The Handbook of EVOLUTIONARY PSYCHOLOGY

Second Edition

Volume 2: Integrations

Edited by

DAVID M. BUSS

WILEY

The Handbook of Evolutionary Psychology

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PART V

GROUP LIVING: COOPERATION AND CONFLICT

DAVID M. BUSS and DANIEL CONROY-BEAM

Homo sapiens has been called "the social animal" for a good reason. Living in groups defines a key mode of human existence. Groups contain a bounty of resources critical to survival and reproduction. They afford safety and protection from predators and from other humans. They are populated with potential friends for mutually beneficial social exchange. They contain reproductively valuable mates. And they are inhabited with kin, precious carriers of our genetic cargo, from whom we can receive aid and in whom we can invest. At the same time, group living intensifies competition over precisely those reproductively relevant resources, creating sources of conflict not faced by more solitary creatures. The chapters in this part describe many of the complexities of the evolutionary psychology of group living, focusing on cooperation and conflict.

In Chapter 25, Leda Cosmides and John Tooby provide a comprehensive review of the extensive body of research, much of it conducted by them and their students, on neurocognitive adaptations for social exchange. They elucidate the many design features that such adaptations theoretically should possess and provide compelling arguments that domain-general mechanisms cannot achieve the specific outcomes needed for successful social exchange. They review competing theories to explain the content effects on the Wason selection task and marshal empirical evidence relevant to adjudicating among those theories. In a display of the sort of methodological pluralism advocated by Simpson and Campbell (Chapter 3, this *Handbook*, Volume 1), Cosmides and Tooby describe cross-cultural studies, studies using traditional methods of cognitive psychology, and studies using neurocognitive techniques.

Martin Daly's chapter (Chapter 26) on interpersonal violence and homicide begins by articulating an evolutionary perspective on conflicts of reproductive interests—a long-standing ingenious strategy pioneered by Daly and his long-time collaborator Margo Wilson. Next, he articulates the rationale for using violence and homicides as assays of social conflicts. Thus, Daly's focus is not so much in explaining violence per se, although key insights into violence do indeed emerge. Rather, his central aim is to exploit patterns of violence to reveal underlying conflicts of evolutionary interests that occur between individuals when they live in groups. He deploys this strategy to make novel scientific discoveries. Kin, for example, who typically have a greater confluence of interest compared to unrelated individuals, display much less violence toward each other, despite the fact that they interact more frequently. Intimate mates, to take another example, can have converging genetic interests, as when they have mutually produced offspring. But conflicts of interest emerge from at least six sources, such as temptations for genetic cuckoldry, temptations to trade up, relationship defection, and channeling pooled resources toward one set of kin at the expense of another (see also Conroy-Beam, Goetz, & Buss, 2015). Violence is more common precisely when these conflicts of interest emerge in intimate mateships.

Anne Campbell's chapter (Chapter 27) provides an overview of theory and research on women's competition and aggression. She explores both the proximate mechanisms (hormones, physiological maturation, neuropsychology) and ultimate selective forces underlying women's competition and aggression. Fear, she argues, acts as a more powerful brake on women's than on men's violent aggression, due to the greater costs of engaging in violent conflict (e.g., costs not only to the woman, but also to her children). But make no mistake, Campbell argues—women's competition, although less ostentatiously violent, can be ferocious. Women compete for the best mates, for example, a form of competition possibly exacerbated by socially imposed monogamy. She argues that appearance (cues to fertility) and fidelity (cues to paternity certainty) become key weapons by which women compete with other women, with tactics that include shunning, stigmatizing, derogating, and ostracizing their rivals. When tactics do escalate to actual violence, they occur in predictable contexts such as resource scarcity and a sex ratio imbalance involving too few men as potential mates. In short, Campbell's excellent chapter provides a detailed analysis of the underlying adaptations for female competition and aggression, the ways in which they are sex-differentiated in design, and the contextual and ecological variables to which they respond.

Prejudice seems to be a ubiquitous feature of human social living. Everywhere, people seem prone to dislike and distrust some others, discriminating against them within groups and even warring with them when they are out-groups. Steven Neuberg and Peter DeScioli (Chapter 28) provide an outstanding chapter on the evolved psychology—threat management systems—designed to deal with adaptive problems arising from within and outside of one's group. These prejudices can cause harm and discrimination in the modern environment, they argue, which makes it all the more important to understand their design features and how they play out in this new world.

Humans are an extraordinarily coalitional species. We form groups, often in competition with other groups. Dominic Johnson's chapter (Chapter 29) on leadership and war focuses on group-on-group conflict. He outlines different hypotheses about the evolution of leader traits in the context of war, or alternatively features of coalitional leadership psychology that could have been coopted for war, and examines the relevant empirical evidence. He makes a compelling case that war has been a major selective force on human psychology, including the evolution of leadership and followership traits—arguments that have critical relevance in a modern world beset with warfare in forms unimaginable in the past, but that exploit the same suite of psychological adaptations.

Group living is what we do as a species. It offers a bounty of benefits through cooperation and an abundance of costs through social conflict. As a consequence, it is reasonable to expect that humans have evolved a large number of specialized adaptations for dealing with other humans, both for within-group interactions and for dealing with other groups. Collectively, these chapters highlight the complexity of human evolutionary psychology for group living and pave the way for the discovery of many more adaptations for grappling with the challenges posed by other humans—challenges centering on cooperation and conflict.

REFERENCE

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CHAPTER 25

Adaptations for Reasoning About Social Exchange

LEDA COSMIDES and JOHN TOOBY

> If a person doesn't give something to me, I won't give anything to that person. If I'm sitting eating, and someone like that comes by, I say, "Uhn, uhn. I'm not going to give any of this to you. When you have food, the things you do with it make me unhappy. If you even once in a while gave me something nice, I would surely give some of this to you."
>
> Nisa from *Nisa: The Life and Words of a !Kung Woman,* Shostak, 1981, p. 89

> Instead of keeping things, [!Kung] use them as gifts to express generosity and friendly intent, and to put people under obligation to make return tokens of friendship . . . . In reciprocating, one does not give the same object back again but something of comparable value.
>
> Eland fat is a very highly valued gift . . . . Toma said that when he had eland fat to give, he took shrewd note of certain objects he might like to have and gave their owners especially generous gifts of fat.
>
> Marshall, 1976, pp. 366–369

NISA AND TOMA were hunter-gatherers, !Kung San people living in Botswana's inhospitable Kalahari desert during the 1960s. Their way of life was as different from that in an industrialized, economically developed society as any on earth, yet their sentiments are as familiar and easy to comprehend as those of your neighbor next door. They involve *social exchange,* interactions in which one party provides a benefit to the other, conditional on the recipient's providing a benefit in return (Cosmides, 1985; Cosmides & Tooby, 1989; Tooby & Cosmides, 1996). Among humans, social exchange can be implicit or explicit, simultaneous or sequential, immediate or deferred, and may involve alternating actions by the two parties or follow more complex structures. In all these cases, however, it is a way people cooperate for mutual benefit. Explicitly agreed-to forms of social exchange are the focus of study in economics (and are known as exchange or trade), while biologists and anthropologists focus more on implicit, deferred cases of exchange, often called *reciprocal altruism* (Trivers, 1971), *reciprocity,* or *reciprocation.* We will refer to the inclusive set of cases of the mutually conditioned provisioning of benefits as social exchange, regardless of subtype. Nisa and Toma are musing about social exchange interactions in which the expectation of reciprocity is implicit and the favor can be returned at a much later date. In their society, as in ours, the benefits given and received need not be physical objects for exchange to exist; they can be services (valued actions) as well. Aid in a fight, support in a political conflict, help with a sick child, permission to hunt and use water holes in your family's territory—all are ways of doing or repaying a favor. Social exchange behavior is both panhuman and ancient. Which cognitive abilities make it possible?

For 25 years, we have been investigating the hypothesis that the enduring presence of social exchange interactions among our ancestors has selected for cognitive mechanisms that are specialized for reasoning about social exchange. Just as a lock and key are designed to fit together to function, our claim is that the proprietary procedures and conceptual elements of the social exchange reasoning specializations evolved to reflect the abstract, evolutionarily recurring relationships present in social exchange interactions (Cosmides & Tooby, 1989).

We picked social exchange reasoning as an initial test case for exploring the empirical power of evolutionary psychological analyses for a number of reasons. First, the topic is intrinsically important: Exchange is central to all human economic activity. If exchange in our species is made possible by evolved, neurocomputational programs specialized for exchange itself, this is surely worth knowing. Such evolved programs would constitute the foundation of economic behavior, and their specific properties would organize exchange interactions in all human societies; thus, if they exist, they deserve to be mapped. The discovery and mapping of such mechanisms would ground economics in the evolutionary and cognitive sciences, cross-connecting economics to the rest of the natural sciences. Social exchange specializations (if they exist) also underlie many aspects of a far broader category of implicit social interaction lying outside economics, involving favors, friendship, and self-organizing cooperation.

There was a second reason for investigating the computational procedures engaged by social exchange. There are many counterhypotheses about social exchange reasoning to test against, but they all spring from the single most central assumption of the traditional social and behavioral sciences—the blank slate view of the mind that lies at the center of what we have called the *standard social science model* (Tooby & Cosmides, 1992). According to this view, humans are endowed with a powerful, general cognitive capacity (intelligence, rationality, learning, instrumental reasoning), which explains human thought and the great majority of human behavior. In this case, humans putatively engage in successful social exchange through exactly the same cognitive faculties that allow them to do everything else: Their general intelligence allows them to recognize, learn, or reason out intelligent, beneficial courses of action. This hypothesis has been central to how most neural, psychological, and social scientists conceptualize human behavior, but it is almost never subjected to potential empirical falsification (unlike theories central to physics or biology). Investigating reasoning about social exchange provided an opportunity to test the blank slate hypothesis empirically in domains (economics and social behavior) where it had been uncritically accepted by almost all traditional researchers. Moreover, the results of these tests would be powerfully telling for the general issue of whether an evolutionary psychological program would lead to far-reaching and fundamental revisions across the human sciences. Why? If mechanisms of general rationality exist and are to genuinely explain anything of significance, they should surely explain social exchange reasoning as one easy application. After all, social exchange is absurdly simple compared to other cognitive activities such as language or vision, it is mutually beneficial and intrinsically rewarding, it is economically rational (Simon, 1990), and it should emerge spontaneously as the result of the ability to pursue goals; even artificially intelligent agents capable of pursuing goals through means-ends analysis should be able to manage it. An organism that was in fact equipped with a powerful, general intelligence would not *need* cognitive specializations for social exchange to be able to engage in it. If it turns out that humans nonetheless have adaptive specializations for social exchange, it would imply that mechanisms of general intelligence (if they exist) are relatively weak, and natural selection has specialized a far larger number of comparable cognitive competences than cognitive and behavioral scientists had anticipated.

Third, we chose to study a form of reasoning because reasoning is widely considered to be the quintessential case of a content-independent, general-purpose cognitive competence. Reasoning is also considered to be the most distinctively human cognitive ability—something that exists in opposition to, and as a replacement for, instinct. If, against all expectation, human reasoning turns out to fractionate into a diverse collection of evolved, content-specialized procedures, then adaptive specializations are far more likely to be widespread and typical in the human psychological architecture, rather than nonexistent or exceptional. Reasoning presents the most difficult test case, and hence the most useful case, to leapfrog the evolutionary debate into genuinely new territory. In contrast, the eventual outcome of debates over the evolutionary origins and organization of motivation (e.g., sexual desire) and emotion (e.g., fear) are not in doubt (despite the persistence of intensely fought rearguard actions by traditional research communities). No blank slate process could, even in principle, acquire the motivational and emotional organization found in humans (Cosmides & Tooby, 1987; Tooby, Cosmides, & Barrett, 2005). Reasoning will be the last redoubt of those who adhere to a blank slate approach to the human psychological architecture.

Fourth, logical reasoning is subject to precise formal computational analysis, so it is possible to derive exact and contrasting predictions from domain-general and domain-specific theories, allowing critical tests to be devised and theories to be potentially or actually falsified.

Finally, we chose the domain of social exchange because it offered the opportunity to explore whether the evolutionary dynamics newly charted by evolutionary game theory (e.g., Maynard Smith, 1982) had sculpted the human brain and mind and, indeed, human moral reasoning. If it could be shown empirically that the kinds of selection pressures modeled in evolutionary game theory had real consequences on the human psychological architecture, then this would help lay the foundations of an evolutionary approach to social psychology, social behavior, and morality (Cosmides & Tooby, 2004). At the time, most social scientists considered morality to be a cultural product free of biological organization. We thought on theoretical grounds there should be an evolved set of domain-specific grammars of moral and social reasoning (Cosmides & Tooby, 1989) and wanted to see if we could clearly establish at least one rich empirical example—a grammar of social exchange. One pleasing feature of the case of social exchange is that it can be clearly traced step by step as a causal chain from replicator dynamics and game theory to details of the computational architecture to specific patterns of reasoning performance to specific cultural phenomena, moral intuitions, and conceptual primitives in moral philosophy—showcasing the broad integrative power of an evolutionary psychological approach. This research is one component of a larger project that includes mapping the evolutionary psychology of moral sentiments and moral emotions alongside moral reasoning (e.g., Cosmides & Tooby, 2004; Lieberman, Tooby, & Cosmides, 2003, 2007; Price, Cosmides, & Tooby, 2002; Tooby & Cosmides, 2010).

What follows are some of the high points of this 25-year research program. We argue that social exchange is ubiquitously woven through the fabric of human life in all human cultures everywhere, and has been taking place among our ancestors for millions and possibly tens of millions of years. This means social exchange interactions are an important and recurrent human activity with sufficient time depth to have selected for specialized neural adaptations. Evolutionary game theory shows that social exchange can evolve and persist only if the cognitive programs that cause it conform to a narrow and complex set of design specifications. The complex pattern of functional and neural dissociations that we discovered reveal so close a fit between adaptive problem and computational solving that a neurocognitive specialization for reasoning about social exchange is implicated, including a subroutine for detecting cheaters. This subroutine develops precocially (by ages 3 to 4) and appears cross-culturally—hunter-horticulturalists in the Amazon detect cheaters as reliably as adults who live in advanced market economies. The detailed patterns of human reasoning performance elicited by situations involving social exchange correspond to the evolutionarily derived predictions of a specialized logic or grammar of social exchange and falsify content-independent, general-purpose reasoning mechanisms as a plausible explanation for reasoning in this domain. A developmental process that is itself specialized for social exchange appears to be responsible for building the neurocognitive specialization found in adults: As we show, the design, ontogenetic timetable, and cross-cultural distribution of social exchange are not consistent with any known domain-general learning process. Taken together, the data showing design specificity, precocious development, cross-cultural universality, and neural dissociability implicate the existence of an evolved, species-typical neurocomputational specialization.

In short, the neurocognitive system that causes reasoning about social exchange shows evidence of being what Pinker (1994) has called a *cognitive instinct:* It is complexly organized for solving a well-defined adaptive problem our ancestors faced in the past, it reliably develops in all normal humans, it develops without any conscious effort and in the absence of explicit instruction, it is applied without any conscious awareness of its underlying logic, and it is functionally and neurally distinct from more general abilities to process information or behave intelligently. We briefly review the evidence that supports this conclusion, along with the evidence that eliminates the alternative by-product hypotheses that have been proposed. (For more comprehensive treatments, see Cosmides, 1985, 1989; Cosmides, Barrett, & Tooby, 2010; Cosmides & Tooby, 1989, 1992, 2005, 2008a; Fiddick, Cosmides, & Tooby, 2000; Stone, Cosmides, Tooby, Kroll, & Knight, 2002; Sugiyama, Tooby, & Cosmides, 2002.)

SOCIAL EXCHANGE IN ZOOLOGICAL AND CULTURAL PERSPECTIVE

Living in daily contact affords many opportunities to see when someone needs help, to monitor when someone fails to help but could have, and, as Nisa explains, to withdraw future help when this happens. Under these conditions, reciprocity can be delayed, understanding of obligations and entitlements can remain tacit, and aid (in addition to objects) can be given and received (Shostak, 1981). But when people do not live side by side, social exchange arrangements typically involve explicit agreements, simultaneous transfers of benefits, and increased trade of objects (rather than intimate acts of aid). Agreements are explicit because neither side can know the other's needs based on daily interaction, objects are traded because neither side is present to provide aid when the opportunity arises, and trades are simultaneous because this reduces the risk of nonreciprocation—neither side needs to trust the other to provide help in the future. Accordingly, explicit or simultaneous trade is usually a sign of social distance (Tooby & Cosmides, 1996). !Kung, for example, will trade hides for knives and other goods with Bantu people but not with fellow band members (Marshall, 1976).

Explicit trades and delayed, implicit reciprocation differ in these superficial ways, but they share a deep structure: *X* provides a benefit to *Y* conditional on *Y* doing something that *X* wants. As humans, we take it for granted that people can make each other better off than they were before by exchanging benefits—goods, services, acts of help and kindness. But when placed in zoological perspective, social exchange stands out as an unusual phenomenon whose existence requires explanation. The magnitude, variety, and complexity of our social exchange relations are among the most distinctive features of human social life and differentiate us strongly from all other animal species (Tooby & DeVore, 1987). Indeed, uncontroversial examples of social exchange in other species are difficult to find, and despite widespread investigation, social exchange has been reported in only a tiny handful of other species, such as chimpanzees, certain monkeys, and vampire bats (see Dugatkin, 1997; Hauser, 2007, for contrasting views of the nonhuman findings).

Practices can be widespread without being the specific product of evolved psychological adaptations. Is social exchange a recent cultural invention? Cultural inventions such as alphabetic writing systems, cereal cultivation, and Arabic numerals are widespread, but they have one or a few points of origin, spread by contact, and are highly elaborated in some cultures and absent in others. Social exchange does not fit this pattern. It is found in every documented culture past and present and is a feature of virtually every human life within each culture, taking on a multiplicity of elaborate forms, such as returning favors, sharing food, reciprocal gift giving, explicit trade, and extending acts of help with the implicit expectation that they will be reciprocated (Cashdan, 1989; Fiske, 1991; Gurven, 2004; Malinowski, 1922; Mauss, 1925/1967). Particular methods or institutions for engaging in exchange—marketplaces, stock exchanges, money, the Kula Ring—are recent cultural inventions, but not social exchange behavior itself.

Moreover, evidence supports the view that social exchange is at least as old as the genus *Homo* and possibly far older than that. Paleoanthropological evidence indicates that before anatomically modern humans evolved, hominids engaged in social exchange (see, e.g., Isaac, 1978). Moreover, the presence of reciprocity in chimpanzees (and even certain monkeys; Brosnan & de Waal, 2003; de Waal, 1989, 1997a, 1997b; de Waal & Luttrell, 1988) suggests it may predate the time, 5 to 7 million years ago, when the hominid line split from chimpanzees. In short, social exchange behavior has been present during the evolutionary history of our line for so long that selection could well have engineered complex cognitive mechanisms specialized for engaging in it.

Natural selection retains and discards properties from a species' design based on how well these properties solve adaptive problems—evolutionarily recurrent problems whose solution promotes reproduction. To have been a target of selection, a design had to produce beneficial effects, measured in reproductive terms, in the environments in which it evolved. Social exchange clearly produced beneficial effects for those who successfully engaged in it, ancestrally as well as now (Cashdan, 1989; Isaac, 1978). A life deprived of the benefits that reciprocal cooperation provides would be a Hobbesian nightmare of poverty and social isolation, punctuated by conflict. But the fact that social exchange produces beneficial effects is not sufficient for showing that the neurocognitive system that enables it was designed by natural selection for that function. To rule out the counterhypothesis that social exchange is a side effect of a system that was designed to solve a different or more inclusive set of adaptive problems, we need to evaluate whether the adaptation shows evidence of special design for the proposed function (Williams, 1966).

So what, exactly, is the nature of the neurocognitive machinery that enables exchange, and how specialized is it for this function? Social exchange is zoologically rare, raising the possibility that natural selection engineered into the human brain information processing circuits that are narrowly specialized for understanding, reasoning about, motivating, and engaging in social exchange. On this view, the circuits involved are neurocognitive adaptations *for* social exchange, evolved cognitive instincts designed by natural selection for that function—the *adaptive specialization hypothesis.* An alternative family of theories derives from the possibility that our ability to reason about and engage in social exchange is a by-product of a neurocognitive system that evolved for a different function. This could be an alternative specific function (e.g., reasoning about obligations). More usually, however, researchers expect that social exchange reasoning is a by-product or expression of a neurocognitive system that evolved to perform a more general function—operant conditioning, logical reasoning, rational decision making, or some sort of general intelligence. We call this family of explanations the *general rationality hypothesis.*

The general rationality hypothesis is so compelling, so self-evident, and so entrenched in our scientific culture that researchers find it difficult to treat it as a scientific hypothesis at all, exempting it from demands of falsifiability, specification, formalization, consistency, and proof they would insist on for any other scientific hypothesis. For example, in dismissing the adaptive specialization hypothesis of social exchange without examining the evidence, Ehrlich (2002) considers it sufficient to advance the folk theory that people just "figure it out." He makes no predictions nor specifies any possible test that could falsify his view. Orr (2003) similarly refuses to engage the evidence, arguing that perhaps "it just pays to behave in a certain way, and an organism with a big-enough brain reasons this out, while evolved instincts and specialized mental modules are beside the point" (p. 18). He packages this argument with the usual and necessarily undocumented claims about the low scientific standards of evolutionary psychology (in this case, voiced by unnamed colleagues in molecular biology).

What is problematic about this debate is not that the general rationality hypothesis is advanced as an alternative explanation. It is a plausible (if hopelessly vague) hypothesis. Indeed, the entire social exchange research program has, from its inception, been designed to systematically test against the major predictions that can be derived from this family of countertheories, to the extent they can be specified. What is problematic is that critics engage in the pretense that tests of the hypothesis they favor have never been carried out; that their favored hypothesis has no empirical burden of its own to bear; and that merely stating the general rationality hypothesis is enough to establish the empirical weakness of the adaptive specialization hypothesis. It is, in reality, what Dawkins (1986) calls the *argument from personal incredulity* masquerading as its opposite—a commitment to high standards of hypothesis testing.

Of course, to a cognitive scientist, Orr's conjecture as stated does not rise to the level of a scientific hypothesis. "Big brains" cause reasoning only by virtue of the neurocognitive programs they contain. Had Orr specified a reasoning mechanism or a learning process, we could empirically test the proposition that it predicts the observed patterns of social exchange reasoning. But he did not. Fortunately, however, a number of cognitive scientists have proposed some well-formulated by-product hypotheses, all of which make different predictions from the adaptive specialization hypothesis. Moreover, even where well-specified theories are lacking, one can derive some general predictions from the class of general rationality theories about possible versus impossible patterns of cultural variation, the effects of familiarity, possible versus impossible patterns of neural dissociation, and so on. We have tested each by-product hypothesis in turn. None can explain the patterns of reasoning performance found, patterns that were previously unknown and predicted in advance by the hypothesis that humans have neurocognitive adaptations designed for social exchange.

SELECTION PRESSURES AND PREDICTED DESIGN FEATURES

To test whether a system is an adaptation that evolved for a particular function, one must produce design evidence. The first step is to demonstrate that the system's properties solve a well-specified adaptive problem in a well-engineered way (Dawkins, 1986; Tooby & Cosmides, 1992, Chapter 1, this *Handbook*, Volume 1; Williams, 1966). This requires a well-specified theory of the adaptive problem in question.

For example, the laws of optics constrain the properties of cameras and eyes: Certain engineering problems must be solved by any information processing system that uses reflected light to project images of objects onto a 2-D surface (film or retina). Once these problems are understood, the eye's design makes sense. The transparency of the cornea, the ability of the iris to constrict the pupillary opening, the shape of the lens, the existence of photoreactive molecules in the retina, the resolution of retinal cells—all are solutions to these problems (and have their counterparts in a camera). Optics constrain the design of the eye, but the design of programs causing social behavior is constrained by the behavior of other agents—more precisely, by the design of the behavior-regulating programs in other agents and the fitness consequences that result from the interactions these programs cause. These constraints can be analyzed using evolutionary game theory (Maynard Smith, 1982).

An *evolutionarily stable strategy* (ESS) is a strategy (a decision rule) that can arise and persist in a population because it produces fitness outcomes greater than or equal to alternative strategies (Maynard Smith, 1982). The rules of reasoning and decision making that guide social exchange in humans would not exist unless they had outcompeted alternatives, so we should expect that they implement an ESS.[1] By using game theory and conducting computer simulations of the evolutionary process, one can determine which strategies for engaging in social exchange are ESSs.

Selection pressures favoring social exchange exist whenever one organism (the provider) can change the behavior of a target organism to the provider's advantage by making the target's receipt of that benefit *conditional* on the target acting in a required manner. In social exchange, individuals agree, either explicitly or implicitly, to abide by a particular *social contract*. For ease of explication, let us define a social contract as a conditional (i.e., *If-then*) rule that fits the following template: "If you accept a benefit from *X*, then you must satisfy *X*'s requirement" (where *X* is an individual or set of individuals). For example, Toma knew that people in his band recognize and implicitly follow a social contract rule: *If you accept a generous gift of eland fat from someone, then you must give that person something valuable in the future.* Nisa's words also express a social contract: *If you are to get food in the future from me, then you must be individual Y* (where *Y* = an individual who has willingly shared food with Nisa in the past). Both realize that the act of accepting a benefit from someone triggers an obligation to behave in a way that somehow benefits the provider, now or in the future.

This mutual provisioning of benefits, each conditional on the other's compliance, is usually modeled by game theorists as a repeated Prisoners' Dilemma (Axelrod & Hamilton, 1981; Boyd, 1988; Trivers, 1971; but see Stevens & Stephens, 2004; Tooby & Cosmides, 1996). The results show that the behavior of cooperators must be generated by programs that perform certain specific tasks very well if they are to be evolutionarily stable (Cosmides, 1985; Cosmides & Tooby, 1989). Here, we focus on one of these requirements: cheater detection. A *cheater* is an individual who fails to reciprocate—who accepts the benefit specified by a social contract without satisfying the requirement that provision of that benefit was made contingent on.

The ability to reliably and systematically detect cheaters is a necessary condition for cooperation in the repeated Prisoners' Dilemma to be an ESS (e.g., Axelrod, 1984; Axelrod & Hamilton, 1981; Boyd, 1988; Trivers, 1971; Williams, 1966).[2] To see this, consider the fate of a program that, because it cannot detect cheaters, bestows benefits

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[1] If the rules regulating reasoning and decision-making about social exchange do not implement an ESS, it would imply that these rules are a by-product of some other adaptation that produces fitness benefits so huge that they compensate for the systematic fitness costs that result from its producing non-ESS forms of social exchange as a side effect. Given how much social exchange humans engage in, this alternative seems unlikely.

[2] Detecting cheaters is necessary for contingent cooperation to evolve, even when providing a benefit is cost free (i.e., even for situations that do not fit the payoff structure of a Prisoners' Dilemma; Tooby & Cosmides, 1996). In such cases, a design that cooperates contingently needs to detect when someone has failed to provide a benefit because it needs to know when to shift partners. In this model (just as in the Prisoners' Dilemma), a design that cannot shift partners will have lower fitness than a design that detects cheaters and directs future cooperation to those who do not cheat. Fitness is lower because of the opportunity cost associated with staying, not because of the cost of providing a benefit to the partner. Failure to understand that social exchange is defined by contingent provision of benefits, not by the suffering of costs, has resulted in some irrelevant experiments and discussion in the psychological literature. For example, showing that cheater detection can still occur when the requirement is not costly (e.g., Cheng & Holyoak, 1989) is a prediction of social contract theory, not a refutation of it (Cosmides, 1985; Cosmides & Tooby, 1989). For the same reason, there is no basis in social contract theory for Cheng and Holyoak's (1989) distinction between "social exchanges" (in which satisfying the requirement involves transferring a good, at some cost) and "social contracts" (in which satisfying a requirement may be cost free). For further discussion, see Fiddick, Cosmides, and Tooby (2000).

on others unconditionally. These unconditional helpers will increase the fitness of any nonreciprocating design they meet in the population. But when a nonreciprocating design is helped, the unconditional helper never recoups the expense of helping: The helper design incurs a net fitness cost while conferring a net fitness advantage on a design that does not help in return. As a result, a population of unconditional helpers is easily invaded and eventually outcompeted by designs that accept the benefits helpers bestow without reciprocating them. Unconditional helping is not an ESS.

In contrast, program designs that cause *conditional* helping—that help those who reciprocate the favor, but not those who fail to reciprocate—can invade a population of nonreciprocators and outcompete them. Moreover, a population of such designs can resist invasion by designs that do not reciprocate (cheater designs). Therefore, conditional helping, which requires the ability to detect cheaters, is an ESS.

Engineers always start with a task analysis before considering possible design solutions. We did, too. By applying ESS analyses to the behavioral ecology of hunter-gatherers, we were able to specify tasks that an information processing program would have to be good at solving for it to implement an evolutionarily stable form of social exchange (Cosmides, 1985; Cosmides & Tooby, 1989). This task analysis of the required computations, *social contract theory,* specifies what counts as good design in this domain.

Because social contract theory provides a standard of good design against which human performance can be measured, there can be a meaningful answer to the question, "Are the programs that cause reasoning about social exchange well engineered for the task?" Well-designed programs for engaging in social exchange—if such exist—should include features that execute the computational requirements specified by social contract theory, and do so reliably, precisely, and economically (Williams, 1966).

From social contract theory's task analyses, we derived a set of predictions about the design features that a neurocognitive system specialized for reasoning about social exchange should have (Cosmides, 1985; Cosmides & Tooby, 1989, 2008a). The following six design features (D1–D6) were among those on the list:

D1. Social exchange is cooperation for mutual *benefit.* If there is nothing in a conditional rule that can be interpreted as a rationed benefit, then interpretive procedures should not categorize that rule as a social contract. To trigger the inferences about obligations and entitlements that are appropriate to social contracts, the rule must be interpreted as restricting access to a benefit to those who have met a requirement. (This is a necessary, but not sufficient, condition; Cosmides & Tooby, 1989; Gigerenzer & Hug, 1992.)

D2. Cheating is a specific way of violating a social contract: It is taking the benefit when you are not entitled to do so. Consequently, the cognitive architecture must define the concept of *cheating* using contentful representational primitives, referring to illicitly taken *benefits.* This implies that a system designed for cheater detection will not know what to look for if the rule specifies no benefit to the potential violator.

D3. The definition of cheating also depends on which agent's point of view is taken. Perspective matters because the item, action, or state of affairs that one party views as a benefit is viewed as a requirement by the other party. The system needs to be able to compute a cost-benefit representation from the perspective of each participant and define cheating with respect to that perspective-relative representation.

D4. To be an ESS, a design for conditional helping must not be outcompeted by alternative *designs.* Accidents and innocent mistakes that result in an individual being cheated are not markers of a design difference. A cheater detection system should look for cheaters: individuals equipped with programs that cheat by design.[3] Hence, intentional cheating should powerfully trigger the detection system whereas mistakes should trigger it weakly or not at all. (Mistakes that result in an individual being cheated are relevant only insofar as they may not be true mistakes.)

D5. The hypothesis that the ability to reason about social exchange is acquired through the operation of some general-purpose learning ability necessarily predicts that good performance should be a function of experience and familiarity. In contrast, an evolved system for social exchange should be designed to recognize and reason about social exchange interactions no matter how unfamiliar the interaction may be, provided it can be mapped onto the abstract structure of a social contract. Individuals need to be able to reason about each new exchange situation as it arises, so rules that fit the template of a social contract should elicit high levels of cheater detection, even if they are unfamiliar.

D6. Inferences made about social contracts should not follow the rules of a content-free, formal logic. They should follow a content-specific adaptive logic, evolutionarily tailored for the domain of social exchange (described in Cosmides & Tooby, 1989, 2008a).

Cheating does involve the violation of a conditional rule, but note that it is a particular *kind* of violation of a particular *kind* of conditional rule. The rule must fit the template for a *social contract*; the violation must be one in which an individual *intentionally* took what *that* individual considered to be a *benefit* and did so without satisfying the requirement.

Formal logics (e.g., the propositional calculus) are content blind; the definition of *violation* in standard logics applies to all conditional rules, whether they are social contracts, threats, or descriptions of how the world works. But, as shown later, the definition of cheating implied by design features D1 through D4 does not map onto this content-blind definition of violation. What counts as cheating in social exchange is so content sensitive that a detection mechanism equipped only with a domain-general definition of violation would not be able to solve the problem of cheater detection. This suggests that there should be a program specialized for cheater detection. To operate, this program would have to function as a subcomponent of a system that, because of its domain-specialized structure, is well designed for detecting social conditionals involving exchange, interpreting their meaning, and successfully solving the inferential problems they pose: *social contract algorithms.*

CONDITIONAL REASONING AND SOCIAL EXCHANGE

Reciprocation is, by definition, social behavior that is conditional: You agree to deliver a benefit *conditionally* (conditional on the other person doing what you required in return). Understanding it therefore requires conditional reasoning.

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[3] *Programs that cheat by design* is a more general formulation of the principle, which does not require the human ability to form mental representations of intentions or to infer the presence of intentional mental states in others. An analogy to deception may be useful: Birds that feign a broken wing to lure predators away from their nests are equipped with programs that are designed to deceive the predator, but the cognitive procedures involved need not include a mental representation of an *intention* to deceive.

Because engaging in social exchange requires conditional reasoning, investigations of conditional reasoning can be used to test for the presence of social contract algorithms. The hypothesis that the brain contains social contract algorithms predicts a dissociation in reasoning performance by *content:* a sharply enhanced ability to reason adaptively about conditional rules when those rules specify a social exchange. The null hypothesis is that there is nothing specialized in the brain for social exchange. This hypothesis follows from the traditional assumption that reasoning is caused by content-independent processes. It predicts no enhanced conditional reasoning performance specifically triggered by social exchanges as compared to other contents.

A standard tool for investigating conditional reasoning is the Wason selection task, which asks you to look for potential violations of a conditional rule of the form *If P, then Q* (Wason, 1966, 1983; Wason & Johnson-Laird, 1972). Using this task, an extensive series of experiments has been conducted that addresses the following questions:

- Do our minds include cognitive machinery that is *specialized* for reasoning about social exchange (alongside other domain-specific mechanisms, each specialized for reasoning about a different adaptive domain involving conditional behavior)? Or,
- Is the cognitive machinery that causes good conditional reasoning general—does it operate well regardless of content?

If the human brain had cognitive machinery that causes good conditional reasoning regardless of content, then people should be good at tasks requiring conditional reasoning. For example, they should be good at detecting violations of conditional rules. Yet studies with the Wason selection task show that they are not. Consider the Wason task in Figure 25.1. The correct answer (choose *P,* choose *not-Q*) would be intuitively obvious if our minds were equipped with reasoning procedures specialized for detecting *logical* violations of conditional rules. But this answer is not obvious to people. Studies in many nations have shown that reasoning performance is low on descriptive (indicative) rules like the rule in Figure 25.1: Only 5% to 30% of people give the logically correct answer, even when the rule involves familiar terms drawn from everyday life (Cosmides, 1989; Manktelow & Evans, 1979; Sugiyama et al., 2002; Wason, 1966, 1983). Interestingly, explicit instruction in logical inference does not boost performance: People who have just completed a semester-long college course in logic perform no better than people without this formal training (Cheng, Holyoak, Nisbett, & Oliver, 1986).

Formal logics, such as the propositional calculus, provide a standard of good design for content-general conditional reasoning: Their inference rules were constructed by philosophers to generate true conclusions from true premises, regardless of the subject matter one is asked to reason about. When human performance is measured against this standard, there is little evidence of good design: Conditional rules with descriptive content fail to elicit logically correct performance from 70% to 95% of people. Therefore, one can reject the hypothesis that the human mind is equipped with cognitive machinery that causes good conditional reasoning across all content domains.

A Dissociation by Content

People are poor at detecting violations of conditional rules when their content is descriptive. Does this result generalize to conditional rules that express a social

Ebbinghaus disease was recently identified and is not yet well understood. So an international committee of physicians who have experience with this disease was assembled. Their goal was to characterize the symptoms, and develop surefire ways of diagnosing it.

Patients afflicted with Ebbinghaus disease have many different symptoms: nosebleeds, headaches, ringing in the ears, and others. Diagnosing it is difficult because a patient may have the disease, yet not manifest all of the symptoms. Dr. Buchner, an expert on the disease, said that the following rule holds:

"If a person has Ebbinghaus disease, then that person will be forgetful."
If *P* *then* *Q*

Dr. Buchner may be wrong, however. You are interested in seeing whether there are any patients whose symptoms violate this rule.

The cards below represent four patients in your hospital. Each card represents one patient. One side of the card tells whether or not the patient has Ebbinghaus disease, and the other side tells whether or not that patient is forgetful.

Which of the following card(s) would you definitely need to turn over to see if any of these cases violate Dr. Buchner's rule: "If a person has Ebbinghaus disease, then that person will be forgetful." Don't turn over any more cards than are absolutely necessary.

has Ebbinghaus disease	does not have Ebbinghaus disease	is forgetful	is not forgetful
P	*not-P*	*Q*	*not-Q*

Figure 25.1 The Wason Selection Task. In a Wason task, there is always a rule of the form, *If P then Q*, and four cards showing the values *P*, *not-P*, *Q*, and *not-Q* (respectively) on the side that the subject can see. From a logical point of view, only the combination of *P* and *not-Q* can violate this rule, so the correct answer is to check the *P* card (to see if it has a *not-Q* on the back), the *not-Q* card (to see if it has a *P* on the back), and no others. Few subjects answer correctly, however, when the conditional rule is descriptive (indicative), even when its content is familiar; for example, only 26% of subjects answered the above problem correctly (by choosing "has Ebbinghaus disease" and "is not forgetful"). Most choose either *P* alone, or *P* and *Q*. (The italicized *P*s and *Q*s are not in problems given to subjects.)

contract? No. People who ordinarily cannot detect violations of if-then rules can do so easily and accurately when that violation represents cheating in a situation of social exchange. This pattern—good violation detection for social contracts but not for descriptive rules—is a dissociation in reasoning elicited by differences in the conditional rule's *content.* It provides (initial) evidence that the mind has reasoning procedures specialized for detecting cheaters.

More specifically, when asked to look for violations of a conditional rule that fits the social contract template—"If you take benefit B, then you must satisfy requirement R" (e.g., "If you borrow my car, then you have to fill up the tank with gas")—people check the individual who accepted the benefit (borrowed the car; *P*) and the individual who did not satisfy the requirement (did not fill the tank; *not-Q*). These are the cases that represent potential cheaters (Figure 25.2a). The adaptively correct answer is immediately obvious to most subjects, who commonly experience a pop-out effect. No formal training is needed. Whenever the content of a problem asks one to look for cheaters in a social exchange, subjects experience the problem as simple to solve, and their performance jumps dramatically. In general, 65% to 80% of subjects get it right, the highest performance found for a task of this kind (for reviews, see Cosmides, 1985, 1989; Cosmides et al., 2010; Cosmides & Tooby, 1992, 1997, 2008a, 2008b; Fiddick et al., 2000; Gigerenzer & Hug, 1992; Platt & Griggs, 1993).

Given the content-blind syntax of formal logic, investigating the person who borrowed the car (*P*) and the person who did not fill the gas tank (*not-Q*) is logically equivalent to investigating the person with Ebbinghaus disease (*P*) and the person who is not forgetful (*not-Q*) for the disease-symptom problem in Figure 25.1. But everywhere it has been tested (adults in the United States, United Kingdom, Germany, Italy, France, Hong Kong, Japan; schoolchildren in Quito, Ecuador; Shiwiar hunter-horticulturalists in the Ecuadorian Amazon), people do not treat social exchange problems as equivalent to other kinds of conditional reasoning problems (Cheng & Holyoak, 1985; Cosmides, 1989; Hasegawa & Hiraishi, 2000; Platt & Griggs, 1993; Sugiyama et al., 2002; supports D5, D6). Their minds distinguish social exchange content from other domains, and reason as if they were translating their terms into representational primitives such as *benefit, cost, obligation, entitlement, intentional,* and *agent* (Figure 25.2b; Cosmides & Tooby, 1992, 2008a; Fiddick et al., 2000). Reasoning problems could be sorted into indefinitely many categories based on their content or structure (including the propositional calculus's two content-free categories, antecedent and consequent). Yet, even in remarkably different cultures, the same mental categorization occurs. This cross-culturally recurrent dissociation by content was predicted in advance of its discovery by social contract theory's adaptationist analysis.

This pattern of good performance on reasoning problems involving social exchange is what we would expect if the mind reliably develops neurocognitive adaptations for reasoning about social exchange. But more design evidence is needed. Later we review experiments conducted to test for design features D1 through D6: features that should be present if a system specialized for social exchange exists.

In addition to producing evidence of good design for social exchange, recall that one must also show that the system's properties are not better explained as a solution to an alternative adaptive problem or by chance (Tooby & Cosmides, 1992, Chapter 1, this *Handbook,* Volume 1). Each experiment testing for a design feature was also constructed to pit the adaptive specialization hypothesis against at least one alternative by-product hypothesis, so by-product and design feature implications are discussed in tandem. As we show, reasoning performance on social contracts is not explained by familiarity effects, by a content-free formal logic, by a permission schema, or by a general deontic logic. Table 25.1 lists the by-product hypotheses that have been tested and eliminated.

DO UNFAMILIAR SOCIAL CONTRACTS ELICIT CHEATER DETECTION? (D5)

An individual needs to understand each new opportunity to exchange as it arises, so it was predicted that social exchange reasoning should operate even for unfamiliar social contract rules (D5). This distinguishes social contract theory

A.

Teenagers who don't have their own cars usually end up borrowing their parents' cars. In return for the privilege of borrowing the car, the Carters have given their kids the rule,

"If you borrow my car, then you have to fill up the tank with gas."

Of course, teenagers are sometimes irresponsible. You are interested in seeing whether any of the Carter teenagers broke this rule.

The cards below represent four of the Carter teenagers. Each card represents one teenager. One side of the card tells whether or not a teenager has borrowed the parents' car on a particular day, and the other side tells whether or not that teenager filled up the tank with gas on that day.

Which of the following card(s) would you definitely need to turn over to see if any of these teenagers are breaking their parents' rule: "If you borrow my car, then you have to fill up the tank with gas." Don't turn over any more cards than are absolutely necessary.

borrowed car	did not borrow car	filled up tank with gas	did not fill up tank with gas

B.

The mind translates social contracts into representations of benefits and requirements, and it inserts concepts such as "entitled to" and "obligated to," whether they are specified or not.

How the mind "sees" the social contract above is shown in ***bold italics***.

"If you borrow my car, then you have to fill up the tank with gas."

If you take the benefit, then you are obligated to satisfy the requirement.

borrowed car	did not borrow car	filled up tank with gas	did not fill up tank with gas
= ***accepted the benefit***	= ***did not accept the benefit***	= ***satisfied the requirement***	= ***did not satisfy the requirement***

Figure 25.2 Wason Task with a Social Contract Rule. (A) In response to this social contract problem, 76% of subjects chose *P and not-Q* ("borrowed the car " and "did not fill the tank with gas")—the cards that represent potential cheaters. Yet only 26% chose this (logically correct) answer in response to the descriptive rule in Figure 25.1. Although this social contract rule involves familiar items, unfamiliar social contracts elicit the same high performance. (B) How the mind represents the social contract shown in (A). According to inferential rules specialized for social exchange (but not according to formal logic), "If you take the benefit, then you are obligated to satisfy the requirement" implies "If you satisfy the requirement, then you are entitled to take the benefit." Consequently, the rule in (A) implies: "If you fill the tank with gas, then you may borrow the car" (see Figure 25.4, switched social contracts).

Table 25.1
Alternative (By-Product) Hypotheses Eliminated

B1. That familiarity can explain the social contract effect.

B2. That social contract content merely activates the rules of inference of the propositional calculus (logic).

B3. That any problem involving payoffs will elicit the detection of logical violations.

B4. That permission schema theory can explain the social contract effect.

B5. That social contract content merely promotes "clear thinking."

B6. That a content-independent deontic logic can explain social contract reasoning.

B7. That a single mechanism operates on all deontic rules involving subjective utilities.

B8. That relevance theory can explain social contract effects (see also Fiddick, Cosmides, & Tooby, 2000).

B9. That standard economic models can explain social contract effects.

B10. That statistical learning produces the mechanisms that cause social contract reasoning.

strongly from theories that explain reasoning performance as the product of general learning strategies plus experience: The most natural prediction for such skill-acquisition theories is that performance should be a function of familiarity.

The evidence supports social contract theory: Cheater detection occurs even when the social contract is wildly unfamiliar (Figure 25.3a). For example, the rule "If a man eats cassava root, then he must have a tattoo on his face" can be made to fit the social contract template by explaining that the people involved consider eating cassava root to be a benefit (the rule then implies that having a tattoo is the requirement an individual must satisfy to be eligible for that benefit). When given this context, this outlandish, culturally alien rule elicits the same high level of cheater detection as highly familiar social exchange rules. This surprising result has been replicated for many different unfamiliar rules (Cosmides, 1985, 1989; Cosmides & Tooby, 1992; Gigerenzer & Hug, 1992; Platt & Griggs, 1993).

Eliminating Familiarity (B1)

The dissociation by content—good performance for social contract rules but not for descriptive ones—has nothing to do with the familiarity of the rules tested. Familiarity is neither necessary nor sufficient for eliciting high performance (B1 of Table 25.1).

First, familiarity does not produce high levels of performance for descriptive rules (Cosmides, 1989; Manktelow & Evans, 1979). Note, for example, that the Ebbinghaus disease problem in Figure 25.1 involves a familiar causal relationship (a disease causing a symptom) embedded in a real-world context. Yet only 26% of 111 college students that we tested produced the logically correct answer, *P & not-Q,* for this problem. If familiarity fails to elicit high performance on descriptive rules, then it also fails as an explanation for high performance on social contracts.

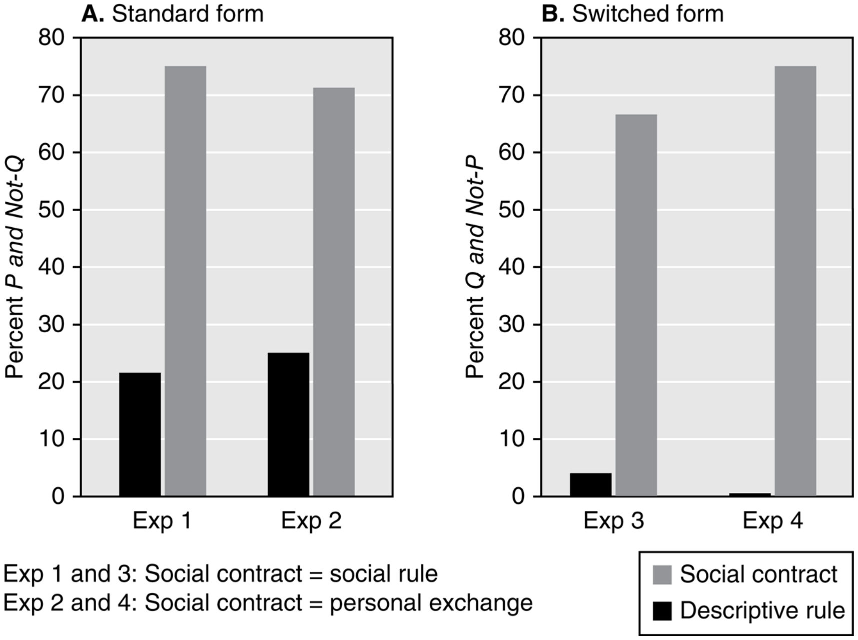

Figure 25.3 Detecting Violations of Unfamiliar Conditional Rules: Social Contracts Versus Descriptive Rules. In these experiments, the same, unfamiliar rule was embedded either in a story that caused it to be interpreted as a social contract or in a story that caused it to be interpreted as a rule describing some state of the world. For social contracts, the correct answer is always to pick the *benefit accepted* card and the *requirement not satisfied* card. (A) For standard social contracts, these correspond to the logical categories *P* and *not-Q*. *P and not-Q* also happens to be the logically correct answer. Over 70% of subjects chose these cards for the social contracts, but fewer than 25% chose them for the matching descriptive rules. (B) For switched social contracts, the *benefit accepted* and *requirement not satisfied* cards correspond to the logical categories *Q* and *not-P*. This is not a logically correct response. Nevertheless, about 70% of subjects chose it for the social contracts; virtually no one chose it for the matching descriptive rules (see Figure 25.4).

Second, the fact that unfamiliar social contracts elicit high performance shows that familiarity is not necessary for eliciting violation detection. Third (and most surprising), people are just as good at detecting cheaters on culturally unfamiliar or imaginary social contracts as they are for ones that are completely familiar (Cosmides, 1985). This provides a challenge for any counterhypothesis resting on a general-learning skill acquisition account (most of which rely on familiarity and repetition).

ADAPTIVE LOGIC, NOT FORMAL LOGIC (D3, D6)

As shown earlier, it is possible to construct social contract problems that will elicit a logically correct answer. But this is not because social exchange content activates logical reasoning.

Good cheater detection is not the same as good detection of logical violations (and vice versa). Hence, problems can be created in which the search for cheaters will result in a logically incorrect response (and the search for logical violations will fail to detect

Consider the following rule:

Standard format:

If you take the ***benefit,*** *then satisfy my* ***requirement*** (e.g., "If I give you $50, then give me your watch.")

If P then Q

Switched format:

If you satisfy my ***requirement,*** *then take the* ***benefit*** (e.g., "If you give me your watch, then I'll give you $50.")

If P then Q

The cards below have information about four people to whom this offer was made. Each card represents one person. One side of a card tells whether the person accepted the benefit, and the other side of the card tells whether that person satisfied the requirement. Indicate only those card(s) you definitely need to turn over to see if any of these people have violated the rule.

	✔			✔
	Benefit accepted	Benefit not accepted	Requirement satisfied	Requirement not satisfied
Standard:	*P*	*not-P*	*Q*	*not-Q*
Switched:	*Q*	*not-Q*	*P*	*not-P*

Figure 25.4 Generic Structure of a Wason Task When the Conditional Rule Is a Social Contract. A social contract can be translated into either social contract terms (benefits and requirements) or logical terms (antecedents and consequents; designated here as *P*s and *Q*s). Check marks indicate the correct card choices if one is looking for cheaters—these should be chosen by a cheater detection subroutine, whether the exchange was expressed in a standard or switched format. This results in a logically incorrect answer (*Q* and *not-P*) when the rule is expressed in the switched format, and a logically correct answer (*P* and *not-Q*) when the rule is expressed in the standard format. By testing switched social contracts, one can see that the reasoning procedures activated cause one to detect cheaters, not logical violations (see Figure 25.3B). Note that a logically correct response to a switched social contract—where *P* = *requirement satisfied* and *not-Q* = *benefit not accepted*—would fail to detect cheaters.

cheaters; see Figure 25.4). When given such problems, people look for cheaters, thereby giving a logically incorrect answer (*Q* and *not-P*).

PERSPECTIVE CHANGE

As predicted (D3), the mind's automatically deployed definition of cheating is tied to the perspective you are taking (Gigerenzer & Hug, 1992). For example, consider the following social contract:

> [1] If an employee is to get a pension, then that employee must have worked for the firm for more than 10 years.

This rule elicits different answers depending on whether subjects are cued into the role of employer or employee. Those in the employer role look for cheating by employees, investigating cases of *P* and *not-Q* (employees with pensions; employees who have worked for fewer than 10 years). Those in the employee role look for cheating by employers, investigating cases of *not-P* and *Q* (employees with no pension; employees who have worked more than 10 years). *Not-P & Q* is correct if the goal is to find out whether the employer is cheating employees. But it is not *logically* correct.[4]

In social exchange, the benefit to one agent is the requirement for the other: For example, giving pensions to employees benefits the employees but is the requirement the employer must satisfy (in exchange for > 10 years of employee service). To capture the distinction between the perspectives of the two agents, rules of inference for social exchange must be content sensitive, defining benefits and requirements relative to the agents involved. Because logical procedures are blind to the content of the propositions over which they operate, they have no way of representing the values of an action to each agent involved.

SWITCHED SOCIAL CONTRACTS

By moving the benefit from the antecedent clause (*P*) to the consequent clause (*Q*), one can construct a social exchange problem for which the adaptively correct cheater detection response is logically incorrect.

According to the propositional calculus (a formal logic), *If B then C* does not imply *If C then B*; therefore, "If you take the benefit, then you are obligated to satisfy the requirement," does not imply, "If you satisfy the requirement, then you are entitled to take the benefit." But inferential rules specialized for social exchange do license the latter inference (Cosmides & Tooby, 1989). Consequently, social exchange inferences (but not logical ones) should cause rule [1] above to be interpreted as implying:

> [2] If an employee has worked for the firm for more than 10 years, then that employee gets a pension.

Assume you are concerned that employees have been cheating and are asked to check whether any employees have violated the rule. Although [2] and [1] are not logically equivalent, our minds interpret them as expressing the same social contract agreement. Hence, in both cases, a subroutine for detecting cheaters should cause you to check employees who have taken the benefit (gotten a pension) and employees who have not met the requirement (worked < 10 years).

But notice that these cards fall into different logical categories when the benefit to the potential cheater is in the antecedent clause versus the consequent clause (standard versus switched format, respectively; Figure 25.4). When the rule is expressed in the switched format, "got a pension" corresponds to the logical category *Q*, and "worked less than 10 years" corresponds to the logical category *not-P*. This answer will correctly detect employees who are cheating, but it is logically incorrect. When the rule is expressed in the standard format, the same two cards correspond to *P* and *not-Q*.

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[4] Moreover, the propositional calculus contains no rules of inference that allow *If B, then C* to be translated as *If C, then B* (i.e., no rule for translating [1] as [2]; see text) and then applying the logical definition of violation to [2] to arrive at the employee perspective answer (see Fiddick et al., 2000).

For standard format social contracts, the cheater detection subroutine will produce the same answer as logical procedures would—not because this response is logically correct, but because it will detect cheaters.

When given switched social contracts like [2], subjects overwhelmingly respond by choosing *Q & not-P,* a logically incorrect answer that correctly detects cheaters (Figure 25.3b; Cosmides, 1985, 1989; Gigerenzer & Hug, 1992; supports D2, D6). Indeed, when subjects' choices are classified by *logical* category, it looks like standard and switched social contracts elicit different responses. But when their choices are classified by *social contract* category, they are invariant: For both rule formats, people choose the cards that represent an agent who took the benefit and an agent who did not meet the requirement.

This robust pattern occurs precisely because social exchange reasoning is sensitive to content: It responds to a syntax of agent-relative benefits and requirements, not antecedents and consequents. Logical procedures would fail to detect cheaters on switched social contracts. Being content blind, their inferential rules are doomed to checking *P* and *not-Q,* even when these cards correspond to potential altruists (or fools)—that is, to people who have fulfilled the requirement and people who have not accepted the benefit.

ELIMINATING LOGIC (B2, B3)

Consider the following by-product hypothesis: The dissociation between social contracts and descriptive rules is not caused by a cheater detection mechanism. Instead, the human cognitive architecture applies content-free rules of logical inference, such as *modus ponens* and *modus tollens.* These logical rules are activated by social contract content but not by other kinds of content, and that causes the spike in *P & not-Q* answers for social contracts.

The results of the switched social contract and the perspective change experiments eliminate this hypothesis. Social contracts elicit a logically incorrect answer, *Q & not-P,* when this answer would correctly detect cheaters. Logical rules applied to the syntax of the material conditionally cannot explain this pattern, because these rules would always choose a true antecedent and false consequent (*P & not-Q*), never a true consequent and false antecedent (*Q & not-P*).

There is an active debate about whether the human cognitive architecture includes content-blind rules of logical inference, which are sometimes dormant and sometimes activated (e.g., Bonatti, 1994; Rips, 1994; Sperber, Cara, & Girotto, 1995). We are agnostic about that issue. What is clear, however, is that such rules cannot explain reasoning about social contracts (for further evidence, see Fiddick et al., 2000).

DEDICATED SYSTEM OR GENERAL INTELLIGENCE?

Social contract reasoning can be maintained in the face of impairments in general logical reasoning. Individuals with schizophrenia manifest deficits on virtually any test of general intellectual functioning they are given (McKenna, Clare, & Baddeley, 1995). Yet their ability to detect cheaters can remain intact. Maljkovic (1987) tested the reasoning of patients suffering from positive symptoms of schizophrenia, comparing their performance with that of hospitalized (nonpsychotic) control patients. Compared to the control patients, the schizophrenic patients were impaired on more general (non-Wason) tests of logical reasoning, in a way typical of individuals with frontal lobe dysfunction. But their ability to detect cheaters on Wason tasks was unimpaired. Indeed, it was indistinguishable from the controls and showed the typical dissociation by content (see also Kornreich, Delle-Vigne, Dubruille, Campanella, Noel, & Ermer, forthcoming). This selective preservation of social exchange reasoning is consistent with the notion that reasoning about social exchange is handled by a dedicated system, which can operate even when the systems responsible for more general reasoning are damaged. It provides further support for the claim that social exchange reasoning is functionally and neurally distinct from more general abilities to process information or behave intelligently.

HOW MANY SPECIALIZATIONS FOR CONDITIONAL REASONING?

Social contracts are not the only conditional rules for which natural selection should have designed specialized reasoning mechanisms (Cosmides, 1989). Indeed, good violation detection is also found for conditional rules drawn from two other domains: threats and precautions. Is good performance across these three domains caused by a single neurocognitive system or by several functionally distinct ones? If a single system causes reasoning about all three domains, then we should not claim that cheater detection is caused by adaptations that evolved for that specific function.

The notion of multiple adaptive specializations is commonplace in physiology: The body is composed of many organs, each designed for a different function. Yet many psychologists cringe at the notion of multiple adaptive specializations when these are computational. Indeed, evolutionary approaches to psychology foundered in the early 1920s on what was seen as an unfounded multiplication of "instincts."

That was before the cognitive revolution, with its language for describing what the brain does in information processing terms and its empirical methods for revealing the structure of representations and processes. Rather than relying on a priori arguments about what should or could be done by a single mechanism, we can now empirically test whether processing about two domains is accomplished by one mechanism or two. We should not imagine that there is a separate specialization for solving each and every adaptive problem. Nor should real differences in processing be ignored in a misguided effort to explain all performance by reference to a single mechanism. As Einstein once said, "Make everything as simple as possible, but no simpler."

Conditional Reasoning About Other Social Domains

Threats specify a conditional rule (*If you don't do what I require, I will harm you*), which the threatener can violate in two ways: by bluffing or by double-crossing. It appears that people are good at detecting bluffs and double-crosses on Wason tasks that test threats (with an interesting sex difference never found for social exchange problems; Tooby & Cosmides, 1989). However, these violations do not map onto the definition of cheating and, therefore, cannot be detected by a cheater detection mechanism. This suggests that reasoning about social contracts and threats is caused by two distinct mechanisms. (So far, no theory advocating a single mechanism for reasoning about these two domains has been proposed. Threats are not deontic; see later discussion.)

Also of adaptive importance is the ability to detect when someone is in danger by virtue of having violated a precautionary rule. These rules have the general form, *"If one is to engage in hazardous activity H, then one must take precaution R"* (e.g., "If you are working with toxic gases, then wear a gas mask"). Using the Wason task, it has been shown that people are very good at detecting potential violators of precautionary rules; that is, individuals who have engaged in a hazardous activity without taking the appropriate precaution (e.g., those working with toxic gases [*P*] and those not wearing a gas mask [*not-Q*]). Indeed, relative to descriptive rules, precautions show a spike in performance, and the magnitude of this content effect is about the same as that for detecting cheaters on social contracts (Cheng & Holyoak, 1989; Fiddick et al., 2000; Manktelow & Over, 1988, 1990, 1991; Stone et al., 2002).

A system well designed for reasoning about hazards and precautions should have properties different from one for detecting cheaters, many of which have been tested for and found (Fiddick, 1998, 2004; Fiddick et al., 2000; Pereyra & Nieto, 2004; Stone et al., 2002). Therefore, alongside a specialization for reasoning about social exchange, the human cognitive architecture should contain computational machinery specialized for managing hazards, which causes good violation detection on precautionary rules. Obsessive-compulsive disorder, with its compulsive worrying, checking, and precaution taking, may be caused by a misfiring of this precautionary system (Boyer & Liénard, 2006; Cosmides & Tooby, 1999; Leckman & Mayes, 1998, 1999; Szechtman & Woody, 2004).

An alternative view is that reasoning about social contracts and precautionary rules is generated by a single mechanism. Some view both social contracts and precautions as deontic rules (i.e., rules specifying obligations and entitlements) and wonder whether there is a general system for reasoning about deontic conditionals. More specifically, Cheng and Holyoak (1985, 1989) have proposed that inferences about both types of rules are generated by a permission schema, which operates over a larger class of problems.[5]

Can positing a permission schema explain the full set of relevant results? Or are they more parsimoniously explained by positing two separate adaptive specializations, one for social contracts and one for precautionary rules? We are looking for a model that is as simple as possible, but no simpler.

SOCIAL CONTRACT ALGORITHMS OR A PERMISSION SCHEMA? LOOKING FOR DISSOCIATIONS *WITHIN* THE CLASS OF PERMISSION RULES (D1, D2, D4)

Permission rules are a species of conditional rule. According to Cheng and Holyoak (1985, 1989), these rules are imposed by an authority to achieve a social purpose, and they specify the conditions under which an individual is permitted to take an action. Cheng and Holyoak speculate that repeated encounters with such social rules cause domain-general learning mechanisms to induce a *permission schema,* consisting of four production rules (see Table 25.2). This schema generates inferences about any conditional rule that fits the following template: "If action A is to be taken, then precondition R must be satisfied."

Social contracts fit this template. In social exchange, an agent *permits* you to take a benefit from him or her, conditional on your having met the agent's requirement.

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[5] Cheng and Holyoak (1985) also propose an obligation schema, but permission and obligation schemas do not lead to different predictions on the kinds of rules usually tested (see Cosmides, 1989; Rips, 1994, p. 413).

Table 25.2
The Permission Schema Is Composed of Four Production Rules[a]

Rule 1:	If the action is to be taken, then the precondition must be satisfied.[b]
Rule 2:	If the action is not to be taken, then the precondition need not be satisfied.
Rule 3:	If the precondition is satisfied, then the action may be taken.
Rule 4:	If the precondition is not satisfied, then the action must not be taken.

[a] Cheng and Holyoak, 1985.

[b] Social contracts and precautions fit the template of Rule 1:
If the benefit is to be taken, then the requirement must be satisfied.
If the hazardous action is to be taken, then the precaution must be taken.

There are, however, many situations other than social exchange in which an action is permitted conditionally. Permission schema theory predicts uniformly high performance for the entire class of permission rules, a set that is larger, more general, and more inclusive than the set of all social contracts (see Figure 25.5).

On this view, a neurocognitive system specialized for reasoning about social exchange, with a subroutine for cheater detection, does not exist. According to their hypothesis, a permission schema causes good violation detection for all permission rules; social contracts are a subset of the class of permission rules; therefore, cheater detection occurs as a by-product of the more domain-general permission schema (Cheng & Holyoak, 1985, 1989).

In contrast, the adaptive specialization hypothesis holds that the design of the reasoning system that causes cheater detection is more precise and functionally specialized than the design of the permission schema. Social contract algorithms should have design features that are lacking from the permission schema, such as responsivity to benefits and intentionality. As a result, removing benefits (D1, D2)

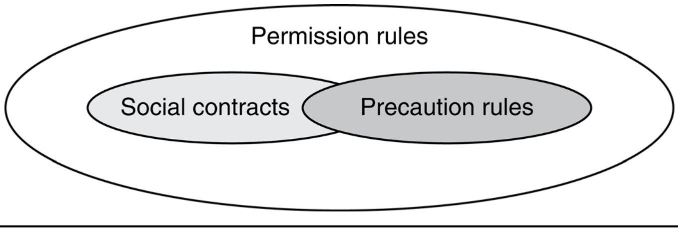

Figure 25.5 The Class of Permission Rules Is Larger Than, and Includes, Social Contracts and Precautionary Rules. Many of the permission rules we encounter in everyday life are neither social contracts nor precautions (white area). Rules of civil society (etiquette, customs, traditions), bureaucratic rules, corporate rules—many of these are conditional rules that do not regulate access to a benefit or involve a danger. Permission schema theory (see Table 25.2) predicts high performance for all permission rules; however, permission rules that fall into the white area do not elicit the high levels of performance that social contracts and precaution rules do. Neuropsychological and cognitive tests show that performance on social contracts dissociates from other permission rules (white area), from precautionary rules, and from the general class of deontic rules involving subjective utilities. These dissociations would be impossible if reasoning about social contracts and precautions were caused by a single schema that is general to the domain of permission rules.

and/or intentionality (D4) from a social contract should produce a permission rule that fails to elicit good violation detection on the Wason task.

As Sherlock Holmes might put it, we are looking for the dog that did not bark: permission rules that do *not* elicit good violation detection. That discovery would falsify permission schema theory. Social contract theory predicts functional dissociations *within* the class of permission rules whereas permission schema theory does not.

NO BENEFITS, NO SOCIAL EXCHANGE REASONING: TESTING D1 AND D2

To trigger cheater detection (D2) and inference procedures specialized for interpreting social exchanges (D1), a rule needs to regulate access to benefits, not actions more generally. Does reasoning performance change when benefits are removed?

BENEFITS ARE NECESSARY FOR CHEATER DETECTION (D1, D2)

The function of a social exchange for each participant is to gain access to benefits that would otherwise be unavailable to them. Therefore, an important cue that a conditional rule is a social contract is the presence in it of a desired benefit under the control of an agent. *Taking a benefit* is a representational primitive within the social contract template: *If you take benefit B, then you must satisfy requirement R.*

The permission schema template has representational primitives with a larger scope than that proposed for social contract algorithms. For example, *taking a benefit* is *taking an action,* but not all cases of taking actions are cases of taking benefits. As a result, all social contracts are permission rules, but not all permission rules are social contracts. Precautionary rules can also be construed as permission rules (although they need not be; see Fiddick et al., 2000, exp. 2). They, too, have a more restricted scope: *Hazardous actions* are a subset of *actions; precautions* are a subset of *preconditions.*

Note, however, that there are permission rules that are neither social contracts nor precautionary rules (see Figure 25.5). This is because there are actions an individual can take that are not *benefits* (social contract theory) and that are not *hazardous* (hazard management theory). Indeed, we encounter many rules like this in everyday life—bureaucratic and corporate rules, for example, often state a procedure that is to be followed without specifying a benefit (or a danger). If the mind has a permission schema, then people should be good at detecting violations of rules that fall into the white area of Figure 25.5, that is, permission rules that are neither social contracts nor precautionary. But they are not. Benefits are necessary for cheater detection.

Using the Wason task, several labs have tested permission rules that involve no benefit (and are not precautionary). As predicted by social contract theory, these do not elicit high levels of violation detection. For example, Cosmides and Tooby (1992; see also Cosmides et al., 2010) constructed Wason tasks in which the elders (authorities) were creating laws governing the conditions under which adolescents are permitted to take certain actions. For all tasks, the law fit the template for a permission rule. The permission rules tested differed in just one respect: whether the action to be taken is a benefit or an unpleasant chore. The critical conditions compared performance on these two rules:

[3] "If one is going out at night, then one must tie a small piece of red volcanic rock around one's ankle."

[4] "If one is taking out the garbage, then one must tie a small piece of red volcanic rock around one's ankle."

A cheater detection subroutine looks for benefits illicitly taken; without a benefit, it doesn't know what kind of violation to look for (D1, D2). When the permitted action was a benefit (getting to go out at night), 80% of subjects answered correctly; when it was a chore (taking out the garbage), only 44% did so (for details, see Cosmides et al., 2010). This dramatic decrease in violation detection was predicted in advance by social contract theory. Moreover, it violates the central prediction of permission schema theory: that being a permission rule is sufficient to facilitate violation detection. There are now many experiments showing poor violation detection with permission rules that lack a benefit (e.g., Barrett, 1999; Beaman, 2002; Cosmides, 1989, exp. 5; Fiddick, 2003; Manktelow & Over, 1991; Platt & Griggs, 1993; for discussion, see Cosmides & Tooby, 2008b).

This is another dissociation by content, but this time it is *within* the domain of permission rules. To elicit cheater detection, a permission rule must be interpreted as restricting access *to a benefit.* It supports the psychological reality of the representational primitives posited by social contract theory, showing that the representations necessary to trigger differential reasoning are more content specific than those of the permission schema.

BENEFITS TRIGGER SOCIAL CONTRACT INTERPRETATIONS (D1)

The Wason experiments just described tested D1 and D2 in tandem. But D1—the claim that benefits are necessary for permission rules to be *interpreted* as social contracts—receives support independent of experiments testing D2, from studies of moral reasoning. Fiddick (2004) asked subjects what justifies various permission rules and when an individual should be allowed to break them. The rules were closely matched for surface content, and context was used to vary their interpretation. The permission rule that lacked a benefit (a precautionary one) elicited different judgments from permission rules that restricted access to a benefit (the social contracts). Whereas social agreement and morality, rather than facts, were more often cited as justifying the social contract rules, facts (about poisons and antidotes) rather than social agreement were seen as justifying the precautionary rule. Whereas most subjects thought it was acceptable to break the social contract rules if you were not a member of the group that created them, they thought the precautionary rule should always be followed by people everywhere. Moreover, the explicit exchange rule triggered very specific inferences about the conditions under which it could be broken: Those who had received a benefit could be released from their obligation to reciprocate, *but only by those who had provided the benefit to them* (i.e., the obligation could not be voided by a group leader or by a consensus of the recipients themselves). The inferences subjects made about the rules restricting access to a benefit follow directly from the grammar of social exchange laid out in social contract theory (Cosmides & Tooby, 1989). These inferences were not—and should not—be applied to precautionary rules (see also Fiddick et al., 2000). The presence of a benefit also predicted inferences about emotional reactions to seeing someone violate a permission rule: Social contract violations were thought to trigger anger whereas precautionary violations were thought to trigger fear (Fiddick, 2004). None of these dissociations within the realm of permission rules are predicted by permission schema theory.

INTENTIONAL VIOLATIONS VERSUS INNOCENT MISTAKES: TESTING D4

Intentionality plays no role in permission schema theory. Whenever the action has been taken but the precondition has not been satisfied, the permission schema should register that a *violation* has occurred. As a result, people should be good at detecting violations of permission rules, whether the violations occurred by accident or by intention. In contrast, social contract theory predicts a mechanism that looks for *intentional* violations (D4).

Program designs that cause unconditional helping are not evolutionarily stable strategies. Conditional helping can be an ESS because cheater detection provides a specific fitness advantage unavailable to unconditional helpers: By identifying cheaters, the conditional helper can avoid squandering costly cooperative efforts in the future on those who, by virtue of having an alternative program design, will not reciprocate. This means the evolutionary function of a cheater detection subroutine is to correctly connect an attributed disposition (to cheat) with a person (a cheater). It is not simply to recognize instances wherein an individual did not get what he or she was entitled to. Violations of social contracts are relevant only insofar as they reveal individuals disposed to cheat—individuals who cheat by design, not by accident. Noncompliance caused by factors other than disposition, such as accidental violations and other innocent mistakes, does not reveal the disposition or design of the exchange partner. Accidents may result in someone being cheated, but without indicating the presence of a cheater.[6]

Therefore, social contract theory predicts an additional level of cognitive specialization beyond looking for violations of a social contract. Accidental violations of social contracts will not fully engage the cheater detection subroutine; intentional violations will (D4).

A DISSOCIATION FOR SOCIAL CONTRACTS

Given the same social exchange rule, one can manipulate contextual factors to change the nature of the violation from intentional cheating to an innocent mistake. One experiment, for example, compared a condition in which the potential rule violator was inattentive but well meaning to a condition in which she had an incentive to intentionally cheat. Varying intentionality caused a radical change in performance, from 68% correct in the intentional cheating condition to 27% correct in the innocent mistake condition (Cosmides et al., 2010; supports D4; disconfirms B1–B8). Fiddick (1998, 2004) found the same effect (as did Gigerenzer & Hug, 1992, using a different context manipulation).

In both scenarios, violating the rule would result in someone being cheated, yet high performance occurred only when being cheated was caused by a cheater. Cosmides et al. (2010; see also Barrett, 1999) conducted a series of parametric studies

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[6] Mistakes can be faked, of course. Too many by a given individual should raise suspicion, as should a single mistake that results in a very large benefit. Although this prediction has not been tested yet, we would expect social contract algorithms to be sensitive to these conditions.

to find out whether the drop in performance in the innocent mistake condition was caused by the violator's lack of intentionality (D4) or by the violator's failure to benefit from her mistake (D2; see earlier discussion, on the necessity of *benefits* to elicit cheater detection). They found that both factors independently contributed to the drop, equally and additively. Thus, the same decrease in performance occurred whether (1) violators would benefit from their innocent mistakes, or (2) violators wanted to break the rule on purpose but would not get the benefit specified in the rule by doing so. For scenarios missing both factors (i.e., accidental violations that do not benefit the violator), performance dropped by twice as much as when just one factor was missing. That is, the more factors relevant to cheater detection are removed, the more performance drops.

In bargaining games, experimental economists have found that subjects are twice as likely to punish defections (failures to reciprocate) when it is clear that the defector intended to cheat as when the defector is a novice who might have simply made a mistake (Hoffman, McCabe, & Smith, 1998). This provides interesting convergent evidence, using entirely different methods, for the claim that programs causing social exchange distinguish between mistakes and intentional cheating.

NO DISSOCIATION FOR PRECAUTIONS

Different results are expected for precautionary rules. Intentionality should not matter if the mechanisms that detect violations of precautionary rules were designed to look for people in danger. For example, a person who is not wearing a gas mask while working with toxic gases is in danger, whether that person forgot the gas mask at home (accidental violation) or left it home on purpose (intentional violation). That is, varying the intentionality of a violation should affect social exchange reasoning but not precautionary reasoning. Fiddick (1998, 2004) tested and confirmed this prediction: Precautionary rules elicited high levels of violation detection whether the violations were accidental or intentional, but performance on social contracts was lower for accidental violations than for intentional ones. This functional distinction between precautionary and social exchange reasoning was predicted in advance based on the divergent adaptive functions proposed for these two systems.

ELIMINATING PERMISSION SCHEMA THEORY (B4)

The preceding results violate central predictions of permission schema theory. According to that theory, (1) all permission rules should elicit high levels of violation detection, whether the permitted action is a benefit or a chore; and (2) all permission rules should elicit high levels of violation detection, whether the violation was committed intentionally or accidentally. Both predictions fail. Permission rules fail to elicit high levels of violation detection when the permitted action is neutral or unpleasant (yet not hazardous). Moreover, people are bad at detecting accidental violations of permission rules that are social contracts. Taken together, these results eliminate the hypothesis that the mind contains or develops a permission schema of the kind postulated by Cheng and Holyoak (1985, 1989).

ELIMINATING CONTENT-FREE DEONTIC LOGICS (B6)

The same results also falsify hypothesis B6: that cheater detection on social contracts is caused by a content-free deontic logic (for discussion of this possibility, see Manktelow & Over, 1987; Cosmides & Tooby, 2008a). All the benefit and intentionality tests described in this section involved deontic rules, but not all elicited high levels of violation detection.

This same set of results also defeats a related claim by Fodor (2000): that "the putative cheater detection effect on the Wason task is actually a materials artifact" (p. 29). This sweeping conclusion is predicated on the (mistaken) notion that the only evidence for cheater detection comes from experiments in which the control problems are indicative (i.e., descriptive) conditional rules (a curious mistake because it is refuted by experiments with deontic controls, which are presented in the single source Fodor cites: Cosmides & Tooby, 1992). According to Fodor, reasoning *from* a deontic conditional rule that is stipulated to hold is more likely to elicit violation detection than reasoning *about* a rule whose truth is in question (even though in both cases the individual is asked to do the same thing: look for rule violations). Fodor's explanation for this purported difference is deeply flawed (among other things, it assumes what it seeks to explain; see Cosmides & Tooby, 2008a, 2008b). But instead of disputing Fodor's reasoning, let us consider whether his artifact explanation can account for the cheater detection results observed. After all, there are many experiments comparing reasoning on social contracts to reasoning about other deontic conditionals.

According to Fodor, high levels of violation detection will be found for any deontic rule that specifies what people are (conditionally) required to do (because all involve reasoning with the law of contradiction). All the permission rules described earlier had precisely this property, all were stipulated to hold, and, in every case, subjects were asked to reason *from* the rule, not about it. If Fodor's artifact hypothesis was correct, all of these rules should have elicited good violation detection. But they did not. Violation detection was poor when the deontic rule lacked a benefit; it was also poor for social contract rules when the potential violator was accused of making innocent mistakes rather than intentional cheating. This pattern is predicted by social contract theory, but not by Fodor's hypothesis that reasoning from a deontic conditional rule is sufficient to elicit good violation detection.

B5—that social contract rules elicit good performance merely because we understand what implications follow from them (e.g., Almor & Sloman, 1996)—is eliminated by the intention versus accident dissociation. The same social contract rule—with the same implications—was used in both conditions. If the rule's implications were understood in the intention condition, they also should have been understood in the accident condition. Yet the accident condition failed to elicit good violation detection. Understanding the implications of a social contract may be necessary for cheater detection (Fiddick et al., 2000), but the accident results show this is not sufficient.

In short, it is not enough to admit that moral reasoning, social reasoning, or deontic reasoning is special: The specificity of design for social exchange is far narrower in scope.

A NEUROPSYCHOLOGICAL DISSOCIATION BETWEEN SOCIAL CONTRACTS AND PRECAUTIONS

Like social contracts, precautionary rules are conditional, deontic, and involve subjective utilities. Moreover, people are as good at detecting violators of precautionary rules as they are at detecting cheaters on social contracts. This has led some to conclude that reasoning about social contracts and precautions is caused by a single, more general mechanism (e.g., general to permissions, to deontic rules, or to deontic rules involving subjective utilities; Cheng & Holyoak, 1989; Manktelow & Over, 1988, 1990, 1991; Sperber et al., 1995). Most of these one-mechanism theories are undermined by the series of very precise, functional dissociations between social exchange reasoning and reasoning about other deontic permission rules (discussed earlier). But a very strong test, one that addresses *all* one-mechanism theories, would be to find a neural dissociation between social exchange and precautionary reasoning.

ONE MECHANISM OR TWO?

If reasoning about social contracts and precautions is caused by a single mechanism, then neurological damage to that mechanism should lower performance on both types of rule. But if reasoning about these two domains is caused by two functionally distinct mechanisms, then it is possible for social contract algorithms to be damaged while leaving precautionary mechanisms unimpaired, and vice versa.

Stone et al. (2002) developed a battery of Wason tasks that tested social contracts, precautionary rules, and descriptive rules. The social contracts and precautionary rules elicited equally high levels of violation detection from normal subjects (who got 70% and 71% correct, respectively). For each subject, a difference score was calculated: percentage correct for precautions minus percentage correct for social contracts. For normal subjects, these difference scores were all close to zero (Mean = 1.2 percentage points, $SD = 11.5$).

Stone and colleagues (2002) administered this battery of Wason tasks to R. M., a patient with bilateral damage to his medial orbitofrontal cortex and anterior temporal cortex (disconnecting both amygdalae). R. M.'s performance on the precaution problems was 70% correct: equivalent to that of the normal controls. In contrast, his performance on the social contract problems was only 39% correct. R. M.'s difference score (precautions minus social contracts) was 31 percentage points. This is 2.7 standard deviations larger than the average difference score of 1.2 percentage points found for control subjects ($p < .005$). In other words, R. M. had a large deficit in his social contract reasoning, alongside normal reasoning about precautionary rules.

Double dissociations are helpful in ruling out differences in task difficulty as a counterexplanation for a given dissociation (Shallice, 1988), but here the tasks were perfectly matched for difficulty. The social contracts and precautionary rules given to R. M. were logically identical, posed identical task demands, and were equally difficult for normal subjects. Moreover, because the performance of the normal controls was not at ceiling, ceiling effects could not be masking real differences in the difficulty of the two sets of problems. In this case, a single dissociation licenses inferences about the underlying mental structures. R. M.'s dissociation supports the hypothesis that reasoning about social exchange is caused by a different computational system than reasoning about precautionary rules: a two-mechanism account.

Although tests of this kind cannot conclusively establish the anatomical location of a mechanism, tests with other patients suggest that damage to a circuit connecting anterior temporal cortex to the amygdalae was important in creating R. M.'s selective deficit.[7] Recent functional imaging (fMRI) studies also support the hypothesis that social contract reasoning is supported by different brain areas than precautionary reasoning, and imply the involvement of several brain areas in addition to temporal cortex (Ermer, Guerin, Cosmides, Tooby, & Miller, 2006; Fiddick, Spampinato, & Grafman, 2005; Reis, Brackett, Shamosh, Kiehl, Salovey, & Gray, 2007; Wegener, Lund, Hede, Ramsøy, Baaré, & Paulson, 2004).

ELIMINATING ONE-MECHANISM HYPOTHESES (B6–B8; B1–B4)

Every alternative explanation of cheater detection proposed so far claims that reasoning about social contracts and precautions is caused by the same neurocognitive system. R. M.'s dissociation is inconsistent with all of these one-mechanism accounts. These accounts include mental logic (Rips, 1994), mental models (Johnson-Laird & Byrne, 1991), decision theory/optimal data selection (Kirby, 1994; Oaksford & Chater, 1994), permission schema theory (Cheng & Holyoak, 1989), relevance theory (Sperber et al., 1995),[8] and Manktelow and Over's (1991, 1995) view implicating a system that is general to any deontic rule that involves subjective utilities. (For further evidence against relevance theory, see Fiddick et al., 2000; for further evidence against Manktelow & Over's theory, see Fiddick & Rutherford, 2006.)

Indeed, no other reasoning theory even distinguishes between precautions and social contract rules; the distinction is derived from evolutionary-functional analyses and is purely in terms of *content.* These results indicate the presence of a very narrow, content-sensitive cognitive specialization within the human reasoning system.

PRECOCIOUS DEVELOPMENT OF SOCIAL EXCHANGE REASONING

Children understand what counts as cheating on a social contract by age 3 (Harris & Núñez, 1996; Harris, Núñez, & Brett, 2001; Núñez & Harris, 1998a).[9] This has been shown repeatedly in experiments by Harris and Núñez using an evaluation task: a task in which the child must decide when a character is violating a rule. Consider, for example, a story in which Carol wants to ride her bicycle but her mom says, "If you ride your bike, then you must wear an apron." This rule restricts access to a benefit (riding the bike) based on whether the child has satisfied an arbitrary requirement. The child is then shown four pictures (Carol riding the bike wearing an apron, Carol riding without an apron, Carol wearing an apron but not riding, and Carol not riding or wearing an apron) and asked to choose the picture in which Carol is doing something naughty. British 3-year-olds chose the correct picture (Carol riding the bike with no apron) 72% to 83% of the time; 4-year-olds, 77% to 100% of the time (Harris & Núñez, 1996; Harris et al., 2001; Núñez & Harris, 1998a). These performance levels were found

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[7] Stone et al. (2002) tested two other patients with overlapping but different patterns of brain damage. R. B. had more extensive bilateral orbitofrontal damage than R. M., and had some anterior temporal damage as well, but his right temporal pole was largely spared (thus he did not have bilateral disconnection of the amygdalae): His scores were 85% correct for precautions and 83% correct for social contracts. B. G. had extensive bilateral temporal pole damage compromising (though not severing) input into both amygdalae, but his orbitofrontal cortex was completely spared: He scored 100% on both sets of problems.

[8] For a full account of the problems relevance theory has explaining social contract reasoning, see Fiddick et al., 2000.

[9] Younger children have not been tested yet.

whether the social contract emanated from the mother or was a consensual swap between two children; that is, the rule did not have to be imposed by an authority figure. A variety of tests showed that, for social contracts, children understood that taking the benefit was *conditional* on meeting the requirement. They were not merely looking for cases in which the requirement was not met; they were looking for cases in which the benefit was taken *and* the requirement was not met. The same effects were found for preschoolers from the United Kingdom, Colombia, and (with minor qualifications) rural Nepal.

The performance of the preschoolers was adultlike in other ways. Like adults, the preschoolers did well whether the social contract was familiar or unfamiliar. Also like adults, intentionality mattered to the children. Núñez and Harris (1998a) varied (1) whether the character had taken the benefit or not and (2) whether the character had failed to fulfill the requirement by accident or deliberately. Children were far more likely to say the character had been naughty when the breach was intentional rather than accidental. Four-year-olds deemed social contract violations naughty 81% of the time when they were intentional versus 10% of the time when they were accidental; for 3-year-olds, the figures were 65% versus 17%, respectively. Children also could match emotions to outcomes for reciprocal exchanges: Given an agreement to swap, they understood that the victim of cheating would feel upset, and that both children would be happy if the swap was completed (Núñez, 2011).

Moreover, the children tested by Harris and Núñez (1996) showed the same dissociation between social contract and descriptive rules as adults: 3- to 4-year-olds chose the correct violation condition only 40% of the time for descriptive rules but 72% to 83% of the time for social contracts. By age 5, children could solve a full-array Wason selection task when the rule was a social contract (Núñez & Harris, 1998b; performance limitations, rather than competence problems, interfered with the Wason performance of the preschoolers).[10]

CROSS-CULTURAL INVARIANCES AND DISSOCIATIONS IN SOCIAL EXCHANGE REASONING

Cognitive neuroscientists have long been aware that neural dissociations are useful for elucidating mental structure. But cultural dissociations may provide a uniquely informative source of converging evidence. Because the ontogenetic experience of people in different cultures varies widely, cross-cultural studies allow one to see whether differences in ontogenetic experience are associated with differences in mental structure.

Most psychologists and anthropologists believe that high-level cognitive competences emerge from general-purpose cognitive abilities trained by culturally specific activities, rather than as part of our evolved, reliably developing, species-typical design. That cheater detection should be well developed across cultures is a falsifiable

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[10] Although the definitive experiments have not yet been done, existing evidence suggests that preschoolers also understand violations of precautionary rules. The rules used by Harris and Núñez (1996) fell into two categories: pure social contracts (“arbitrary permissions” and “swaps,” in their terminology) and hybrid rules (ones that can be interpreted either as social contracts or precautionary). The hybrids were rules that restricted access to a benefit on the condition that a precaution was taken, for example, *If you play outside, you must wear a coat* (to keep warm). Cummins (1996) tested a more purely precautionary rule, but the context still involved restrictions on access to a benefit (playing outside).

prediction of the evolutionary account, which posits that this competence should be distributed in a species-typical, human universal fashion. More precisely, because detecting cheaters is necessary for social exchange to be an ESS, the development of cheater detection should be buffered against cultural variation and, therefore, be uniform. In contrast, the development of ESS-irrelevant aspects of performance (e.g., interest in acts of generosity) is under no selection to be uniform across cultures and should, therefore, be free to vary with cultural circumstance.

Sugiyama et al. (2002) tested these predictions among the Shiwiar, a hunter-horticultural population in a remote part of the Ecuadorian Amazon. Good cheater detection had already been established in the United States, Europe, Hong Kong, and Japan. But adults in advanced market economies engage in more trade—especially with strangers—than people who hunt and garden in remote parts of the Amazon. Anonymity facilitates cheating; markets increase the volume of transactions experienced by each individual. If no evolved specialization is involved—that is, if general-purpose processes induce a cheater detection subroutine through repeated experience with cheating—then this subroutine might not be found outside the Western world.

The Shiwiar were raised and continue to live in a culture as different from that of American college students as any on the planet. Nevertheless, Shiwiar were just as good at detecting cheaters on Wason tasks as Harvard undergraduates were (Figure 25.6). For cheater-relevant cards, the performance of Shiwiar hunter-horticulturalists was identical to that of Harvard students. Shiwiar differed only in that they were more likely to also show interest in cheater-irrelevant cards—the ones that could reveal acts of generosity. (Their excellence at cheater detection did not result from indiscriminate interest in all cards. Controlling for logical category, Shiwiar were more than twice as likely to choose a card when it was cheater-relevant than when it was not; $p < .005$.) In short, there was no dissociation between cultures in the parts of the mechanism necessary to its performing its evolved function. The only "cultural dissociation" was in ESS-irrelevant aspects of performance.

Is cheater detection invariant because the sociocultural experience of Shiwiar and American subjects is too similar to cause differences in reasoning performance? Clearly not; if that were true, the two populations would perform identically on cheater-irrelevant cards as well as on cheater-relevant ones. That did not happen.

This is the only research we know of to show identical performance across very different cultural groups on those aspects of a reasoning problem that are relevant to a cognitive adaptation functioning as an evolutionarily stable strategy, yet different performance on those aspects that are irrelevant to the adaptation functioning as an ESS. That performance in detecting cheaters was invariant across very disparate cultural settings suggests that the brain mechanism responsible is a reliably developing neurocognitive system. That is, its development is canalized in a way that buffers it against idiosyncratic variations in ontogenetic experience.

DOES DOMAIN-GENERAL LEARNING BUILD THE SPECIALIZATION FOR SOCIAL EXCHANGE?

The empirical evidence reviewed earlier strongly supports the claim that reasoning about social exchange is caused by neurocognitive machinery that is specialized for

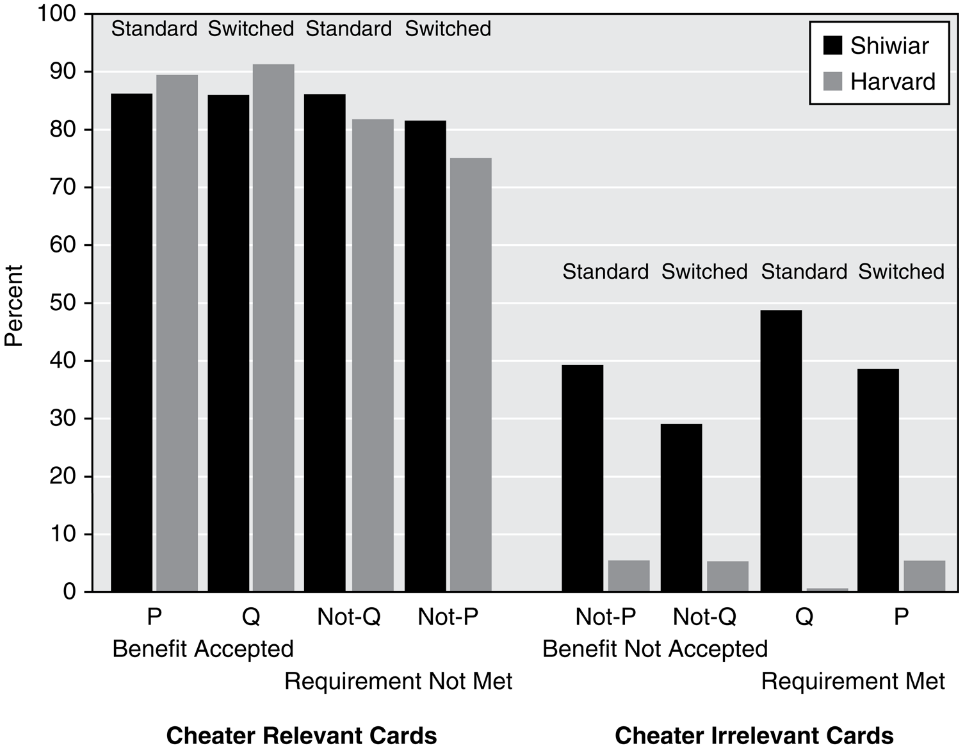

Figure 25.6 Performance of Shiwiar Hunter-Horticulturalists and Harvard Undergraduates on Standard and Switched Social Contracts (percent of subjects choosing each card). There was no difference between the two populations in their choice of cheater relevant cards (*benefit accepted*, *requirement not satisfied*). They differed only in their choice of cheater-irrelevant cards (Shiwiar showing more interest in cards that could reveal acts of generosity or fair play). Shiwiar high performance on cheater-relevant cards is not caused by indiscriminate interest in all cards. Holding logical category constant, Shiwiar always chose a card more frequently when it was relevant to cheater detection than when it was not. This can be shown by comparing performance on standard versus switched social contracts (e.g., the *P* card is cheater-relevant for a standard social contract, but not for a switched one; see Figure 25.4).

this function in adults: social contract algorithms. This conclusion was supported not just by evidence from Wason tasks but also from experimental economics games, moral reasoning protocols, emotion attribution tasks, and developmental studies. What makes the Wason results particularly interesting, however, is that the Wason task requires information search. The Wason results indicate the presence of a subroutine that is narrowly specialized for *seeking out* information that would *reveal* the presence of cheaters. This subroutine is not designed to seek out information that would reveal the presence of cheating (when this occurs by mistake), or permission violations, or violations in general.

But how was this very precisely designed computational specialization produced? Are the developmental mechanisms that build social contract algorithms domain-specific and specialized for this function? Or are social contract specializations in adults built by domain-general learning mechanisms?

If computational specializations for social exchange are acquired via some general-purpose learning process, then we should not claim that the specialization is an evolved adaptation *for* social exchange. Instead, the social exchange specialization would be the product of a learning mechanism that evolved to solve a different, perhaps more general, adaptive problem.

General Purpose Learning Is a Nonstarter

Evidence of an adaptive specialization in the adult human mind often meets the following rejoinder: Although the adult mechanism is specialized, the mechanisms that built it are not—the adult specialization was acquired via a general purpose learning process (e.g., Elman et al., 1996; Gauthier & Tarr, 2002; Orr, 2003; Rumelhart & McClelland, 1986; for discussion, see Duchaine, 2001; Duchaine, Yovel, Butterworth, & Nakayama, 2006; Pinker, 2002; Tooby & Cosmides, 1992).

There is a fundamental problem with this view: No general purpose learning process is known to science (Gallistel, 2000). This is not because scientists are in the dark about animal learning. Learning processes specialized for solving specific adaptive problems have been found in many species, including dead reckoning in desert ants, learned food aversions in rats, star navigation in birds, snake fear in primates, and language acquisition in humans (Gallistel, 1990, 2000; Garcia, 1990; Garcia & Koelling, 1966; Mineka & Cook, 1993; Pinker, 1994). Indeed, even classical conditioning, considered by many to be the premier example of general purpose learning, is anything but (Staddon, 1988). The empirical evidence shows that this form of learning is adaptively specialized for a specific computational task common in foraging and predator avoidance: multivariate nonstationary time series analysis (Gallistel & Gibbon, 2000).

Classical and operant conditioning are adaptive specializations, but it is true that they operate over inputs from many different domains (i.e., they are somewhat content-general). So let us reframe the rejoinder thus: Are adult specializations for reasoning about social exchange acquired via classical or operant conditioning?

At the root of operant and classical conditioning is the ability to respond contingently to reward and punishment (Gallistel & Gibbon, 2000; Staddon, 1988). Social exchange entails such contingencies: I offer to provide a benefit to you, contingent on your satisfying a requirement that I specify. I impose that requirement in the hope that your satisfying it will create a situation that benefits me in some way.

Yet the ability to respond contingently to reward and punishment is not sufficient for social exchange to emerge in a species. All animal species can be classically and operantly conditioned (Staddon, 1988), but few species engage in social exchange. If classical and/or operant conditioning caused the acquisition of social exchange specializations, then social exchange should be zoologically widespread. The fact that it is so rare means that it is not the consequence of any behavior-regulation or learning process that is zoologically common.

Although reciprocity is rare in the animal kingdom, it is found in a number of nonhuman primate species (Brosnan & de Waal, 2003; de Waal, 1989, 1997a, 1997b; de Waal & Luttrell, 1988). Its presence in other primates means that social exchange behavior can arise in the absence of language. This means the conditioning hypothesis cannot be rescued by arguing that the development of social exchange requires the joint presence of language and conditioning mechanisms.

STANDARD ECONOMIC MODELS CANNOT EXPLAIN THE RESULTS (B9)

Can the development of neurocognitive specializations for reasoning about social exchange be accounted for by the fact that reciprocity is economically advantageous? An economic folk theory exists and was articulated by Orr (2003, p. 18):

> An evolutionary psychologist might counter that the fact that a behavior conforms so closely to what's expected of an adaptive one is evidence that it's a bona fide biological adaptation. And here we arrive at another problem. For the same logic that makes a behavior evolutionarily advantageous might also make it "economically" advantageous . . . . The point is that when evolutionary and economic considerations yield the same prediction, conformity to Darwinian predictions cannot be taken as decisive.

This would be a good point if economists had a theory of the computations that give rise to economic learning and decision making. But they do not. Having no account of how economic reasoning is accomplished, economists have relied on a Homo economicus (economic man) model, an *as if* approach. According to Homo economicus models, people reason *as if* they were equipped with neurocognitive mechanisms that compute (in some as yet unspecified way) the subjective expected utility of alternative actions, and choose the one that maximizes personal utility (Savage, 1954).

Homo economicus models make very precise predictions about the choices people should make when engaging in social exchange and other economic games. Contrary to Orr's assumption, however, these economic models and the evolutionarily functional theory of social exchange make different predictions about human behavior (Delton, Krasnow, Cosmides, & Tooby, 2011; Hoffman, McCabe, & Smith, 1998). There is now a large body of results from experimental economics showing that people rarely behave as the Homo economicus model predicts and that this is not due to inexperience with the experimental situation—even experienced subjects violate the model's predictions (e.g., Fehr & Gächter, 2000a, 2000b; Henrich et al., 2005; Hoffman et al., 1998; Krasnow, Cosmides, Pedersen, & Tooby, 2012). For example, when given the opportunity to engage in social exchange, people routinely and systematically choose to cooperate with others when they would earn a higher payoff by defecting; they also punish acts of cheating when they would earn more by not doing so. That is, they cooperate and punish in circumstances, such as the one-shot Prisoners' Dilemma, where these choices are not utility maximizing (Hoffman et al., 1998). As Hoffman and colleagues argue, these are precisely the responses one would expect of specializations designed to operate in small hunter-gatherer bands, where repeated interactions are the norm and one-shot interactions are rare (for agent-based simulations supporting this point, see Delton et al., 2011; Krasnow, Delton, Tooby, & Cosmides, 2013). The results reported earlier on accidental versus intentional violations of social contracts are also inconsistent with economic prediction. Economic man theories predict mechanisms that respond to the payoff structure of situations, not to intentions, and cheating produces the same negative payoff whether it was accidental or intentional. Thus, a system designed for maximizing utility should detect cheating, not cheaters. Yet that is not the empirical finding.

Rational or *economically advantageous* has to refer to some kind of reasoning process if it is to serve as an explanation of anything, and the most completely axiomatized normative model of rational economic behavior fails to predict or explain the facts of when humans choose to cooperate and punish, either in social exchange

(Hoffman et al., 1998) or in public goods games (Fehr & Gächter, 2000a, 2000b; Henrich et al., 2005; Kurzban, McCabe, Smith, & Wilson, 2001). Because the facts of social exchange reasoning and behavior contradict central predictions of this standard economic model, this economic by-product hypothesis cannot explain the features of the neurocognitive specialization found in adults, or the development of these features (B9 eliminated). In light of this failure, a number of economists are turning to evolutionary psychological accounts of social exchange and judgment under uncertainty to explain human economic behavior (Gigerenzer & Selten, 2001; Hoffman et al., 1998; Romer, 2000).

Statistical Learning and Content-Free Inductive Inference: More Dogs That Do Not Bark (B10)

Various accounts of inductive learning have been proposed: Bayesian learning machines, connectionist systems that compute a multiple regression, contingency calculators. Some posit highly domain-specific, inductive learning systems (e.g., Marcus, 2001; Staddon, 1988), but most do not (e.g., Elman et al., 1996; Quartz & Sejnowski, 1997).

The domain-general proposals foreground the role of content-blind inductive inference procedures in the construction of mental content.[11] These extract statistical relationships from patterns that are objectively present in the external world. Indeed, they are constrained to do so: The world is the only source of content for these statistical learning mechanisms. As a result, we should see certain dogs barking. For example, 20th-century Chicago schoolchildren should fear things that are dangerous to children living in 20th-century urban Chicago—electric sockets, cars, streets, hot stoves. The content of their fears should reflect the frequency and statistical distribution of dangers in the modern world because it was constructed by content-free mechanisms operating on information derived from these distributions.

By contrast, domain-specific learning mechanisms are content rich: They allow inferences that go beyond the information given, so the mental content constructed may be richer than (or merely different from) the statistical distribution of information in the external world of individual experience. For example, when asked what they are most afraid of, Chicago schoolchildren name lions, tigers, wild animals, "monsters" (dangerous but unspecified animal or humanlike creatures), snakes, and spiders (Maurer, 1965). The content of their fears reflects the statistical distribution of dangers in an ancestral world they have never experienced (Marks, 1987). It does not reflect the statistical distribution of dangers in urban Chicago—that is, the modern dogs are not barking.

People reliably develop—apparently by age 3—social contract algorithms with the properties discussed in this review. These properties make that neurocognitive system very good at solving an adaptive problem of the ancestral world: seeking out information that would reveal cheaters. We know there is good design for this ancestral problem because very precise patterns of dissociations by content—both functional and neural—were predicted in advance of their discovery on the basis of ESS analyses applied to the behavioral ecology of hunter-gatherers. However,

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[11] Attentional biases (e.g., for faces) play a role in some of the domain-general theories (e.g., Elman et al., 1996), but these are thought to be few in number and, crucially, to not contain the mental content that is eventually constructed (the source of which is patterns in the world).

statistical learning theories cannot even retrodict this pattern of dissociations (let alone predict them in advance).

The explanatory variables that drive statistical learning are experience, repetition, and their consequence, familiarity. If these variables caused the development of reasoning specializations, we should observe a different set of reasoning specializations than are found, including ones that produce good violation detection for permission rules and even descriptive ones. But these modern dogs are not barking either.

Where Is the Specialization for Finding Violations of Descriptive Rules? Descriptive rules are not rare, exotic occurrences. They are claims about how the world works, commonplaces of everyday conversation (*If you wait until November, the clinic will be out of flu shots. If she eats hot chili, she likes a cold beer. If you use that pan, the casserole will stick. If you wash with bleach, your clothes will be whiter.*). Actions are more likely to succeed when they are based on true rather than false information, so violations of these claims should be salient. Consistent with this, people do know what counts as a violation: They can tell you that cases in which *P* happens but *Q* does not violate a descriptive rule, even when the rule is abstract or unfamiliar (Manktelow & Over, 1987).

But this knowledge does not translate into efficacious information search. Although people *recognize* violations of descriptive rules when they occur, they do not *seek out* information that could reveal such violations, even when they are explicitly asked to do so on a Wason task (see instructions for Figure 25.1; for discussion, see Fiddick et al., 2000; Cosmides & Tooby, 2008a). That is, humans do not reliably develop reasoning specializations that cause them to *look for* potential violations of descriptive rules. This dissociation between people's knowledge and what information they search for is found for descriptive rules but not for social contracts. Descriptive rules are ubiquitous. If experience with a type of rule were sufficient for statistical learning to build a specialization for information search, then we should observe good violation detection on Wason tasks using descriptive rules (even unfamiliar ones), just as we do for social contracts.

Even worse, experience with *specific* descriptive rules does nothing to improve performance. Early research using the Wason task explored whether violation detection for descriptive rules was better when the rule, relation, or any of its terms were familiar. It was not (Cheng et al., 1986; Cosmides, 1985; Manktelow & Evans, 1979; Wason, 1983). Furthermore, people who had repeated experience with instances that violated a particular concrete rule performed no better than people who did not have these experiences (Manktelow & Evans, 1979). The impotence of repeated experience with concrete violations is mirrored in the social contract results, where high performance is observed regardless of experience. College students are intimately familiar with rules restricting access to alcohol (e.g., *If you drink beer, then you must be over 21*), and break them regularly, yet Cosmides (1985) found they are no better at detecting violations of this familiar rule than they are for never-experienced rules about cassava root and tattoos.

Where Is the Specialization for Finding Violations of Permission Rules? The failure of statistical learning theories becomes even clearer when we consider that social exchange rules are but a small subset of all permission rules (which are, in turn, a subset of deontic rules, which are themselves a subset of all conditional rules). By class inclusion, humans necessarily have far more experience with permission rules than with social contracts (legend, Figure 25.5). It was on this basis that Cheng and

Holyoak (1985, 1989) argued that domain-general inductive processes *should* produce the more abstract and inclusive permission schema, rather than social contract algorithms, and that this schema should operate not only on social contracts but also on precautionary rules and indeed on any social norm that gives conditional permission. Yet careful tests showed that the permission schema they predicted does not exist.

Poor performance in detecting violations of conditional permission rules drawn from the white zone of Figure 25.5 cannot be explained by claiming that all the permission rules we happen to encounter are either social contracts or precautions. Conditional social norms that fit neither category permeate our society (*If one eats red meat, then one drinks red wine. If you live east of Milpas Street, then vote at Cleveland Elementary School. If the blue inventory form is filled out, file it in the metal bin.* See, e.g., Cosmides et al., 2010, Exp 2.). Yet we do not develop information search strategies specialized for detecting violations of such rules.

Where Is the Specialization for Detecting Negative Payoffs? Statistical learning theorists might respond by saying that learning occurs in response to negative payoffs (see Manktelow & Over, 1995, for a related proposal). This view predicts an information search specialization for detecting when a negative payoff might occur, whether it is produced by cheating on a social contract or failing to take precautions in hazardous situations (Manktelow & Over, 1991, 1995).

Fiddick and Rutherford (2006) show that no such specialization exists: Information search on Wason tasks using social contracts and related rules bears no relationship to subjects' judgments about which outcomes produce negative payoffs. Moreover, R. M.'s neural dissociation (preserved search for violations of precautionary rules with impaired search for cheaters) shows that the mind does not contain a unitary specialization for detecting negative payoffs.

Where Is the Specialization for Detecting Cheating, Rather Than Cheaters? What if statistical learning is triggered by negative payoffs, but only within the domain of social exchange? (This is hardly a domain-general proposal, but never mind.) A person can be cheated—receive a negative payoff due to the violation of a social exchange agreement—by accident or by intention. Both kinds of violation damage personal utility, both are useful to detect, and both require detection if the participant in an exchange is to get what he or she wants and is entitled to. Moreover, because innocent mistakes and intentional cheating both result in someone being cheated, situations in which a person *was cheated* are statistically more common than situations in which someone was cheated *by a cheater.* Hence, this domain-restricted version of statistical learning predicts the development of an information search specialization that looks for acts in which someone was cheated, regardless of cause. This specialization would be easy to engineer: A mechanism that indiscriminately scrutinizes cases in which the benefit was accepted and cases in which the requirement was not met would reveal both accidental and intentional violations. But this specialization does not exist: People are not good at detecting acts of cheating when there is evidence that they occurred by accident rather than intention.

In contrast, it is specifically the detection of intentional cheaters that makes contingent exchange evolutionarily stable against exploitation by cheaters (i.e., an ESS). That people are good at detecting intentional cheating but not accidental mistakes is a unique prediction of the evolutionary task analysis of exchange.

Variables That Affect Statistical Learning Do Not Seem to Affect the Development of Cheater Detection An information search specialization for detecting cheaters reliably develops across large variations in experience, repetition, and familiarity. For example:

- Precocious performance is neither necessary nor sufficient for sustaining an adaptationist hypothesis (Cosmides & Tooby, 1997). It is, however, relevant for evaluating claims of content-free inductive learning because these predict that the development of reasoning skills will reflect the child's experience (e.g., Markman, 1989). The early age at which children understand social exchange reasoning undermines the hypothesis that social contract specializations were constructed by content-independent procedures operating on individual experience.
- Preschool-age children are not noted for the accuracy and consistency of their reasoning in many domains, even ones with which they have considerable experience. For example, many children this age will say that a raccoon can change into a skunk; that there are more daisies than flowers; that the amount of liquid changes when poured from a short fat beaker into a tall thin one; that they have a sister but their sister does not (Boden, 1980; Carey, 1984; Keil, 1989; Piaget, 1950). When reasoning about social exchange, however, preschool-age children show virtually all the features of special design that adults do.
- When a child has had experience in a number of domains, it is difficult to explain how or why a content-blind statistical learning mechanism would cause the early and uniform acquisition of a reasoning skill for one of these domains, yet fail to do so for the others. When one considers that adults have massive experience with permission rules, yet fail to develop specializations for detecting violations of this more general and, therefore, more common class, the presence of accurate cheater detection in 3- and 4-year-olds is even more surprising.
- Cultural experience is often invoked as a schema-building factor. Yet, despite a massive difference in experience with trade and cheating, there was no difference between Shiwiar and American adults in cheater detection.

Statistical Learning Summary Neither experience, repetition, nor familiarity explain which reasoning skills develop and which do not, yet they should if specializations develop via statistical learning. In contrast, the hypothesis that social contract algorithms were built by a developmental process designed for that function neatly accounts for all the developmental facts: that cheater detection develops invariantly across widely divergent cultures (whereas other aspects dissociate); that social exchange reasoning and cheater detection develop precocially; that the mechanisms responsible operate smoothly regardless of experience and familiarity; that they detect cheaters and not other kinds of violators; and that the developmental process results in a social contract specialization rather than one for more inclusive classes such as permission rules.

CONCLUSIONS

There are strict standards of evidence for claiming that an organic system is an evolved adaptation. The system that causes reasoning about social exchange meets these standards. Reasoning about social exchange narrowly dissociates from other forms of reasoning, both cognitively and neurally. The pattern of results reveals a system equipped with exactly those computational properties necessary to produce an evolutionarily stable form of conditional helping (as opposed to the many kinds of unconditional helping that are culturally encouraged). These properties include, but are not limited to, the six design features discussed herein, all of which were predicted in advance from the task analyses contained in social contract theory (see Cosmides & Tooby, 1992, 2008a, 2008b; Fiddick et al., 2000 for others). Importantly, the pattern of results cannot be explained as a by-product of a reasoning adaptation designed for some different, or more general, function. Every by-product hypothesis proposed in the literature has been tested and eliminated as an explanation for social exchange reasoning (see Table 25.1).

The design of the computational specialization that causes social exchange reasoning in adults (and preschoolers) places limits on any theory purporting to account for its development. No known domain-general process can account for the fact that social contract specializations with these particular design features reliably develop across cultures, whereas specializations for more commonly encountered reasoning problems do not develop at all. Indeed, the social contract specialization has properties that are better adapted to the small-group living conditions of ancestral hunter-gatherers than to modern industrial societies. Experience of the world may well be necessary for its development during ontogeny, but the developmental process implicated appears to be a domain-specific one, designed by natural selection to produce an evolutionarily stable strategy for conditional helping.

The simplest, most parsimonious explanation that can account for all the results—developmental, neuropsychological, cognitive, and behavioral—is that the human brain contains a neurocognitive adaptation designed for reasoning about social exchange. Because the developmental process that builds it is specialized for doing so, this neurocognitive specialization for social exchange reliably develops across striking variations in cultural experience. It is one component of a complex and universal human nature.

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CHAPTER 26

Interpersonal Conflict and Violence

MARTIN DALY

AN EVOLUTIONARY PERSPECTIVE ON CONFLICTS OF INTEREST

THIS CHAPTER MAKES the case that the discovery and interpretation of basic facts about conflict and violence can be facilitated by having a sound theory of the nature of self-interest, and that the requisite theory is necessarily grounded in the theory of evolution by selection.

The basic facts about conflict and violence to which I refer are social, familial, demographic, epidemiological, and motivational. Who is more or less likely to come into conflict with whom, and over what substantive issues? What considerations affect the intensity of interpersonal disagreements and their potential for violence? Answers to these questions clearly differ according to specific social relationships—strangers, same-sex rivals, parent–offspring and other kin relationships, romantic partners, potential mates, in-laws, and so on—as well as in relation to the parties' ages, sexes, social positions, and reproductive histories. The ways in which these variables affect conflict are consequences, I suggest, of actors' perceptions of where their interests reside and of whether the actions and inclinations of others are then experienced as antagonistic to, or facilitating of, the satisfaction of those perceived interests.

It is essential to be clear about what one means by "interests." The dictionary definition that is closest to my meaning here is an "advantage or benefit" to the party in question (see, e.g., http://www.oxforddictionaries.com/definition/english/interest). Defining interests in this way justifies the popular evolutionary theoretical equation of an individual's interests with the relative replicative success of that individual's alleles (loosely, "fitness"), but it also justifies a more psychological interpretation whereby one's interests correspond with one's preferred states, whether fitness-promoting or not. I will use the term "fitness interests" to refer to the former, evolutionary meaning, and "perceived interests" (with no implications about conscious awareness) to refer to the latter, psychological meaning. This distinction is essentially the same as that which Tinbergen (1963) made between "function" and "cause."[1]

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[1] I prefer Tinbergen's terminology to the currently popular "proximate" versus "ultimate," because the latter obscures the fact that both causes and functions can be relatively proximal or distal. A relatively proximal function of eating, for example, is energy acquisition, while a more distal function is reproduction.

The cause/function distinction is easily blurred. "Strategy," for example, is such a compelling metaphor for adaptively conditional responsiveness within an integrated hierarchy of functions that it is now used by evolutionists primarily in this functional sense (e.g., Shuster & Wade, 2003). This is unproblematic when the so-called strategists are brainless organisms such as plants (e.g., DeJong & Klinkhamer, 2005), but in its literal sense, strategy is a causal concept (and moreover one that implies conscious planning), so "reproductive strategy" is sometimes misunderstood as implying a literal pursuit of fitness rather than as the pursuit of goals that contributed to ancestral fitness. Trying to clarify one's meaning by adding that alleged efforts to "maximize fitness" are "unconscious" doesn't eliminate the potential for confusion. Consciousness or its absence is again a meaningful distinction only within the domain of proximate causation.

This sort of failure to carefully distinguish cause from function encourages two common fallacies. One is that Darwinism entitles us to expect that organisms will do whatever it takes to maximize their fitness, even in evolutionarily novel circumstances. Symons (1987, 1989, 1990) provided a series of critiques of such thinking and elicited great indignation from Darwinians whose oxen he gored, but his cogent analysis retains its bite to this day. The second fallacy that often follows from treating fitness as a goal is to think that because evolutionary explanations invoke fitness consequences, maladaptive behavior must require some alternative sort of explanation that is "not evolutionary." The problem here is that maladaptive action and even extreme psychopathology are the outputs of brains/minds whose evolved structures and processes generate *all* behavior. An evolution-minded taxonomy of the sources of maladaptation is essential (e.g., Baron-Cohen, 1997; Williams & Nesse, 1991). Failures of adaptation can result not only from brain damage and insanity, but also from mismatches between adaptations and modern environments, from bad luck in domains where behavior is successful only on average, from hijackings of the actors' adaptations by other organisms, and from wasteful intragenomic conflicts (Nesse, Chapter 43, this volume; Tooby & Cosmides, Chapter 1, this *Handbook*, this volume).

The point of these cautions is not to deny that *perceived interests* and *fitness interests* often look very much alike. They do, of course, because the former have been shaped by selection to be means to the end of the latter. Unrelated same-sex individuals who are competitors for access to limited resources are threats to one another's fitness and are therefore apt to respond to one another as rivals. Being cuckolded harms a man's expected fitness, and his partner's sexual infidelities are therefore intensely disliked (Shackelford, Goetz, LaMunyon, Pham, & Pound, Chapter 15, this *Handbook*, Volume 1). However, it must never be forgotten that organisms are not seeking fitness in a literal sense, but simply responding to cues and pursuing goal states that were statistical predictors of expected fitness consequences in ancestral environments. Rats in a Skinner box will continue to work for hypothalamic stimulation that has been divorced from fitness-related outcomes, and vasectomized men will continue to lust after sexually appealing women.

The fitness interests of two individuals may overlap to varying degrees, or may be strictly antithetical, and the basic sources of commonality versus conflict of fitness interests are ancient and enduring. It is thus a reasonable working hypothesis that the evolved psychology of interpersonal conflict will be responsive to evolutionarily reliable cues of the extent to which fitness interests are shared, as well as the delimited contexts or circumstances in which they are shared or in conflict. The genetic relatedness between two parties, for example, is the most obvious and often the main determinant of the degree to which their fitness interests overlap, and we are therefore justified in postulating positive social responses to cues of genetic relatedness (e.g., DeBruine, 2002; Hames, Chapter 19, this *Handbook*, Volume 1; Krupp, DeBruine, & Jones, 2011). The other primary source of overlapping fitness interests is the fact that sexual reproduction gives individuals who are not themselves close kin a shared stake in the welfare of young who are close kin to both, and we are therefore justified in postulating effects of offspring on the quality of relations between mates, and between in-laws who are related through a mateship, as well as strong emotional responses to cues of fidelity and paternity (Shackelford, Goetz, LaMunyon, Pham, & Pound, this volume).

VIOLENCE AS A WINDOW ON INTERPERSONAL CONFLICT

Intraspecific violence has attracted the attention of evolutionists for a variety of reasons. The fact that direct aggression is a risky competitive tactic has motivated extensive theoretical and empirical analysis of the factors that make animals more or less likely to resort to it (Hardy & Briffa, 2013; Maynard Smith & Price, 1973). Moreover, because intraspecific violence can be a significant source of mortality in some species, including human beings in small-scale, nonstate societies like those in which basic human attributes evolved (P. L. Walker, 2001; R. S. Walker & Bailey, 2013), its selective impacts warrant investigation. However, this review of the topic, and my own research on human violence in collaboration with the late Margo Wilson, are motivated not so much by the possible evolutionary significance of violence itself, as by the fact that it provides a useful assay of conflict, and a way to test theoretically derived hypotheses about the factors that affect conflict's intensity in different relationships.

It is, of course, possible and sometimes illuminating to investigate interpersonal conflict through its nonviolent manifestations. However, such research programs face potential threats to validity. Opportunities for direct observation of conflict behavior are limited, and researchers have relied heavily on questionnaires and interviews, but data derived from these self-report methods must be interpreted skeptically in any domain in which issues of social desirability, self-presentation, and self-justification are prominent. A cautionary example is provided by a large literature on violence between intimate partners and other family members that has relied on a self-report tool called the Conflict Tactics Scales (CTS; Straus, 1979). CTS respondents are asked to affirm or deny that they and their partners or other family members have performed each of a long list of "acts" in conflict situations within a specified period, usually the past year. It has long been apparent that the reliability of these measures is poor: When intimate partners are both tested, the correlations between their accounts of their respective actions are often negligible (R. P. Dobash, Dobash, Wilson, & Daly, 1992; Jouriles & O'Leary, 1985; Szinovacz, 1983). It is therefore unsurprising that CTS research has repeatedly generated "findings" that contradict those based on less equivocal manifestations of violence and that are almost certainly not valid; examples include an alleged absence of sex differences in intimate partner violence that is unique to CTS studies (reviewed and critiqued by R. P. Dobash et al., 1992), and supposedly identical levels of assaults on children by genetic and stepparents as reported by Gelles and Harrop (1991; see Daly & Wilson, 2008).

The poor validity of such measures is presumably due mainly to biased self-presentation. However, there is also some reason to doubt that people have the introspective ability that they would need to portray their social conflicts accurately, even if they were sincerely trying to be forthcoming (Nisbett & Wilson, 1977; Wegner, 2002). For these reasons, self-report data are of limited value in this area.

The experimental methods of behavioral economics afford opportunities for participants to select how cooperatively or competitively they will behave toward specific others in a variety of allocation decisions. To date, the literature on economic games has been overwhelmingly focused on stranger and/or anonymous interactions (see, e.g., Plott & Smith, 2008), but the methods are certainly amenable to the study of participants' "welfare trade-off ratios" (Cosmides & Tooby, 2013) with various sorts of relationship partners. The external validity of such methods remains questionable, however, not only because of the same self-presentation concerns that bedevil self-report studies, but also because of the likelihood that research participants may often be motivated to simply maximize joint profits in games played with close social partners, in the shadow of an expectation of post-experimental reallocation.

Thus, despite the limitations of nonexperimental research, the investigation of interpersonal solidarity versus conflict must still rely on spontaneous real-world manifestations thereof, such as legal proceedings, bequests, divorces, and violence. Unfortunately, none of these manifestations can provide a completely unbiased window on the real distribution of conflict. The subsets of people who launch civil lawsuits, who register marriages and divorces, and who die intestate are surely not random samples of human decision makers, and persons charged with assault are not a random subset of actual assailants. It is for this reason that Margo Wilson and I were first drawn to the study of *lethal* interpersonal violence. It is a truism among criminologists that homicide is the crime that is least vulnerable to biased detection and recording. Although there are surely exceptions necessitating continued caution, by and large the bodies are found and the causes of death are investigated. Consider, for example, the question of whether child maltreatment is disproportionately perpetrated by stepparents. In a U.S. study, Wilson, Daly, and Weghorst (1980) were the first researchers to estimate rates of reported physical abuse of children in stepparent-plus-genetic-parent versus two-genetic-parent, and found a large excess in the former. It is easy to imagine, however, that stepparents' abusive acts might be especially likely to be detected or recorded, and for that reason, Wilson and colleagues (1980) noted and stressed that the differences between household types were much larger in the relatively rare lethal cases than in nonlethal abuse, a result that is hard to reconcile with an explanation in terms of biased detection. Greater stepparental overrepresentation in lethal beatings than in nonlethal maltreatment has proven to be a robust result, and provides some of the best evidence that "Cinderella effects"—elevated risks at the hands of stepparents—are genuine (Daly & Wilson, 2008).

KINSHIP MITIGATES LETHAL VIOLENCE

According to the leading theory of social evolution, Hamilton's (1964) inclusive fitness theory, the fundamental basis of shared fitness interests is genealogical kinship (Hames, Chapter 19, this *Handbook*, Volume 1). An obvious hypothesis, then, is that perceived interests will follow suit and social motives will be effectively "nepotistic." Creatures cherish close kin because they are vehicles of inclusive fitness and selection has favored valuing their welfare if they can be identified with any degree of reliability. The flip side is that we should be more reluctant to harm kin than nonkin.

Bohannan's (1960) study of homicides among the Tiv of central Nigeria during the colonial period provides a nice illustration of such nepotistic restraint. The society was strictly patrilocal, such that men's daily interactions were predominantly with close patrilineal kin. A highly successful Tiv man might have as many as 20 wives, not all of whom he could easily guard, and competition among agnates (patrilineal kin) was intense. But Bohannan was able to show that close kinship typically prevented that competition from becoming lethal:

> In a community in which 83% of the adult males are agnatic kinsmen of one another, the chances that a woman's lover will be a kinsman of her husband are obviously extremely high. . . . In the eight cases in which men killed their wives' lovers, only [two cases] show any kinship relation between the husband and the lover. Any fieldworker in Tivland realizes that adulteries between women and their husbands' kinsmen occur frequently. Tiv do not suggest that such adultery does not occur. They insist, however—and the cases prove them right—that a wife's adulteries must not be allowed to disturb relationships among kinsmen. (Bohannon, 1960, p. 42)

The tendency for patrilineal kinsmen to form political and military alliances that compete against other patrilineages is of course well known to anthropologists, who have dubbed such coalitions "fraternal interest groups" (e.g., Göhlen, 1990; Otterbein, 1968). Anti-Darwinians such as Sahlins (1976) have asserted that these practices have "nothing to do with biology," and while such arguments prove only their authors' incomprehension and hostility, there *are* legitimate questions about the degree to which fraternal interest groups are effectively nepotistic. How well do clan memberships and patronyms serve as proxies for actual relatedness? And does terminological kinship "crowd out" other potential cues of relatedness in the social and psychological control of nepotism?

Napoleon Chagnon's studies of Yanomamö horticulturalists in Venezuela speak to these issues with unusual clarity. The Yanomamö use an "Iroquois" kinship system, in which all men who can trace their patrilineage to the same male ancestor at the same generational depth are called "brother." But this does not mean they treat their patrilateral parallel cousins and their "real" brothers identically. To the contrary, genetic relatedness as estimated from recited genealogies is a better predictor of who lines up with whom in a violent conflict situation than is mere kin terminology (Alvard, 2009; Chagnon, 1981; Chagnon & Bugos, 1979). Relatedly, kin stick together in space. When Yanomamö villages grow unmanageably large, disputes arise, mainly over adulteries, and the villages then "fission," with each man having to choose in which of the two new smaller villages he will reside. Because of generations of cross-cousin marriage, virtually everyone is related to everyone else, often by multiple loops, such that the "correct" characterization of particular people's relationships (and hence their entitlements to marry) may even be contested, and yet it is a striking fact that the average genetic relatedness of pairs residing in the same village is elevated by a fissioning event (Chagnon, 1981). In sum, the Yanomamö behave as if they know their degrees of relatedness to one another more accurately than one could infer from knowing only the kin terms that dyads use to address one another, and they use that awareness to form alliances both for protection and for aggressive exploitation of others.

It isn't only in tribal societies with semichronic warfare between villages that you might be wise to stick close to your close genetic relatives. In tough times, close kin can be one's salvation. Several analyses of the sources of differential mortality in disasters have reached the conclusion that when mortality rates skyrocket, the density of kin in your immediate vicinity is a major determinant of your chances of surviving, sometimes mattering even more than your age, sex, or wealth (Grayson, 1993, 1996; McCullough & Barton, 1991). Part of the reason for this—but only part—is that those people who have no relatives to protect and avenge them are fair game for homicide and even cannibalism.

In modern mass society, the importance of kinship has surely diminished, so one might reasonably wonder whether nepotistic biases are still detectable in action. Decades ago, as newcomers to the study of family violence, Margo Wilson and I were startled to encounter allegations that close kin relations are *routinely* violent! Not only were psychoanalysts seemingly convinced that parricidal and filicidal impulses are universal components of human nature, but even number-crunching social scientists were on board. According to the two best-known investigators of family violence in the United States, for example:

> The family is the most frequent locus of all types of violence ranging from slaps, to beatings, to torture, to murder. Students of homicide are well aware that more murder victims are members of the same family than any other category of murderer–victim relationship . . . In fact, violence is so common in the family that we have said it is at least as typical of family relations as is love. (Gelles & Straus, 1979, p. 188)

This would be astonishing if it were true. But it is not true. Intrafamilial homicides are in fact quite rare in the United States, as they are elsewhere (Daly & Wilson, 1982, 1988b).

A small part of the obfuscation here derives from an excessively broad definition of "family." Since Wolfgang (1958), mainstream criminologists who partition the victim–killer relationship have typically recognized just three categories: strangers, acquaintances, and family members. This taxonomy, extraordinarily naïve from an evolutionary perspective, has persisted through a half century of studies. Some researchers now at least distinguish "intimate" or "romantic" partners (who almost always comprise a large majority of "family" victims) from "other relatives," but this latter basket category still typically includes the killer's children, parents, other genetic kin, step-relations, and in-laws (e.g., Kubrin, 2003). This is of course unsatisfactory because it conflates relationships that are qualitatively distinct, not only in degrees of their genetic relatedness, but even in whether they are consanguineal or marital—distinctions critically important to an evolution-minded theorist. The conflicts between intimate partners are utterly different in their substance and triggers than those between other family members, and the same goes for conflicts involving genetic versus marital relatives, as well as conflicts among the various more specific kinds of genetic relatives (Daly & Wilson, 1988a, 1988b).

But even if "family" is defined in the encompassing way that most criminologists thoughtlessly favor, Gelles and Straus's assertions about its dangers are still clearly false: Family homicides are *not* more numerous than those in any and all other categories of victim–killer relationship. Instead, in the United States and also in the world as a whole, the two broad categories of stranger homicides and lethal contests between acquainted nonrelatives both substantially outnumber killings of family members. According to the FBI's data for the years 2000 through 2010, for example, marital partners and genetic relatives together comprised fewer than 20% of the victims of solved U.S. homicides, whereas about a quarter were strangers; more than half were persons who were known to, but not related to, their killers (Puzzanchera, Chamberlin, & Kang, 2013). Moreover, even these numbers almost certainly exaggerate the prevalence of family murders. Over 40% of cases remained unsolved and therefore lack any victim–killer relationship code, and because unsolved homicides are disproportionately cases that occur in public places rather than homes and that exhibit evidence of other criminal victimization (especially robbery and gang violence), it is very likely that they are proportionately more often committed by strangers and acquaintances than solved homicides.

So homicide is less of a family affair than some would portray it. But how can we take the matter further? In order to assess whether and to what extent kinship might be associated with a reduction in lethal conflict, we need some sort of reasonable null model that would generate an "expected" incidence of related victims under the assumption that kinship is *not* relevant. Daly and Wilson (1982, 1988b) tackled this issue of base rate expectations in two ways. First, they analyzed a set of Detroit homicides in which victims and their killers resided in the same household, and generated the required expected values for various relationship categories from survey-based household composition data for the city. The result was that a homicide was more than 10 times as likely between genetically unrelated coresiding persons, regardless of whether they were intimate partners or other nonrelatives such as roommates, than between coresiding genetic relatives.

Daly and Wilson's other approach to this issue exploited the fact that some homicides have multiple perpetrators. The logic was this: Although we cannot know the base rate of the average individual's interactions with kin versus nonkin, we can postulate that *if* kinship were without effect on conflict versus solidarity, such that both arise in frequencies proportionate to the availability and intensity of interactions with others, then the distribution of the social relationships between those who collaborate in homicide should approximate the distribution of victim-killer relationships. With that as our null hypothesis, we assembled every data set containing the requisite information on both co-killer relationships and those between victims and killers that we could find. The resultant samples represented the urban United States, several horticultural or agricultural societies, and an historical registry from late medieval England. In every case, we found that the average relatedness of collaborative killers greatly exceeded that between killers and their victims. In the U.S. urban samples and in 13th-century England, for example, the average relatedness between pairs of co-killers ranged from .08 to .09, and that between killers and victims between .01 and .03.

In more traditional societies, fraternal closeness entails a bitter irony: Brothers may be natural allies, but the very fact of close kinship also forces them into intense rivalries. Not only are close kinsmen likely to be the sole claimants to a title or to the family farm, but where extensive genealogical links dictate who can and cannot marry whom, as is often the case in nonstate societies, brothers must find their brides within the same limited pool of legitimate marriage partners. It is little wonder, then, that stories of fratricide abound in such societies, often in close association with origin myths, as exemplified by the story of Cain and Abel. Can fraternal solidarity survive these social structural pressures? In the analyses described above, the sample included four strongly patrilocal indigenous peoples in India: the Bison-Horn Maria, Bhil, Munda, and Oraon. In these societies, as among the Tiv studied by Bohannan, most of a man's routine social interactions are necessarily with his agnates. Primogeniture in land inheritance created fierce rivalries between brothers, and fratricides in these societies constituted about 10% of all homicides. (In contrast, fratricides comprise about 2% of homicides in modern countries with low homicide rates such as Japan, and fewer than 1% in the United States; Daly, Wilson, Salmon, Hiraiwa-Hasegawa, & Hasegawa, 2001.) But even so, men in these patrilineal Indian societies were substantially *less* likely to kill close agnates than to join forces with them in lethal quarrels with other unrelated or distantly related men; whereas the average victim–killer relatedness for the four societies as a whole was .07, the average relatedness between collaborating killers was .24.

Citing anthropological and historical sources, Daly and Wilson (1988b) concluded their discussion of fratricide by suggesting that it became a problem only after the invention of agriculture led to the inheritance of land. (We were then unable to find even one account of a fratricide in hunter-gatherer ethnographies, but in a personal communication in about 1990, Thomas Headland then drew a single such case to our attention.)

> Where the temptation to fratricide really gets out of hand is in the circumstance where brothers are rivals for a position of enormous value, and yet agnatic kinsmen are not themselves a crucial source of a man's power. . . . In a feudal society . . . vassalage at least partially replaces kinship as a basis of loyalty and power, and rivalrous power blocs may line up behind related pretenders to the same throne. Here, surely, is a situation designed to overwhelm brotherly affection, and indeed the history of royal families in feudal empires is a seemingly endless tale of fraternal bloodletting. (Daly & Wilson, 1988b, p. 31)

It seems that we underestimated nepotistic restraint, however, for there is now evidence that it tempered even feudal disputes over royal succession. S. B. Johnson and Johnson (1991) analyzed the historical struggles among rival claimants to the Earldom of the Orkney Islands, and found an apparent mitigating effect of close kinship: When two men had simultaneous claims to rule, brothers were almost always able to partition the perquisites amicably, whereas a homicide was typically required to resolve analogous competitions between more distant agnatic kin. Dunbar, Clark, and Hurst (1995) extended these analyses by showing that the infrequent killings of agnatic kinsmen occurred only in the context of clear and substantial incentives, quite unlike killings of nonkin, which were often the dénouements of relatively minor disputes with little at stake. Analyses of lethal conflict over the English crown tell a similar story (S. B. Johnson & Johnson, 1991; McCullough, Heath, & Fields, 2006): Although both near and distant kin were certainly slain in battles over succession, fratricides, parricides, and filicides were nevertheless inhibited relative to the enthusiasm with which aspirant kings went about "culling the cousins."

INTIMATE PARTNER VIOLENCE

The reasons for solidarity and conflict between opposite-sex mates are peculiar to that relationship, but as with genetic kinship, those reasons ultimately derive from overlapping fitness interests: Sexual reproduction creates a situation in which unrelated mates combine their prospects for direct fitness, and the young that they produce constitute a powerful source of shared goals. Couples who are faithful monogamists, and who engage in little or no nepotistic investment in their distinct collateral kindreds, attain a commonality of fitness interests that surpasses that of the closest nonclonal genetic relatives (Alexander, 1987). This gibes with, and perhaps explains, the commonplace observation that the tastes, ambitions, and worldviews of long-standing couples often converge.

Despite this powerful source of shared fitness interests, the solidarity of mates is easily and often undermined. Your genetic kin are yours for life, and no betrayal can erase the fact that their reproduction enhances your genetic posterity; that is presumably why the psychology of forgiveness and reconciliation seems to cut kin more slack than friends. Not so for mateship: If a couple is *not* sexually monogamous, then that which enhances one party's fitness may be systematically damaging to the other party's, and this of course explains the peculiar emotional potency of issues related to infidelity and cuckoldry (Gangestad, Thornhill, & Garver-Apgar, Chapter 14, this *Handbook*, Volume 1; Shackelford, Goetz, LaMunyon, Pham, & Pound, Chapter 15, this *Handbook*, Volume 1). Unfortunately, fidelity alone cannot eliminate partner conflict. Even in a population in which couples invest only in joint progeny whose well-being will contribute equally to both parents' direct fitness, selection will still favor those parents who shirk and let their partners pay the lion's share of child rearing costs, *unless* two conditions are met: There is absolutely no chance that either partner will ever remate (e.g., in the event of one's death) *and* there is absolutely no chance that either partner can ever promote his or her inclusive fitness by diverting resources to nondescendant kin. These conditions are not likely to be met in any pair-forming biparental species, and they are certainly not met in human beings.

An evolution-minded analysis of the relationship between mates points to at least the following six, more or less distinct, sources of conflict, many of which clearly match lay notions of the most important threats to a happy marriage:

1. Covert extra-pair fertilization. (The cuckoldry problem.)
2. Dependent offspring of prior unions. (The stepchild problem.)
3. Nepotistic interests in distinct sets of collateral kin. (The in-law problem.)
4. Temptations to free-ride on the partner's efforts. (The lazy spouse problem.)
5. Temptations to sample the mate pool and perhaps upgrade. (The defection problem.)
6. Aspirations to be a polygamist, felt primarily, but not solely, by men. (The polygamy problem.)

Except for the sexually asymmetrical risk of cuckoldry, all of these apply in principle to both women and men, although not necessarily with equal force.

A large majority of the couple conflicts that culminate in a homicide, across the gamut of human societies, are precipitated by male sexual jealousy, if that term is defined to encompass men's resentment of both partner infidelity and partner desertion (Daly & Wilson, 1988b; Daly, Wilson, & Weghorst, 1982). To the best of my knowledge, this conclusion has not been contravened. Some authors have suggested that it was overstated, but the data that supposedly challenge it are invariably informationally impoverished; for example, it may be noted that the police coded only a minority of some set of spousal homicides as "jealousy" cases, while a larger number were coded instead as "arguments" instead, but of course the latter label is mute about the substance of conflicts. In later writings, we have preferred to characterize the issue as one of "proprietariness" rather than "jealousy" to focus attention on men's tendency to construe wives as property, and hence to react similarly to their (suspected) infidelities and their efforts to terminate marriages, both of which are resented as violations of husbands' property rights (Wilson & Daly, 1992, 1996, 1998). This conceptualization captured the imagination of many feminist researchers who had been wary, at best, of evolutionary psychology, and helped create a space for interdisciplinary dialogue (see, e.g., Campbell, 2012; R. E. Dobash & Dobash, 2012; H. Johnson, 2012).

To be useful, an evolution-minded analysis of the relationship between mates should do more than just provide compelling terminology; it should help scientists generate fruitful new hypotheses. The "stepchild problem" provides an illustrative case in point. Whereas a couple's children create a commonality of fitness interests and therefore facilitate consensus on difficult issues such as the ideal uses of the couple's resources, children of former unions have precisely the opposite impact (Daly & Wilson, 1996). This may seem an obvious hypothesis, but although the presence of stepchildren had long been known to be associated with elevated rates of divorce (Becker, Landes, & Michael, 1977; White & Booth, 1985), no one had assessed whether their presence might also be associated with elevated rates of marital violence before Daly, Singh, and Wilson (1993) showed that women with children sired by previous partners were disproportionately heavy users of a women's shelter. In a Canadian study (Daly, Wiseman, & Wilson, 1997), we subsequently showed that such women also incurred a much greater risk of uxoricide than mothers whose children were all sired by the current partner, a result that has been replicated in a U.S. sample (Brewer & Paulsen, 1999). Meanwhile, Jacquelyn Campbell and collaborators were developing tools to assess the risk that intimate partner violence will escalate to lethality, a very difficult task because the risk factors for lethal and nonlethal partner violence are largely the same (Wilson, Johnson, & Daly, 1995). The stepfamily findings persuaded these researchers to include this measure in their assessment battery, and it proved to be one of their most useful. Given that a woman has already been a victim of recurrent physical assaults by her male partner, the evidence to date pinpoints three statistical predictors that he will eventually kill her: a history of his threatening suicide, a gun in the home, and the presence of a child sired by a predecessor (Campbell, 2012; Campbell et al., 2003).

Another important general point that the study of intimate partner homicide can be used to illustrate is that there is seldom a single privileged "evolutionary hypothesis" that can be contrasted with those generated from other perspectives. Instead, evolutionary psychologists and biologists can and often do generate competing hypotheses that are equally Darwinian. Thirty years ago, relationship-specific demographic patterns of homicide risk were virtually unstudied, and no one had investigated how age might be related to differential risk. Reasoning that the value that men place on their female partners should be a function of reproductive value (and influenced, perhaps unduly, by three notorious cases in which high-status Canadian men had hired "hit men" to kill their middle-aged wives), I hypothesized that women's risk of being slain would increase prior to or at menopause, both because of planned disposals and, more importantly, because angry men would be less inhibited by the danger of doing an older wife serious harm. But Margo Wilson predicted that the risk would be maximal for young wives of the highest reproductive value, reasoning that violence against wives is functionally controlling, and that men are most inclined to exert coercive control when their partners are especially attractive to rival males and thus especially likely to confront temptations to defect. Margo's hypothesis, which assumes that uxoricides are mainly functionless by-products of anger and are rarely strategic disposals, was the evident winner: We found a substantial negative relationship between age and uxoricide risk in Canada, with no hint of an elevation at menopause (Daly & Wilson, 1988b; Wilson, Johnson, & Daly, 1995), and this pattern has proven to be replicable in the United States, the United Kingdom, and Australia (Mercy & Saltzman, 1989; Shackelford & Mouzos, 2005; Wilson & Daly, 2001).

A further major risk factor for intimate partner homicide revealed by Daly and Wilson's (1988b) early analyses was common-law or *de facto* status: Both partners were victimized at rates very much higher in coresiding couples than in registered marriage couples, and this, too, has been replicated in other English-speaking countries (Mouzos & Shackelford, 2004; Shackelford & Mouzos, 2005; Wilson & Daly, 2001). Suggested reasons for this include socioeconomic confounds, conflicts arising from lower commitment and higher rates of infidelity in common-law unions, and the much higher incidence of stepchildren in the homes of co-residing couples who have not registered their marriages; a distinct age pattern such that risk in co-residing couples is maximal in middle age, which has also been replicated internationally, lends some support to the stepfamily hypothesis. Surprisingly, however, the large and seemingly robust difference in homicide rates between registered and common-law marriages has been shrinking since 1990 in the United States, and had disappeared completely by 2005 (James & Daly, 2012), and the same appears to be true in Canada (James, 2011). James and Daly (2012) could find no evidence that the two types of unions have been converging in other attributes, and the reasons for this striking change remain to be discovered, as indeed do the reasons for large changes over time, including recent declines, in intimate partner homicide rates as a whole. An evolution-minded understanding of couple conflict will surely remain a crucial element of any satisfactory future explication of these trends.

LETHAL CONFLICT IN OTHER RELATIONSHIPS

Other categories of interpersonal relationships have specific sources of conflict that are manifested in distinct patterns of homicide risk. Trivers's (1974) famous parent–offspring conflict theory laid bare the reasons why parents neither love their young more than they love themselves, nor cherish all of their children equally. The insights that the theory yields about variability in the intensity of parent–offspring conflict as a function of the parties' ages have been supported in a number of studies of age-related trajectories of both maternally and paternally perpetrated filicides, as well as parricides (Daly & Wilson, 1988a; Wilson & Daly, 1994). Trivers's theory also succeeds when its predictions are pitted against Sigmund Freud's notorious theory that parent–offspring conflict is essentially a matter of same-sex rivalry, a theory that is a priori implausible, since human parents and their same-sex offspring rarely compete for mates at all and sons do not lust after their own mothers, as Freud supposed (Daly & Wilson, 1990a).

The relationship that engenders the largest number of homicides by far is that between unrelated male rivals (Daly & Wilson, 1988b, 1990b), and an evolutionary perspective is essential for understanding the cases themselves and their highly variable incidence. That is a topic that we and others have dealt with extensively elsewhere (Courtwright, 1996; Daly & Wilson, 1988b, 1990b, 1997, 2001, 2010; Eisner, 2003; Pinker, 2011; Wilson & Daly, 1985), and that I will not discuss further here.

When using homicides as an "assay" for testing adaptationist hypotheses about the variables that aggravate and alleviate interpersonal conflicts, my collaborators and I have adopted a stance of agnosticism about whether the lethality itself is an adaptive function of the fatal attacks or is a nonadaptive minority outcome that would have reduced the killers' fitness, on average, even in ancestral environments (e.g., Daly & Wilson, 1988b). There is no question that violent capability is an adaptation, nor that the intensity of violent action is modulated by our evolved psychology (e.g., Sell, 2011), and it may well be the case that the human mind contains adaptations for killing. But an evolutionarily informed theory of relationship-specific conflicts is a valuable source of hypotheses about homicide risk regardless of whether most killings are by-products of adaptations for domination and coercion or are instead reflections of adaptations for lethality.

This agnostic stance has been criticized by Buss (1999, 2000) and by Duntley and Buss (2008, 2011). These authors argue that because many killings are intentional rather than being accidental "slips," because most people say that they would kill in certain dire circumstances such as to protect their children, and because large numbers of people admit to homicidal fantasies, lethality is therefore unlikely to be a nonadaptive by-product of adaptations designed to achieve other results. They propose instead that people have been equipped by natural selection with a suite of relationship-specific psychological adaptations both for killing and for avoiding being killed. Unfortunately, identifying aspects of the mind that might have been designed for the specific function of killing is not that easy, and in my view, fantasy, intent, and professed willingness to kill are all beside the point. Even larger numbers of male undergraduates report fantasies of video game playing than of killing (Kai, unpublished, cited by Wilson, Daly, & Pound, 2009) although there are certainly no adaptations for video game playing, and high proportions of people profess willingness and formulate intentions to do myriad things that were never targets of selection, ranging from watching their favorite TV shows to having their pets spayed. Finally, with respect to certain specific relationships for which Duntley and Buss have proposed dedicated homicide "modules," such as wife-killing and stepchild-killing, I can find no ethnographic evidence indicating that these killings might have been either fitness-promoting, on average, in small-scale, face-to-face societies like those in which humans evolved, or frequent enough to be plausible candidates for dedicated evolved psychological machinery. Thus, although I grant that lethal violence has surely been an agent of selection in human evolution, and that killers may even have enjoyed fitness advantages that have had selective consequences (Chagnon, 1988), we have no sound basis for concluding that most, or indeed any, homicides reflect "homicide adaptations" (see also Durrant, 2009).

And in a certain sense, it doesn't matter: This controversy can be set aside in the present context because the predictions that one would make about the patterning of homicide risk are largely unaffected by its resolution. Regardless of whether killing is typically a by-product of adaptations or a more direct reflection of what the relevant adaptations are designed to achieve, we should expect similar effects of cues of infidelity, reproductive value, kinship, and other conflict-related variables. New evidence and ideas may eventually clarify and resolve these points of contention, but of this we can already be sure: Homicides will continue to provide a rich source of data for testing evolution-minded hypotheses about interpersonal conflict.

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CHAPTER 27

Women's Competition and Aggression

ANNE CAMPBELL

The past 25 years have been revolutionary for our understanding of the psychology of sex differences in aggression. Prior to this, the social science orthodoxy was that these differences emerged as a result of early socialization by parents and later conformity to society's gendered division of labor. The fact that these sex differences are early-appearing, universal, and similar to those seen in other species was dismissed (Tieger, 1980). With the publication of Daly and Wilson's book *Homicide* (1988), social scientists were introduced to an evolutionary viewpoint: Across sexually reproducing species, the greater parental investment made by females leads to a male-biased operational sex ratio and heightened competition between males for access to fertile females. Successful males copulate with more partners and leave more sons who carry their fathers' aggressive genetic legacy. This formed the initial framework for an impressive body of supporting research on male aggression but some issues remain to be resolved. Are females exempt from intrasexual competition? If so, is their role merely to act as quality controllers of male genes? When and how did monogamy evolve (Henrich, Boyd, & Richerson, 2012)? What consequences did it have in terms of creating two-way sexual selection and competition (Clutton-Brock & Huchard, 2013)?

These questions inform this chapter. So dazzling were male courtship displays and so ferocious was male aggression that evolutionary biologists have only recently turned their attention to female forms of competition (Stockley & Campbell, 2013). Evolutionary psychologists have a special contribution to make in identifying sex-linked psychological mechanisms that mediate behavioral differences between the sexes. Some of these we share with our phylogenetic cousins. Others may be unique to humans with their capacity for representational thought, reflective control over lower-level reflexive responses, and cultural transmission.

REWARDS AND COSTS OF FEMALE AGGRESSION

For aggression to evolve as a strategy, the rewards must exceed the costs (both measured in terms of reproductive success). For many years it was assumed that because females did not need to fight for copulations, there was nothing of consequence for them to fight about and therefore, there were no rewards for female aggression. But copulation is only the start of reproductive success—offspring must be nourished and protected until they are able to reproduce themselves. Pregnant women need an extra 300 calories every day, and 500 more when they are lactating (Institute of Medicine, 1990). Once on solid food, a toddler needs to consume 1,300 calories a day. Like most primates, humans are a group-living species, which means that food can be a contested resource. In addition, mothers must supervise and protect their offspring from ecological dangers, infanticidal males, and harassment by other females. Now the rewards for female competition become more apparent: Provisioning and protecting offspring are tasks that are easier for a dominant female than a subordinate one. Status elicits deference and compliance from those of lower rank. Dominant female primates produce offspring more rapidly than subordinates and their offspring have higher survival rates (Pusey, Williams, & Goodall, 1997). This makes it all the more puzzling that competition for dominance and status among females is so much less evident than it is among males. Dominance hierarchies are chiefly restricted to female-bonded species (Sterck, Watts, & van Schaik, 1997) in which they are organized around matrilines and rank is inherited rather than fought for. Females rarely risk their lives to achieve dominance (Chapais, 2002). Dominance offers substantial rewards, yet competitive striving for dominance was not strongly selected in females when it entailed direct combat. This suggests that the rewards were offset by higher costs.

One cost that constrains the evolution of female aggressiveness is hormonal. Testosterone is associated with male aggression, but it is even more closely associated with competition for dominance (Johnson, Leedom, & Muhtadie, 2012). In many species, male testosterone levels rise during the breeding season and in response to challenge (Archer, 2006). Hyenas are atypical mammals in which levels of female dominance and aggression match or even exceed those of males. During pregnancy, maternal androgen levels are raised, creating a uterine environment that masculinizes female fetuses. Gestational androgen levels are higher in dominant females, and the fetus's androgen exposure is correlated with greater aggression in later life (French, Mustoe, Cavanaugh, & Birnie, 2013). However, this exposure virilizes the female genitalia, resulting in a 7-inch clitoris with a diameter of 1 inch through which the adult female must deliver a 2-pound cub. These maladaptive side effects likely limit the extent to which female dominance and aggression can evolve by hormonal means (Clutton-Brock, 2007). Testosterone carries other costs in terms of compromising the immune system (Schroderus et al., 2010), which may partially explain males' earlier senescence and death relative to females. In young men, through its effects on aggressiveness and risk taking, testosterone also increases deaths from external causes. This cost is particularly relevant for females because, as I argue below, reproductive success depends on mothers' continued survival.

The prospect of death (or severe injury) is not appealing to either sex. But the sexes differ in the impact of mortality on reproductive success measured in terms of surviving offspring. For a male, death removes the possibility of future matings, but is less likely to compromise the reproductive success he has achieved to date because he can rely on the offsprings' mother to ensure their survival. A father's death may be a tragedy for the child, but "the consequences of losing a mother very early in life are catastrophic" (Sear & Mace, 2008, p. 5). Sear and Mace (2008) examined the impact of parental death on offspring survival in populations ranging from 18th-century China to 20th-century Nepal, from Burkina Faso to New York state. In every case, a mother's survival reduced the likelihood of her children dying. The percentage of children surviving a mother's death ranged from 2% to 50%. The beneficial effects are stronger before children are weaned: In rural Gambia, a mother's death multiplied the odds of her child's death by 6.2 in infancy, 5.2 in toddlerhood, and 1.4 in childhood (Sear, Steele, McGregor, & Mace, 2002). Pavard, Gagnon, Desjardins, and Heyer (2005) examined data from 17th-century Quebec, controlling for a range of variables including the possibility of transmitted infection and shared genetic vulnerability. If a mother died while her infant was still a neonate, the odds of the child dying in the neonatal period were multiplied by 5.52, dropping to 1.27 when the child was aged 5 to 15 years. The effect of a mother's death was consistently more serious than that of any other relative. Their importance to offspring survival increases the selection pressure on females to safeguard their own lives (Campbell, 2013). Sex differences in aggression are the result not only of selection pressures on males to compete for dominance, but selection pressures on women to avoid dangerous competition.

The results of many hundreds of studies of sex differences in aggression using a range of techniques, including laboratory experiments, observation, personality assessment, and self- and peer-reported behavior, fit a clear pattern: The more dangerous and risky the form of aggression, the larger the sex difference. This appears to be true cross-culturally (Archer, 2009). For physical acts such as hitting, punching, and kicking, the effect size lies between $d = 0.59$ and $d = 0.91$, while for verbal acts such as abuse and threats, the effect size is between $d = 0.28$ and $d = 0.46$ (Knight, Fabes, & Higgins, 1996; Knight, Guthrie, Page, & Fabes, 2002). Indirect aggression includes acts such as spreading stories, excluding, and stigmatizing by which the aggressor can remain anonymous and the possibility of retaliation is consequently reduced. Here the sex difference is negligible and nonsignificant, $d = -0.02$ (Archer, 2004).

PROXIMATE MEDIATORS AND MECHANISMS

The sex difference in risky aggression might be mediated by men's greater attraction to reward, reflecting a stronger approach motivation and manifested at the proximate level in the emotion of *anger*, or it might be the result of women's greater sensitivity to costs, reflecting a stronger avoidance motivation and manifested in greater female *fear*. A sex difference in the threshold for experiencing one or both of these emotions might therefore represent a proximate psychological mechanism for the sex difference in aggression.

Anger is a universal emotion, recognized in all cultures and visible early in life. Anger signals goal obstruction: The goal may be respect, resources, or survival. It is only recently that lateralization studies have established unequivocally that anger triggers approach behavior. As evolutionary psychologists would expect, lateralization of emotion is better understood in terms of functionality (approach or avoidance) than valence (pleasant or unpleasant). Results clearly show that anger is left-lateralized, as are other approach motivations (for review, see Carver & Harmon-Jones, 2009). For example, Harmon-Jones and Sigelman (2001) provoked participants by gratuitously insulting them and then allowed them to respond aggressively. Insulted participants showed greater left frontal activity than the control group and the strength of left-hemisphere activation positively correlated with both their reported anger and level of aggression. Other studies have used transcranial magnetic stimulation paradigms to reach the same conclusions (d'Alfonso, van Honk, Hermans, Postma, &

de Haan, 2000). Beyond the laboratory, anger correlates positively with psychometric scales measuring approach motivation and negatively with avoidance motivation (e.g., Smits & Kuppens, 2005).

However, there is little evidence that men exceed women on anger. Archer (2004) performed a meta-analysis of 46 studies of psychometric anger inventories and found no sex difference. National and international surveys find either no sex differences in anger frequency, with both sexes reporting anger about six times a week (Brebner, 2003; Fischer, Mosquera, van Vianen, & Manstead, 2004), or that women experience anger more often (Mirowsky & Ross, 1995). The intensity of experimentally evoked anger does not vary between the sexes (Kring, 2000), nor is men's anger greater in response to hypothetical or remembered provocation (Milovchevich, Howells, Drew, & Day, 2001). In short, data do not support lower anger in women as an adequate explanation of sex differences in aggression. Nor is the proposal satisfactory at a conceptual level: A higher threshold for anger in women might protect them from aggressive confrontations but not from other forms of risky behavior. Yet there is ample evidence that women are more risk averse than men.

By contrast, there is much evidence that the sexes differ in the frequency and intensity of fear (Else-Quest, Hyde, Goldsmith, & Van Hulle, 2006). The fear system is "designed to detect danger and produce responses that maximize the probability of surviving" (LeDoux, 1998, p. 128). Extreme fear triggers freezing: Inhibitory neural connections allow anticipatory activity in the fear system to suppress behavioral approach that might lead the organism into a harmful situation (Derryberry & Rothbart, 1997). Developmentally, girls express fear earlier than boys, and in a large longitudinal study of personality development, more girls than boys were on a high fearfulness trajectory (Cote, Tremblay, Nagin, Zoccolillo, & Vitaro, 2002). Among adults, women experience fear more intensely than men (Gullone, 2000). International studies find significant sex differences in the frequency, intensity, and duration of fear (Brebner, 2003; Fischer & Manstead, 2000). Women express their fear more intensely than men, both verbally and nonverbally (see Madden, Feldman Barrett, & Pietromonaco, 2000). While women are superior to men in accurately identifying emotions, they show a greater accuracy for decoding fear than other emotions (Hall, Carter, & Horgan, 2000). In response to physically threatening scenes, women show greater increases in skin conductance and a more marked startle reflex (McManis, Bradley, Berg, Cuthbert, & Lang, 2001). A single dose of testosterone administered to women significantly reduces their potentiated startle response to anticipated electric shock (Hermans, Putman, Baas, Koppeschaar, & van Honk, 2006). These findings extend rodent research that has robustly established that the hypothalamic pituitary axis response to stress is inhibited by androgens and enhanced by estrogens (Lund, Munson, Haldy, & Handa, 2004). Taken together, these findings suggest that gonadal hormones cause the fear system to develop and function differently in males and females.

This sex difference in fear may explain why men make riskier decisions than women. This is especially marked when the risks are life threatening and when actual risky behaviors, rather than hypothetical choices, are examined. In a review of risk-taking studies, Byrnes, Miller, and Schafer (1999, p. 378) conclude that "fear responses may explain gender differences in risk taking more adequately than the cognitive processes involved in the reflective evaluation of options." Women's lower participation in risky real-world activities is best explained by their stronger anticipation of possible negative consequences and by their higher ratings of the severity of those consequences should they occur (Harris, Jenkins, & Glaser, 2006; Wang, Kruger, & Wilke, 2009). Women's risk taking, but not men's, is especially reduced when their risky decisions have consequences for infants (Fischera & Hills, 2012). A meta-analysis (Cross, Copping, & Campbell, 2011) revealed that although women and men do not differ in their sensitivity to reward, women are consistently more sensitive to punishment than men. This dovetails with the proposal that women have evolved greater sensitivity to negative outcomes than men, manifested in their lower threshold for fear. This lower threshold has direct consequences for aggressive behavior. Two independent meta-analyses have found that women evaluate the same objective situation as more dangerous and more fear-provoking than men, and these appraisals significantly explain the sex difference in aggressive behavior (Bettencourt & Miller, 1996; Eagly & Steffen, 1986). Fear acts as a brake on aggression, and women's brakes respond to danger more sensitively than men's.

THE NEUROPSYCHOLOGY OF SEX DIFFERENCES IN RESPONSE TO THREAT

Increasingly, we are able to access internal affective states through the use of functional magnetic resonance imaging. The chief focus of such studies has been the amygdala, an almond-shaped subcortical structure (composed of more than 10 nuclei) in the temporal lobe. LeDoux's (1998) pioneering work implicated the amygdala in the registration of fear, although it is now thought to process other emotions associated with salient or unexpected events (Sergerie, Chochol, & Armony, 2008). Its role seems to be to rapidly detect stimuli that are biologically relevant (Sander, Grafman, & Zalla, 2003), especially where they may require an immediate response, which is often the case when they are unexpected, threatening, or dangerous (Adolphs & Spezio, 2006). Afferent sensory inputs to the lateral nucleus of the amygdala are coordinated with efferent outputs from the central nucleus that control behavioral, autonomic, and endocrine fear responses.

We would expect to see a stronger amygdala response to threat in women reflecting their greater fearfulness. Meta-analyses generally conclude that women show greater activation to threat in the limbic system, especially the amygdala (Stevens & Hamann, 2012; Whittle, Yucel, Yap, & Allen, 2011; but see also Sergerie et al., 2008). This suggests that women may register external threat more strongly and more persistently than men. However, because the majority of neuroimaging studies use participants of only one sex, meta-analytic conclusions are based on comparisons of men's and women's neural responses to different stimuli.

In many studies, researchers use facial expressions of fear and anger as "threat" signals, collapsing these stimuli in their analyses. This makes it hard to tease apart the neural and emotional response to being personally threatened (viewing an angry face) as compared to being alerted to environmental hazard (viewing a fearful face). We might expect that these two social messages would activate somewhat separate circuits, and that the sexes might differ in their response to them. Both men and women would be expected to show a similar response to a fearful face (indicating nonspecific local danger). However, an angry face (indicating a possible aggressive attack) might trigger hostility in men and fear in women. McClure et al. (2004) compared men's and women's reactivity to angry and fearful faces. The relative engagement of the amygdala bilaterally to angry faces was greater in women, suggesting that women react more fearfully than men to unambiguously threatening (angry) faces. Relative to baseline fixation, women showed significantly greater activation than men over the whole "fear circuit" (amygdala, orbitofrontal, and anterior cingulate cortex) to angry but not fearful faces. By contrast, men showed a less specific pattern of increased orbitofrontal (but not amygdala) activation to both stimuli. There is, then, some support for the proposal that amygdala activation may be more closely associated with fear in response to aggressive threat in women, while men show a less differentiated pattern of reactivity to "threatening" stimuli in general.

These problems of interpretation (the amygdala can respond to facial expressions of both fear and anger, and amygdala activation may correspond to the registration of both these emotions) become particularly evident in research that examines the effect of gonadal hormones. As with other regions that are sexually dimorphic in size, the amygdala contains a high concentration of sex hormone receptors. On one hand, it decreases fear, and one study reported that, in men only, endogenous testosterone levels were negatively correlated with amygdala reactivity to angry faces (Stanton, Wirth, Waugh, & Schultheiss, 2009). On the other hand, testosterone levels have been linked to increased amygdala activation in response to threat, with this activation interpreted as reflecting anger and approach motivation. In both sexes, endogenous testosterone levels are positively associated with amygdala response to threatening stimuli (van Wingen, Ossewaarde, Backstrom, Hermans, & Fernandez, 2011). Administration of testosterone to young women is associated with increased persistence of amygdala reactivity to angry faces (Hermans, Ramsey, & van Honk, 2008). In one study that attempted to disambiguate men's neural response to angry and fearful faces (Derntl et al., 2009), amygdala reactivity did not differ significantly between the two, and their endogenous testosterone levels were equally correlated with their amygdala responses to both types of stimuli.

Underpinning much of this research is the questionable assumption that testosterone has similar effects in men and women. In men, but not women, circulating testosterone interacts with a brain that has been prenatally primed by androgens. In addition, testosterone effects may differ between the sexes as a result of sexually dimorphic gene expression. Testosterone may trigger the expression of autosomal genes in one sex but not the other, or different genes in the two sexes. In the dark-eyed junco, 651 genes in the medial amygdala differed in expression between males and females, and testosterone administration altered the expression of different genes in the two sexes (Peterson et al., 2013). Many genes are subject to correlated expression and may be coregulated, and this functional modularity may allow suites of responses to differ in men and women in response to the same hormonal milieu (Rosvall, 2013b). (A recent vivid example of the dangers of assuming common or sex-neutral effects comes from studies of the peptide hormone oxytocin. S. E. Taylor and colleagues, 2000, proposed that the calming effect of oxytocin was responsible for women's "tend-and-befriend" response to threat. This was supported by studies showing that administration of oxytocin did indeed have anxiolytic effects [e.g., Kirsch et al., 2005]. However, these studies employed male participants. When female participants were examined, oxytocin *increased* rather than decreased amygdala responsiveness to threat [Domes et al., 2010; Lischke et al., 2012]). Further studies are needed to examine the circuitry of fear and anger, identifying common and unique pathways. This will allow examination of the role of these emotions in explaining sex difference in aggression, as well as the effects of gonadal hormones on their relative activation.

These fundamental affective tendencies to approach or avoid stimuli are located in the limbic system and are part of a "reflexive" behavioral control system sculpted in many animal species by evolutionary forces. But in humans, these tendencies are subject to higher-level "reflective" control. Emotional intensity and behavioral response can be modulated by the prefrontal cortex, especially the orbitofrontal (OFC) region, which has direct connections to the amygdala. In neuroimaging studies, negative correlations are found between amygdala and OFC activity in impulsively aggressive individuals (Coccaro, McCloskey, Fitzgerald, & Phan, 2007). When participants are instructed to imagine aggressing against (Pietrini, Guazzelli, Basso, Jaffe, & Grafman, 2000) or harming another person (Decety & Porges, 2011), deactivation of the OFC has been found. Given the modulatory role of the prefrontal cortex, studies have looked for sex differences in these regions. Women have a larger ventromedial prefrontal cortex and right lateral OFC (Welbourne et al., 2009). A meta-analysis of 88 studies reported greater OFC activity in women to facial stimuli depicting negative emotion (Stevens & Hamann, 2012). This suggests that women may be more efficient in spontaneously regulating emotional responses.

Testosterone reduces functional connectivity between the amygdala and the prefrontal cortex, while leaving connectivity to the brain stem unaffected (Manuck et al., 2010; Bos, Hermans, Ramsey, & Van Honk, 2012). (Progesterone has the opposite effect, enhancing amygdala-frontal connectivity; van Wingen et al., 2008). Serotonin (5-HT) plays a key role in the functional connectivity between the PFC and the amygdala. There is a dense concentration of 5-HT receptors in the limbic system (including the amygdala) with projections to the prefrontal cortex. Dietary tryptophan depletion (which reduces 5-HT levels) reduces connectivity in the prefrontal-amygdala circuitry, specifically when viewing angry faces (Passamonti et al., 2012). Women have higher 5-HT transporter availability, and because this regulates 5-HT neurotransmission, baseline serotonin may be higher in women than men. Studies have reported a higher density of 5-HT_{1A} receptors in women in areas including the amygdala and medial and orbital PFC (Parsey et al., 2002). Receptor density in these areas is significantly negatively correlated with lifetime aggression. In animal research, 5-HT receptor density is also negatively correlated with testosterone. Although this has not been replicated with humans, men (but not women) with high levels of aggression are characterized by a combination of high T and low 5-HT (Montoya, Terburg, Bos, & van Honk, 2012). Reduced availability or uptake of serotonin, associated with high T, may explain men's diminished prefrontal control over emotion-driven behavior.

TWO-WAY SELECTION, WOMEN, AND COMPETITION

Female competition and aggression, once considered a fascinating but inexplicable anomaly, is now a documented fact (Stockley & Campbell, 2013). But what are females competing for? The traditional model of sexual selection makes it clear that it cannot be copulations. Under polygyny, it is males not females who must compete for sexual access, hence their gaudy plumage (the better to advertise their genetic quality) and combative attitude (the better to deter and intimidate rival males). Yet in our own species, a cursory inspection reveals that women expend a considerable amount of their energy and resources on increasing their attractiveness to men via cosmetics, surgery, toxin injections, dieting, and clothing. This behavior bears the hallmark of two-way sexual selection. Like men, women are actively competing to obtain the best mates, which suggests that our species is less polygynous than has been assumed. But if polygyny is the optimal strategy for male reproductive success, why would men forego it in favor of committing themselves to a single woman and costly parental investment?

According to the traditional Bateman model, gestation and lactation remove women from the mating pool, creating a male-biased operational sex ratio. This increases competition between males for access to reproductively available females. But the logic of this has been questioned by Kokko and Jennions (2008), who argue that a male-heavy operational sex ratio should generate frequency-dependent selection favoring increased parental care by the sex that faces more intense competition. In short, there is no logical reason why male competition should generate a positive feedback loop over evolutionary time. As competition becomes more intense among males, there is selective advantage for those males who opt out of mating competition in favor of infant care.

Explanations of the evolution of paternal care predict that it should occur where the number of surviving infants with paternal care is greater than the number of surviving infants without such care multiplied by the number of females that a bachelor male can inseminate (e.g., Clutton-Brock, 1991). It has been suggested that paternal care is especially important in humans as a result of the infants' long period of dependency, which suggests that men might enhance their reproductive success more effectively by paternal investment and attendant monogamy than by polygyny. Yet there is evidence that paternal care does not improve offspring survival. Sear and Mace (2008) examined the impact of parental death in 28 hunter-gatherer and foraging populations. In 68% of cases, a father's death had no impact on the survival chances of his child. In 32% of cases, it actually improved the child's odds of surviving. Even among the Tsimane of Bolivia, who have low divorce rates and high levels of paternal provisioning, the early death of a father had no impact on their children's age of first reproduction, completed fertility, or number of surviving offspring (Winking, Gurven, Kaplan, & Stieglitz, 2009). Across five foraging populations, returns on paternal investment in terms of child survival were *less* than those obtained by serial mating (Winking & Gurven, 2011). In ecologies similar to the ones in which humans evolved, there are not strong grounds for believing that there was positive sexual selection on men for paternal care. (This is not to say that paternal investment in contemporary societies does not bring social, emotional, and financial benefits to children; see Geary, Chapter 20, this *Handbook*, Volume 1).

An alternative view of the evolution of biparental care focuses not on sexual selection but *sexual conflict* between men and women. This occurs when a sexual selection pressure acting to augment the spread of a gene-based trait advantageous to one sex is modulated, constrained, or opposed by the coevolution of a counterresponse by the other sex (Arnqvist & Rowe, 2005). Sexual conflict has been studied chiefly at the genetic level, but the basic premise—that males and females are locked in a coevolutionary arms race—can be extended to phenotypic behavior (itself underpinned by gene complexes). Bipedalism and the resulting need for "premature" delivery of babies increased the energetic demands on mothers. The presence of a male partner would have been advantageous, not because it increased offspring survival, but because it decreased the workload on mothers. A synthesis of data from 10 intensive studies of gatherer societies (Kaplan, Hill, Lancaster, & Hurtado, 2000) suggests that between 60% (among the Nukak) and 84% (among the Ache) of the calories consumed are contributed by men. More than half of calories consumed come from meat, hunted almost exclusively by men. With men relieving women of the full burden of provisioning, women were better able to feed their dependent children, sustain pregnancy and lactation, and return to normal cycling more quickly, thus shortening interbirth intervals (Worthman, Jenkins, Stallings, & Daina, 1993). A permanent male assistant was in a woman's best interests, and she had a bargaining chip. By restricting sexual access to men who were willing to make a paternal contribution, women could act as a selecting force countering men's predilection for promiscuity. Due to high male demand and restricted supply, sex has always been a resource that women can trade. Women can use it to obtain short-term and extra-pair mates of high genetic quality (Gangestad & Simpson, 2000; Thornhill & Gangestad, 2008). However, if too many women pursue this strategy, the marketplace will reflect it in a lower value for female sexual access, ultimately diminishing its utility as a bargaining chip. Indeed, female hostility to women who are too sexually available may function to protect the female sex from losing its leverage (Baumeister & Twenge, 2002; Baumeister & Vohs, 2004). Paternal investment offers the best long-term benefits to women by easing the resource costs of motherhood.

Did biparental care arise sufficiently long ago that there has been time for selection to act on it? Neonate size and adult skeletal remains date it to the start of the *Homo* line, 1.5 to 2 million years ago (Eastwick, 2009). Other archaeological findings place it even earlier, with *Australopithecus afarensis,* the predecessors of *Homo* (Reno, Meindl, McCollum, & Lovejoy, 2003). Selection operates faster on sexually, rather than naturally, selected traits: It is estimated that sexual selection can produce a 0.37 standard deviation shift in the average value of a fitness-relevant trait in a single generation of directional selection (Courtiol, Pettay, Jokela, Rotkirch, & Lummaa, 2012). Evidence of an evolved adaptation to paternal investment can be seen in the down-regulation of men's testosterone levels following pair bonding and fatherhood (Gray & Anderson, 2010), and the rise in oxytocin levels in fathers (as well as mothers) after the birth of a baby and during interaction with them (Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010).

The effects of biparental care and pair bonding are profound. Monogamy reduces the ability of men to exploit women by creating greater equality between them in their reproductive output. Holland and Rice (1999) demonstrated this by forcing monogamy on the naturally polygynous fly *Drosophila melanogaster.* Individual males and females were housed together over 32 generations. Under polygyny, males can exploit females quite ruthlessly without suffering any costs themselves, but monogamy means that anything that hurts a female (prevents her from achieving her reproductive potential) hurts her male partner just as much. After several generations of monogamy, Holland and Rice examined the effects. When the control group of polygynous females were allowed to mate with the monogamous "new males," the females benefitted from the decreased toxicity of the male's seminal fluid (a side effect of male sperm competition), which is normally harmful to them. Reciprocally, when the newly monogamous females were returned to the polygynous males, a larger proportion of them died compared to the females who had been allowed to coevolve with male polygyny. As a result of imposed monogamy, males behaved in a less exploitative way toward female partners and so the monogamous females did not need to evolve counterstrategies of resistance.

In many species, monogamy evolves where females are spatially dispersed and each male is forced to associate with an individual female. But this scenario is implausible for humans, who are a group-living species. An alternative model proposes that, if females were willing to forego extra-pair matings and preferred males who provided resources, male provisioning would increase, driven chiefly by low-ranking males who would otherwise fail to reproduce at all (Gavrilets, 2012). Because these males outnumber elite males, selection acts more strongly on them and their strategy. This is not to say that either sex becomes completely faithful, as both have something to gain by extra-pair copulation: Females gain "better" genes and males gain increased paternity. But a basically monogamous mating system, through its effects on individual behavior, brings with it societal rewards in terms of reduced crime rates and stronger within-group alliances. For women, it reduces gender inequality and domestic conflict, while increasing child survival (Henrich et al., 2012).

The cost for women is that sexual selection becomes two-way, increasing competition between women to secure the highest-quality males within the marketplace of assortative mating. The currency of female competition is the qualities that men value in a prospective mate. In many domains, men and women are more similar than different in what they seek in a long-term partner (Buss et al., 1990). There are no sex differences in minimum acceptable percentile for qualities such as intelligence, sexiness, exciting personality, creativity, friendliness, sense of humor, easygoing temperament, health, religiosity, desire for children, kindness, and understanding (Kenrick, Sadalla, Groth, & Trost, 1990). Because men and women are locked together under monogamy and biparental care, both sexes seek qualities that will contribute to the day-to-day cooperation and compromise that such an arrangement requires. But men more than women place a premium on youth (Buss, 1989; Kenrick & Keefe, 1992), physical attractiveness (Buss & Schmitt, 1993), and body shape (Singh, 1993). Female intersexual competition for mates often centers on advertising these qualities. While men are more likely to compete with each other by exaggerating their sporting ability, promiscuity, and popularity, women are more likely to compete with each other in terms of their appearance, using aids such as makeup, nail polish, fake tans, and tight clothing (Cashdan, 1998; Buss, 1988). Both parties are concerned about commitment, but men, who must live with the risk of misplaced paternity, are particularly sensitive to the possibility of sexual infidelity (Sagarin et al., 2012).

Appearance and fidelity can become key weapons when women's competition escalates to indirect or relational aggression. These are acts that stigmatize, ostracize, and otherwise exclude others from social interaction and they can be used without direct physical confrontation. Such acts do not eliminate or physically injure the target, but they do inflict stress and diminish the opponents' reputation and social support. A key component of indirect aggression is the use of gossip to undermine an opponent's reputation and decrease their social capital (Owens, Shute, & Slee, 2000). Pejorative comments about other girls' appearance rank high in girls' topics of gossip (Duncan, 1999) and are used to derogate rivals more often by women than men (Buss & Dedden, 1990). These circuitous attacks are directed particularly at attractive young women (Vaillancourt, 2013). But attractiveness combined with a self-confident flaunting of it seems particularly provocative. Girls who advertise their attractiveness or sexuality too overtly through dress, make-up, or demeanor are often targeted (Miller & Mullins, 2006). These girls offend on two fronts: They attract more than their fair share of boys and they communicate their felt superiority over other girls. This becomes a form of "disrespect," which adds to the antagonism. Women can also benefit competitively by undermining their rivals' sexual reputation and terms such as "slag," "tart," or "whore" are powerful sources of reputation challenge among women (Campbell, 1995, 1999; Lees, 1993; Marsh & Paton, 1986). These tactics are as visible among university students (Buss & Dedden, 1990; Milhausen & Herold, 1999) as among girl gang members in deprived inner-city areas (Campbell, 1984; Ness, 2004).

ESCALATION TO VIOLENCE: ECOLOGICAL AND CULTURAL MODERATORS

Although women engage in same-sex physical confrontations less frequently and less seriously than men, fights do occur. In the United States, girls account for 33% of arrests for simple assault and 24% of aggravated assaults (Girls Study Group, 2008), with the larger gender gap for aggravated assault reflecting girls' less injurious behavior and lower likelihood of using weapons. Surveys indicate that in the previous year, 40.5% of boys and 25.1% of girls had been in a physical fight (Grunbaum et al., 2004). In the previous month, 60% of girls had called another girl names, 50% had sworn at them, and 35% had pushed or shoved them (Artz, Nicholson, & Magnuson, 2008). Female assaults most commonly occur among 15- to 24-year-olds, predominantly between friends and acquaintances, and the most frequent forms of attack are pushing, shoving, grabbing, tripping, slapping, kicking, and punching (Campbell, 1986; Ness, 2004). The reasons for fighting are often connected directly or indirectly to young men and fall broadly into three categories. The first is defending a sexual reputation. Gossip about a girl's promiscuity gives rise to rumor that may find its way back to the target, triggering an attack as a means of reclaiming her threatened identity. A second source of provocation is competition for potential partners. Around the world, access to men and their resources is responsible for the majority of women's fights (Burbank, 1987). Thirdly, jealousy about proprietary ownership of a current partner is a frequent source of conflict.

But the probability of escalating from indirect aggression to outright physical attack is not randomly distributed. There are ecological and demographic factors that concentrate it among the young in the poorest neighborhoods. Men and women show a curvilinear age–violence relationship, with aggression rising in the early teenage years and falling away in the mid-20s. Although male violence is far more prevalent than female violence, the shape of the curve is very similar for both sexes—with one exception. Violence rises and peaks earlier in girls by about 2 years, corresponding to girls' 2-year-earlier attainment of sexual maturity (Campbell, 1995). Early menarche is predictive of girls' aggression. Life history theory forms the basis for expecting that age of menarche should be responsive to cues from the local environment that canalize development toward a "fast" or "slow" reproductive tempo. Resource scarcity, high rates of early mortality, psychosocial stress, low-quality parental investment, father absence, and stepfather presence signal environmental uncertainty and unpredictability, accelerating pubertal timing and reproduction in an adaptive fashion. In deprived neighborhoods, girls may experience many of these risk factors simultaneously. These girls begin their sexual careers earlier, putting them at a significant advantage over their peers. In addition, older girls are acutely sensitive to the entry of younger competitors into the mating arena and this may increase their likelihood of victimization and retaliation. Girls who reach menarche early are more likely to be involved in delinquent and aggressive behavior, and this is especially true for maltreated girls (Negriff & Trickett, 2010) and those living in disadvantaged neighborhoods (Obeidallah, Brennan, Brooks-Gunn, & Earls, 2004).

The operational sex ratio is an index of the availability of prospective mates. Women are most likely to find a partner in the immediate neighborhood, and to the extent that the local male–female ratio drops below unity, competition between women increases. The mortality rate among men is considerably higher than among women, especially between the ages of 15 and 35 (Kruger & Nesse, 2006). At the age of 25, men are 3 times more likely to die from all causes than women, and 4 times more likely to die from external causes. Urban areas are more likely to have a female-biased sex ratio (Edlund, 2005). In the U.S. Black population especially, there is a severe shortage of men. As a result of high male mortality and incarceration rates in the 20-to-29 age group (Tucker & Mitchell-Kernan, 1995), there are 85 men for every 100 women compared to 99 men for every 100 women among Whites. When the local male–female ratio drops below unity, competition between women increases. It also means that men find themselves in an excellent bargaining position. Usually only a very few well-resourced and highly desirable men are in a position to successfully pursue a polygynous strategy, but when men are in short supply, market forces mean that men are in a position to call the shots, effectively enforcing a "short-term only" mating strategy on women (Campbell, 1984). This may be far from ideal from young women's point of view, but the laws of supply and demand mean that such men often get their way, with young women adapting their resource-extraction tactics accordingly. As one young woman advised: "I tell her take all his paper, all of it, 'cause it's just a matter of time and he's gonna do some rotten dog shit on her. . . . Got to get it when you can. You never know when it's gonna stop and you better get much as you can while you can. . . . When fellas get tired of your pussy, it's good-bye girl, naw, it's get the fuck out of my life bitch! Next bitch!" (Taylor, 1993, pp. 97, 131).

High variation in men's resources further intensifies female competition. Among middle-class young women, the costs of escalating to direct competition are rarely worth it: The difference between marrying a doctor or an accountant is not sufficiently great. But in deprived areas, the difference between the desperate poverty of "dope fiends" and the conspicuous consumption of "high rollers" is extreme. The desirability of access to material resources means that well-resourced men are worth fighting for. Antagonism can be heightened further after a young woman bears a man's child: Even after the relationship has ended, a BM ("baby momma") feels entitled to make claims on the father's income and to repel rival women who threaten to divert his resources (Ness, 2004). Young men's preference for sexual novelty is a constant threat to relationships (Symons, 1979), and young women are especially sensitive to attractive or newly arrived girls: "It's like, if another girl gets attention, she's taking it away from you. It's as if she's saying she's better than you. So you gonna knock her down a notch" (Ness, 2004, p. 40).

Cultural norms support the use of women's violence in deprived inner-city neighborhoods where it is most common (Leventhal & Brooks-Gunn, 2000). For families in such neighborhoods, the frequent absence of a consistent father figure means that mothers (and grandmothers) play a pivotal role. They are strong figures who must cope alone with the daily stresses of subsistence living. Many mothers are themselves involved in fighting, especially in defense of their family's good name. Some become actively involved in their daughter's fights and, in doing so, become role models and allies (Ness, 2004). Mothers' concern for their daughters' welfare translates into tolerance (and sometimes encouragement) of fighting. Most mothers acknowledge that a girl needs to be able to "stand her ground" and "hold her own."

The strength and resilience of women is not seen as incompatible with femininity: Indeed, passivity is viewed as a weakness rather than an asset. As Irwin and Adler (2012, p. 319) noted, "Given the emphasis on female strength, girls lost respect for and even targeted other girls who fell short in fulfilling idealized notions of feminine resilience circulating in the local communities."

If weakness makes a girl a target, an important benefit of willingness to fight is the avoidance of victimization. Girls' reports of their fights present aggression as a form of self-defense by emphasizing that their opponent "started it." In some cases, "starting it" refers to a physical assault, but more often to rumor spreading or verbal taunts to which physical aggression is seen as the appropriate response. The slippery divide between physical and verbal provocation is mirrored in the fuzzy distinction between self-defense and reputation enhancement. For many girls, success in a public fight achieves more than the immediate goal of causing an opponent to back off: It promotes a "crazy" or "mean" reputation that will deter others from future attacks (Jones, 2004; Miller & Mullins, 2006). Reputation enhancement involves a disproportionate response to any perceived act of "disrespect," including pejorative gossip, staring, and a demeanor that presumes social superiority (a girl who "thinks she's all that"). Once established, reputations must be defended against others who are seeking to enhance their own. One response is for tough girls to get their retaliation in first. In this way, a self-reinforcing cycle develops between sensitivity to challenge, self-defense, reputation enhancement, and preemptive aggression. Although many disputes appear to be about securing and defending status-enhancing relationships with desirable boys, the motivations can be a complex mixture of rivalry, jealousy, and reputation management. As one girl explained, "I don't care about the guy or anything but I'm gonna mess that girl up cause she deserves it. The bitch just be asking for it. The way I see it, I ain't fighting over the boy. I'm fighting the girl because she be acting in a way that says she thinks I'm a punk" (Ness, 2010, p. 84). The right to be treated with appropriate respect lies at the heart of impression management theories of aggression (Felson, 1978) and public disrespect is a common trigger for anger and aggression. This is as true for inner-city girls as it is for others (Ness, 2010). Young women's fights are triggered by challenges to personal integrity in a range of domains, but slurs on a girl's attractiveness and sexual continence are potent and pervasive sources of conflict.

Young women's verbal bluster and bravado should not be taken as an indication of fearlessness. A theme that recurs in ethnographic reports is the need to control fear and suppress its expression in order to avoid victimization. This is as true in Philadelphia ("If I seem like I'm scared to fight, some girl is gonna think she can mess with me all the time" [Ness, 2004, p. 38]) as it is in Glasgow ("Cos if you show fear of somebody, they're just gonna walk all over the top of you. If you show fear of them, they always come back tae you" [Batchelor, Burman, & Brown, 2001, p. 130]). Growing up in these communities, fear is an emotion that signals weakness and young women must learn to master its expression.

SUMMARY AND CONCLUSION

At a proximate psychological level, evidence suggests that women's lower level of aggression is not explained by their more placid temperament (women experience anger as often and as intensely as men) nor by a sex difference in impulsivity (women can and do act on impulse but are less likely to do so when such acts carry potentially risky consequences; Cross et al., 2011). Rather, it is women's greater fear that restrains their use of overt aggression. Their greater sensitivity to danger is also manifested in their higher levels of subclinical and clinical anxiety, stronger risk aversion, and lower levels of sensation seeking. At an ultimate evolutionary level, the sex difference in the calibration of the fear threshold is predicated on the greater importance of the mother than the father in assuring offspring survival. Reproductively, women are quality, not quantity, specialists. Their output is limited by lengthy infertile periods of gestation and lactation, and truncated by menopause long before somatic senescence. Their investment in each offspring is measured in years as a result of babies' long and demanding period of dependency. Despite this, women are unusual among primates in their short interbirth intervals, resulting in the need to care simultaneously for more than one dependent child. Such a feat requires assistance, and I have suggested that ancestral women traded genetic diversity of offspring for paternal help in resource provision. Because paternal care does not enhance offspring survival sufficiently to compensate for the abandonment of a polygynous strategy, an explanation in terms of male sexual selection is problematic. A plausible alternative scenario is that biparental care arose as a result of sexual conflict in which women granted exclusive sexual access preferentially to men who were willing to invest in their offspring. But with biparental care and monogamy came two-way sexual selection: Men became increasingly choosy in their choice of long-term partners and in response, women competed with one another to advertise qualities that were attractive to men. This is not to deny that mothers created strong bonds of mutual cooperation with one another, despite or because of female emigration from the natal group. (Whether or not such bonds are evidence of "cooperative breeding" depends on one's definition of the term. In most cooperatively breeding species, a single female aggressively monopolizes breeding [Young & Bennett, 2013], a situation that clearly does not apply to humans. Other researchers [e.g., Mace, 2013] treat the term as effectively interchangeable with kin selection since the helpers have a genetic interest in the offspring [e.g., siblings, grandmothers]). Under extreme conditions of resource scarcity, the limits of mutual benevolence between genetically unrelated women would have been sorely tested. Mothers and fathers may be unrelated, but they share a common genetic investment in their offspring, and a substantial history of monogamy has shaped hormonal and neural adaptations for emotional bonding in both sexes (De Boer, Van Buel, & Ter Horst, 2012). The extremity and visibility of female competition is moderated by interlinked ecological and cultural factors. Harsh environments recalibrate life history tempos and increase competition in women as they do in men: Correlations between the sexes' rates of violence across geographic regions exceed .90 (Campbell, 1999). Community tolerance for women's aggression is correspondingly adjusted, so that the concept of "femininity" embraces strength, resilience, and the public denial of fear.

The past few years have seen a surge of interest in female competition by evolutionary biologists (e.g., Rosvall, 2013a; Stockley & Bro-Jørgensen, 2011). To add to their insights, evolutionary psychologists are increasingly stepping up to the special challenges of understanding competition in our own species (Benenson, 2014; Fisher, Garcia, & Chang, 2013; Vaillancourt, 2013) with our capacity for representational thought, symbolic language, and cultural transmission. Yet these impressive human abilities interact with and serve an ancient stratum of affective adaptation, shared with other species, which have been shaped by universal principles of natural and sexual selection.

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CHAPTER 28

Prejudices: Managing Perceived Threats to Group Life

STEVEN L. NEUBERG and PETER DESCIOLI

PEOPLE ARE OFTEN prejudiced against foreigners. They are also prejudiced against those who are obese, physically disabled, or elderly. They are prejudiced against people with schizophrenia and young outgroup men. They are prejudiced against those on social welfare and those who are so wealthy that they and generations of their descendants will never need such help. They are prejudiced against gay men, religious fundamentalists, atheists, and members of this or that political party or advocacy group. As the English essayist Charles Lamb wrote in *Imperfect Sympathies*, humans are a "bundle of prejudices" (Lamb, 1821).

Why? Traditional theoretical approaches posit that prejudices, stereotypes, and discrimination result from a range of proximate processes, including simple ingroup–outgroup categorizations, desires to boost one's self-esteem, authoritarian values, fear of death, and the need to justify oppressive actions against others. We will see, however, that people think about and behave towards others in ways that these approaches cannot predict.

We suggest that understanding prejudices requires a deeper theoretical framework—an evolutionary psychological framework. From this perspective, prejudices, stereotypes, and discriminatory behaviors can be viewed as functionally organized strategies designed to manage the threats posed by the human forms of sociality.

Life was challenging for our ancestors. Food was often scarce, unpredictable, and difficult to extract and secure. Predators and pathogens caused injury, incapacitation, and death. In the face of such challenges, individuals who cooperated with others gained significant reproductive advantages over more solitary, independent individuals (Campbell, 1982; Richerson & Boyd, 1995). Thus, human sociality reflects an evolved set of adaptations to provide safety from danger and to exploit opportunities in challenging environments (Brewer, 1997; Brewer & Caporael, 1990; Leakey, 1978).

Human sociality can also be costly, however. Proximity increases exposure to contagious diseases, and makes people susceptible to theft and violence; cooperation makes contributors vulnerable to others free-riding on their efforts. One general approach to managing the benefits and costs of social life is *discriminate sociality*—the careful selection of social partners (Kurzban & Leary, 2001). Indeed, our choices of social affiliates are far from random, and tend to favor those presenting cues suggesting they'll provide more benefits than costs. We're more likely to select partners who appear to be kin, cooperative, and trustworthy; who are able to coordinate their efforts with ours and are available for future interactions; and who offer other beneficial traits (for reviews, see Kurzban & Neuberg, 2005; Neuberg & Cottrell, 2008). Selecting some individuals into one's coalition and excluding others constitutes one form of discrimination. As we'll discuss, many cues that heuristically identify individuals as potentially costly social partners also constitute the basis of many contemporary social prejudices.

We focus, however, on two other sets of processes. First, we explore the evolved psychological mechanisms by which individuals (1) identify those who afford fitness threats and opportunities and (2) respond to them in threat-mitigating and opportunity-enhancing ways. These *affordance management systems* (Gibson, 1979; McArthur & Baron, 1983; Neuberg, Kenrick, & Schaller, 2010, 2011; Zebrowitz & Montepare, 2006), contribute significantly to stigma, prejudices, and discrimination. Second, people create within-group coalitions to counter threats posed by other group members, and we explore the implications of alliance-based processes for prejudices and group-on-group conflict. We then extend these analyses to understand prejudices against foreigners, especially as these prejudices manifest in warfare and issues of immigration and emigration. Last, we discuss the implications of evolutionary approaches for reducing prejudices and intergroup conflict. Throughout, we'll see that by identifying new prejudice phenomena and by anticipating undiscovered nuances in known phenomena, the evolutionary approach poses significant challenges to traditional social psychological and sociological approaches.

THE EVOLVED THREAT-MANAGEMENT PSYCHOLOGY UNDERLYING PREJUDICES, STEREOTYPES, AND DISCRIMINATION

An affordance-management view holds that prejudices, stereotypes, and discrimination are responses for managing recurring threats to reproductive fitness over human evolutionary history (Schaller & Neuberg, 2012). Like all affordance-management systems, threat-management systems share a common template: Cues in the environment heuristically (and imperfectly) imply specific threats. These perceived threats, in turn, elicit a suite of functionally relevant cognitions, emotions, and behavioral inclinations designed to manage the threats.

There are several important implications of this perspective, each of which we expand on: (a) Qualitatively different psychological systems are likely to have evolved to manage different threats. (b) Different threats are cued by different kinds of information. (c) Upon activation by cues, these distinct systems engage qualitatively different prejudice syndromes of specific cognitions and beliefs (i.e., stereotypes), emotions (i.e., prejudices), and behavioral inclinations (i.e., discrimination). Thus, to the extent that different groups are perceived to pose different threats, they are likely to be targeted by different prejudice syndromes. (d) Threat management systems are biased to avoid costly mistakes, erring on the side of perceiving greater (rather than lesser) threat; consequently, people err on the side of discriminating against individuals who, actually, may afford no threat at all. And (e) deployment of prejudice syndromes depends on an individual's perceived vulnerabilities to particular threats.

People who feel vulnerable to different threats will engage different prejudices and forms of discrimination.

TO WHAT THREATS WOULD AN EVOLVED PSYCHOLOGY BE ATTUNED?

Fitness is the extent to which one's genes are passed into subsequent generations. From this perspective, mechanisms that led our ancestors to be attuned to cues suggesting threats to their (and to their kin's) physical safety, to their ability to acquire necessary resources (e.g., food), and to their health would have been adaptive. Indeed, much of the research from an evolutionary approach has focused on prejudices towards those perceived to threaten others via physical violence or disease (Schaller & Neuberg, 2012).

Because our ancestors benefited from coalitional action, people are also expected to monitor threats both to coalition resources (e.g., access to territory) and the coalition's operational integrity—the social structures that enable coalitions to be effective. Effective coalitions tend to exhibit trust, reciprocity, common values, socialization practices, and authority structures for organizing individual effort and distributing group resources (e.g., Brown, 1991). As a result, people should be wary of those who threaten these group structures (Neuberg, Smith, & Asher, 2000).

DETECTING THREAT

How can one anticipate whether someone is likely to threaten safety, health, resources, and the like? One cannot directly perceive another's pathogens or intentions to harm. Rather, people must rely on cues—features of morphology, behavior, or reputation—that correlate (even if only weakly) with threats.

Because threats are qualitatively distinct—threats to physical safety are different, for instance, than are threats to fair trade—the cues implying different threats will also often be distinct. For example, threats of violence are cued by features (imperfectly) implying the capacity to do harm (e.g., prominent upper-body musculature, maleness, presence of a weapon) and the intention to do harm (e.g., angry facial expressions, looming approach, maleness, and outgroup-linked features related to morphology, language, skin color, clothing; e.g., McDonald, Asher, Kerr, & Navarrete, 2011; Navarrete, McDonald, Molina, & Sidanius, 2010; Navarrete, Olsson, Ho, Mendes, Thomsen, & Sidanius, 2009; Sell, Tooby, & Cosmides, 2009). Threats to health are cued by features linked to pathogens (e.g., skin lesions, coughing spasms) and relevant behavioral and physical abnormalities (e.g., nonfunctioning limbs, facial scars, extreme thinness or obesity; Kurzban & Leary, 2001; Oaten, Stevenson, & Case, 2011; Park, Faulkner, & Schaller, 2003; Schaller, Park, & Faulkner, 2003; Tybur, Lieberman, Kurzban, & DeScioli, 2013), and by features that increase contact with pathogens (e.g., lack of normative hygiene and food preparation practices). Threats to group integrity are cued by features suggesting, for instance, an unwillingness to contribute to collective group action (e.g., facial morphologies suggestive of untrustworthiness or membership in another coalition; Yamagishi, Tanida, Mashima, Shimoma, & Kanazawa, 2003; Zebrowitz, Voinescu, & Collins, 1996) or an inability to do so (e.g., physical features and behaviors implying physical or mental disability). In short, different threats are implied by different cues.

THREAT PERCEPTION AND STEREOTYPES: IT'S BEST TO BE ACCURATE BUT, IF NOT, BETTER SAFE THAN SORRY

If social perception is designed to manage threats and opportunities, then the perceived association between cues and affordances will reflect, to a nontrivial degree, actual associations. Indeed, many stereotypes are meaningfully accurate (Jussim, Cain, Crawford, Harber, & Cohen, 2009; Swim, 1994). Of course, stereotypes are not perfectly diagnostic but rather are statistically associated such that perceivers can make more predictive inferences by using stereotypes (even when this also harms stereotyped individuals). For example, to hold the stereotype that young men are competitive implies that maleness and youth are statistically correlated with competitiveness. Although there has been much research on the content of stereotypes, only recently has an evolutionary approach been used to better make sense of this content (Neuberg & Sng, 2013).

Consider, for example, sex and age stereotypes as traditionally represented by the social psychological literature. People are seen as stereotyping men (and young people) as competitive and agentic, and women (and elderly people) as communal and caring (e.g., Eagly & Steffen, 1984; Hummert, Garstka, Shaner, & Strahm, 1995). Moreover, these sex and age stereotypes are conceptualized as independent of one another. Recent research suggests, however, that people's actual stereotypes are much more nuanced than this.

As predicted from a life history perspective (Kaplan & Gangestad, 2005; Stearns, 1976), the means by which males and females accomplish their major life tasks (e.g., growth, learning, mating, parenting) differ as they age. For example, because of differential parental investment (Trivers, 1972), the sex difference in competitiveness is greater in those years in which mating (relative to parenting) is prioritized. Second, competition tends to be *intrasexual*—it is directed toward (relatively young) adults of one's own sex. If the task of the social perceiver is to manage the threats and opportunities posed by others, stereotypes should be attuned to these nuances—to the ways in which sex and age interact to drive strategic behaviors, and to the fact that others' strategic behaviors tend to be focused on some targets and not others.

And they are (Sng, Williams, & Neuberg, 2015). Instead of possessing independent sex and age stereotypes, people actually possess interactive "SexAge" stereotypes of the specific forms predicted. Moreover, instead of possessing stereotypes in the form of general traits (e.g., "men are competitive"), people possess *directed stereotypes*—stereotypes that account for whom stereotyped behavior is directed towards (e.g., "men are competitive towards young men"). Stereotypes are not only more complex than suggested by the traditional literature, but sometimes contradict these previous theories. For example, rather than holding the stereotype that women are less competitive than men, people actually believe—accurately—that women are *more* competitive towards young women than are young men.

Because social perception relies on imperfect cues, errors are inevitable. Although all errors are potentially costly, some are more costly than others. Social perceivers are biased toward reducing inference errors most costly to reproductive fitness (Haselton & Buss, 2000; Haselton & Nettle, 2006), as illustrated by analogy to a smoke detector (Nesse, 2005). Just as smoke detectors are biased to err on the side of false positives, so too are evolved threat-detection systems designed to err on the side of assuming threats when there are none, rather than missing (potentially fatal) threats. For prejudice, this means people will be biased to overperceive the threats that others pose.

Many people and groups who actually pose no risk may thus be perceived as threatening. For instance, because pathogens often altered body shape and movements, people who are extremely overweight, have limited control over limbs, or are otherwise physically atypical may be (unconsciously) perceived as pathogen risks—even when no actual risk is present. Similarly, because individuals were, ancestrally, indifferent to the welfare of members of other groups, people who bear marks of "outgroupness"—for example, unusual accents or the practice of different rituals—may be perceived as untrustworthy, even if these individuals are actually highly invested in the groups they're entering. "Better safe than sorry" is the operating principle of the contemporary human mind as it perceives such individuals and groups and enacts prejudices against them (Schaller & Neuberg, 2012).

DIFFERENT PERCEIVED THREATS, DIFFERENT PREJUDICES, DIFFERENT BEHAVIORS

Behaviors that mitigate some threats may do little to mitigate others. Whereas a physical confrontation might help get money back from a cheat, it's unlikely to prevent pathogen transmission from a disease-carrying individual. There are good reasons to expect that different behavioral routines evolved to address different perceived threats.

Emotions play a critical role in driving functional, threat-relevant behaviors. Fear, disgust, and anger serve as alarms that interrupt ongoing activities, focus attention, and activate behaviors to address threats. For example, when we perceive a large object moving rapidly towards us, we feel fear and become aware of danger while physiological systems generate a burst of energy and send blood to the large muscles. This syndrome of responses prepares us to flee or fight, thereby mitigating threats of predation. In contrast, smelling dead flesh leads us to feel disgust, constrict our nasal passages, turn away, and create physical distance—all of which, in combination, reduces our exposure to contagious disease. In sum, different threats elicit different emotional alarms and accompanying functional syndromes of cognitions, physiological responses, and behavioral routines (Izard, 1991; Plutchik, 1980; Roseman, Wiest, & Swartz, 1994; Tooby & Cosmides, 1990).

One would predict that responses to different categories of people will also often be very different (Cottrell & Neuberg, 2005). For example, because many Americans perceive Muslim fundamentalists as threatening physical safety, they show fear and mistrust in encounters with them. Because facial disfigurements are (unconscious) cues for disease, people respond with disgust, implicitly activate disease concepts in memory, and avoid physical contact. Because reciprocity creates a vulnerability to cheating, people show anger toward those seen as taking more than their fair share (e.g., welfare recipients), stereotype them as lazy or selfish, and implement policies such as reducing welfare programs and taxation. Because shared values facilitate coordination and socialization into group norms, deviation from these values elicits contempt, disgust, anger, accusations of immorality, and discriminatory actions to exclude and disempower these individuals. Indeed, research shows links between perceived threats, emotional responses, and functionally related discriminatory behaviors (e.g., Cottrell & Neuberg, 2005; Cottrell, Richards, & Neuberg, 2015; Cottrell, Richards, & Nichols, 2010).

Traditional theoretical approaches to prejudice (e.g., ingroup–outgroup, social identity and other self-esteem-based theories) are unable to explain why there exist qualitatively different prejudices toward different groups. From these perspectives, prejudice has been viewed and operationalized as a general undifferentiated attitude towards groups and their members—as simple valence: We like or dislike others, view them favorably or unfavorably, and so on, and prejudice is assessed using "thermometer" measures of how "warm" or "cold" participants feel toward different groups, aggregated responses to "favorable" versus "unfavorable" statements about groups, and implicit associations between groups and "good" or "bad" stimuli. Yet when measures of specific emotions are assessed, rather than only valence, people show textured feelings and beliefs about groups that can look quite different for different target groups—even for groups that elicit similar reactions on traditional valence measures (e.g., Brewer & Alexander, 2002; Cottrell & Neuberg, 2005; Esses, Haddock, & Zanna, 1993; Fiske, Cuddy, Glick, & Xu, 2002; Mackie, Devos, & Smith, 2000). Such findings, and the fact that these different emotion profiles are predicted by the different threats people perceive these groups as posing, challenge in fundamental ways traditional theoretical explanations of stigma, prejudice, stereotypes, and discrimination.

Prejudice Syndromes in Context: Functional Flexibility

Evolved threat-management systems can increase reproductive fitness but can also be costly to deploy. Discriminatory behavior is metabolically costly, distracts one from potential opportunities related to other goals, and can result in lost opportunities for future cooperation with targeted individuals. Moreover, discrimination against people can lead to confrontations that cause injury and damage to reputations, relationships, and coalitions. To minimize these costs, threat-management systems are expected to be engaged primarily when the expected benefits outweigh the damage they might cause.

This benefit–cost ratio will be more favorable when perceived vulnerability is high due to features of the environment and the individual's dispositional concerns. Threat-management systems should be sensitive to cues—external or internal—of apparent threat, and engage strenuously in threat mitigation when vulnerability appears to be great but not when vulnerability appears to be low. There is now much evidence for this form of functional flexibility.

Consider, for example, self-protective concerns. Given the costs of hypervigilance, preparation for flight or fight, and fearfully avoiding others, self-protective mechanisms are likely to be engaged only when cues suggest higher-than-usual risk of danger. Indeed, experiments show that activating perceptions of danger alters a wide range of cognitive and affective processes in ways that bias perceivers towards not missing potential threats (Neuberg & Schaller, 2014). For example, increasing people's felt vulnerability to violence increases perceptions of anger in neutrally expressive faces of young outgroup men and increases the likelihood that people identify ambiguously categorizable persons as outgroup members (Maner et al., 2005; Miller, Maner, & Becker, 2010). Moreover, just as being in a darkened room (a cue for humans of vulnerability to physical attack) increases the intensity of the startle response to a blast of noise (Grillon, Pellowski, Merikangas, & Davis, 1997), being in a darkened room increases for North American Whites and Asians the activation of stereotypic links between Black or Iraqi persons and danger concepts such as "hostile" or "criminal" (Schaller, Park, & Faulkner, 2003; Schaller, Park, & Mueller, 2003). It's instructive that this effect holds primarily for those who dispositionally view the world as a dangerous place—who especially view themselves as vulnerable to violence. Moreover, the activation of these threat-linked concepts is specific to outgroup targets (and not to ingroup targets), and to physical-threat stereotypes (and not to other equally negative, but nonthreat, stereotypes, such as lazy and ignorant). These nuances reveal the functionally focused nature of the system.

Similar functional flexibility is apparent in people's responses to cues for contagious disease: For people who feel especially vulnerable to infectious disease, or when people are in circumstances that make salient the presence of pathogens, disease-avoidance prejudice syndromes are prone to activation. For instance, when disease concerns are salient, people focus greater attention to blemished or disfigured faces (Ackerman, Becker, Mortensen, Sasaki, Neuberg, & Kenrick, 2009; Miller & Maner, 2012). Concerns with disease, whether dispositional or situational, also increase negativity toward individuals with cues of disease such as people with asymmetrical faces (Little, DeBruine, & Jones, 2011; Young, Sacco, & Hugenberg, 2011), who are significantly overweight (Kenrick, Shapiro, & Neuberg, 2013; Park, Schaller, & Crandall, 2007), or who belong to unfamiliar outgroups (Faulkner, Schaller, Park, & Duncan, 2004; Navarrete, Fessler, & Eng, 2007; see Schaller & Neuberg, 2012, for a review).

Although less research is available, there is also evidence for functional flexibility in the application of prejudice syndromes within other threat-management systems as well. For instance, when concerns about resource scarcity become salient, people categorize others to exclude more ambiguous-looking individuals (i.e., apparently biracial persons) from their ingroups (Rodeheffer, Hill, & Lord, 2012), and when concerns about economic competition are made salient, prejudices are heightened especially against groups stereotypically viewed as strong economic competitors (Butz & Yogeeswaran, 2011). Moreover, prejudices against groups seen as threatening group values may be particularly pronounced when concerns about socialization practices are salient, as when prejudices against gay men are particularly strong when heterosexuals think about them within the context of socialization domains (e.g., elementary schools, religious institutions; Saad, 1996).

We see, then, that the engagement of threat-management systems and their functional prejudice syndromes are directed specifically toward targets who exhibit cues for specific threats and especially under circumstances in which people perceive their own vulnerability to the threat in question.

INTERIM SUMMARY

The findings briefly reviewed pose a great challenge to traditional theories of prejudice and stereotyping. Those approaches lack the conceptual architecture to *a priori* account for the nuanced psychology people actually possess: that people apply different stereotypes, prejudices, and discriminatory inclinations toward different groups, based on the specific threats these groups are seen to pose; that these sets of responses are enhanced when people feel themselves to be vulnerable to the particular threats; and that people's responses to apparently quite distinct groups (gay men, obese persons) are nonetheless similar because they are at least partially generated by the same threat-management systems. In contrast, the approach we highlight here impressively predicts these findings.

We have focused on the evolved psychology through which individuals attempt to manage threats posed by other individuals. Some of these threats are inferred from cues that others may belong to out-coalitions—groups of allied individuals working toward common interests, who support one another in disputes against individuals outside their coalition. Indeed, by definition, members of coalitional outgroups will generally be more invested in their own groups than in one's own, and it's thus reasonable for individuals—as individuals—to stereotype members of other coalitions as less trustworthy, more willing to engage them in physical conflict, and so on. We turn now to explore how members of coalitions interact with one another *as coalition members* and, thereby, create the potential for group-on-group conflict.

ALLIANCE-BASED PREJUDICES AND CONFLICT

For animals that live in groups, there are plenty of opportunities to bang heads with other group members, given limited resources to go around. Hence, social animals use fighting strategies to compete for the group's resources. At the same time, conflict is costly. Fighting risks physical injury and damaging valuable cooperative relationships. Animals thus require strategies that increase access to resources while reducing both the likelihood of injury and damage to cooperative relationships.

There is a large theoretical and empirical literature in evolutionary biology about animal fighting (Arnott & Elwood, 2009; Dawkins, 1976; Maynard Smith, 1982; Parker, 1974). Much of this work centers on the Hawk-Dove game, in which two players choose to either fight (hawk) or flee (dove). Each player receives their highest payoff if they fight and their opponent flees, but the most costly outcome occurs if both fight. This research points to a few broad conclusions. First, evolution favors a judicious mixture of fighting and fleeing rather than all-out aggression or all-out acquiescence. Second, when there are asymmetries in fighting ability, more formidable disputants will fight and weaker disputants will flee (all else equal). Third, animals also use other asymmetries, independent of fighting ability, to decide conflicts, such as which player first discovered or possessed the resource.

Fighting is a *coordination game* (Schelling, 1960). Although fighters disagree about who should acquire the resource, they also typically share an interest in avoiding the costs of fighting. This implies that fighters will attend to information or signals that might help coordinate their fighting decisions to prevent deadlock and escalation. This includes cues of relative formidability, precedents set by previous fights, and communicative displays of submission and dominance.

In many social animals, the result of these individual strategies is the creation of linear dominance hierarchies (Boehm, 1999; Krebs & Davies, 1993). Individuals learn which group members they can defeat and attribute to them lower status, and which members they cannot defeat and attribute to them higher status. Higher-status individuals can then win disputes merely by displaying dominance, whereas lower-status individuals can avoid the escalation of conflict and further loss of resources by displaying submissiveness. These communicative strategies persist because they reduce conflict costs for both senders and recipients. Low-status individuals are considerably disadvantaged by this coordination scheme, as they are forced to forgo many of the potential benefits of living in the group. We should expect evolution to favor adaptations designed to help individuals avoid this predicament. A small number of social animals, including humans, have evolved a novel adaptation to the problem of being dominated by more powerful individuals—forming alliances.

THE EVOLUTION OF GROUP-BASED DOMINANCE HIERARCHIES

The original adaptive problem that coalitions are designed to solve is being dominated by a more powerful individual. By teaming up, a few weaker individuals can gain the upper hand against a single more powerful one. The same logic of asymmetric fights applies to the combined power of the coalition, in which sole individuals stand to gain by backing down when they are outmatched by a team.

When one coalition is formed within a group, this creates a new adaptive problem—being dominated by a powerful coalition. The solution to this quandary is to form a coalition in response. In this way, coalitions beget more coalitions until all members are split into teams (Snyder, 1984). Further, small coalitions can increase their power by merging with other small coalitions, which occurs until the group consists of a small number of massive nested coalitions. Individuals can seek cross-cutting alliances with members of other coalitions to bolster their power within their original coalition, creating a complex interlaced network of alliances. Due to this complexity, coalitions are better conceptualized not as fixed and cohesive groups, but instead as arising from interlaced networks of ranked loyalties (DeScioli & Kurzban, 2009, 2011, 2013; DeScioli, Kurzban, Koch, & Liben-Nowell, 2011).

Once coalitions are formed, they have the same problem as individual fighters—avoiding costly fights—and they can apply similar tactics including fighting assessment, fighting displays, dominance and submission signals, and the use of arbitrary asymmetries or conventions. The result is a group-based dominance hierarchy, analogous to individual dominance hierarchies. The existence of group-based dominance hierarchies sets the stage for certain forms of intergroup prejudices and discrimination.

SOCIAL DOMINANCE THEORY AND COALITIONAL PREJUDICE

Social dominance theory holds that the evolution of group-based dominance hierarchies explains coalition-based forms of prejudice, discrimination, and oppression (Pratto, Sidanius, & Levin, 2006; Sidanius & Pratto, 1999). From this perspective, coalitions broadcast their memberships, group boundaries, and power advantages over other groups through individual acts of prejudice, institutional discrimination, and legitimizing myths (Pratto et al., 2006). As in individual disputes, both higher-status and lower-status groups gain by using dominance and submission signals because these signals help individuals avoid the costs of violent confrontations (Sidanius & Pratto, 1993). Due to this dominance scheme, individuals in lower-status groups receive a smaller share of the available resources. Moreover, oppression by higher-status groups can become extreme, such as the historically widespread practice of slavery.

From this perspective, then, certain prejudices begin with evolved cognitive adaptations for coalition formation. In supporting an ally, one is exhibiting prejudice and discrimination in favor of one's ally against their opponent. Even supporting family or friends in an argument against strangers is prejudiced, in this sense.

Social dominance theory focuses on three types of group-based hierarchy based on age, sex, and arbitrary sets (Pratto et al., 2006). In the age system, adults as coalitions have disproportionate power compared to children. In the gender system, men allied in coalition have disproportionate power relative to women. In the arbitrary-set system, people construct rival coalitions on arbitrary distinctions such as race, nationality, political ideologies, or religion.

Social dominance theorists argue that, historically, the most damaging prejudices and acts of discrimination have been those used by these arbitrary groups of men to dominate other men (Pratto et al., 2006). They further argue that this gender difference is explained by parental investment theory, which implies high stakes for human male–male competition leading males to fight more intensely than females (McDonald, Navarrete, & Sidanius, 2011; McDonald, Navarrete, & van Vugt, 2012; Pratto et al., 2006). Particularly important in this account are the *legitimizing myths*—which include unflattering stereotypes about lower-status groups—used to stabilize otherwise arbitrary coalitional alignments to enable dominant groups to oppress weaker groups.

The idea of prejudice based on arbitrary sets fits well with game theoretic models showing indeterminacy and instability in coalition formation (Von Neumann & Morgenstern, 1944). In these models, individuals aim to form teams to gain advantages over other teams, but these motives can lead to many possible partitions of the group. Even after coalitions are formed, individuals often have incentives to switch to a new coalition and these switches can, in some cases, occur indefinitely. Humans appear to be attuned to this game of theoretic logic with psychological mechanisms for tracking coalition membership by adaptively and flexibly alternating among a variety of cues including race, accent, and even tags as arbitrary as shirt color (Kinzler, Shutts, DeJesus, & Spelke, 2009; Kurzban, Tooby, & Cosmides, 2001; Pietraszewski, Cosmides, & Tooby, 2014).

COMMON COALITION-BASED PREJUDICES

Although coalitions tend to be unstable and shifting, certain special interests among individuals make it more likely that specific kinds of coalitions will form and be relatively stable. Perhaps the most biologically important source of shared interests is family relationships. Kin deeply share fitness interests (Hamilton, 1964), and kin selection favors adaptations for helping kin in conflicts with nonkin. These psychological mechanisms can be viewed as an evolved prejudice—nepotism—for supporting kin against nonkin, and are observed both in humans and nonhuman animals (e.g., Cheney & Seyfarth, 2007; Silk, 2002).

Racial prejudices might be extensions of an evolved kin-based coalitional prejudice. People might perceive racial and ethnic differences as cues indicating low genetic relatedness. Because our ancestors were unlikely to encounter "racially" different individuals within the range of their life experiences, there was little opportunity for race-focused prejudice, per se, to be selected for (Kurzban et al., 2001). There likely did often exist, however, observable differences between competing coalitions—cued by different physical appearances, language or accents, and cultural artifacts and practices—that would enable individuals to evolve a coalitional psychology sensitive to features implying difference. The features denoting "race" may thus serve as super-cues of difference, and be used heuristically by a kin-based coalitional psychology to generate so-called racial prejudices and acts of discrimination).

Age and sex are also potential sources of special interest groups. Life history strategies (Kaplan & Gangestad, 2005) and parent-offspring conflict (Trivers, 1974) can give rise to systematically different evolved preferences for individuals of different ages. For example, children often try to extract more resources than parents want to provide. Parents can potentially work together to suppress their children's extraction efforts, exhibiting a self-serving ageism. For example, the consensus among adults that children should obey their parents can be understood as a strategy for limiting children's demands for resources. For sex, parental investment theory and sexual selection (Trivers, 1972) imply that men and women will have a variety of different preferences. Each sex can potentially ally and conspire to advance its own interests at the expense of the opposite sex, showing self-serving sexism. For example, men and women might disagree about sexual activity outside of long-term relationships, such as prostitution and pornography, due to differences in mating strategies.

Simple ingroup–outgroup coalitional views of race, sex, and age prejudices are likely insufficient, however. Research reveals that coalition-based prejudices are most frequently directed by and toward young men (relative to other sex/age categories). Moreover, the particular stereotypes ascribed to intersectional categories—Sex × Age × Race—are closely linked to the specific threats and opportunities associated with them (Neuberg & Sng, 2013; Sng, Williams, & Neuberg, 2015). An integrative approach that combines both threat-management and coalition dynamics will be especially informative.

Other special interest groups might include those ostensibly based on values—on broad orientations regarding the goals people ought to have and how they ought to behave. Although values themselves appear to be abstract, they often serve as bases for creating or maintaining particular rules, laws, and societal policies that place real, tangible constraints on other people's behaviors—constraints they often wish to avoid. Political parties, for instance, are coalitions that compete over how resources within a society are allocated, the manner in which rule violators should be controlled, and so on. Religious groups, as a second example, are coalitions that compete over similar concerns but also tend to seek to control the sexual strategies pursued by group members (Weeden & Kurzban, 2013). It should not be surprising that activist religious groups often exhibit strong prejudices against one another and engage in extreme forms of conflict (Neuberg et al., 2014).

PREJUDICE AGAINST FOREIGNERS: WARFARE, IMMIGRATION, AND EMIGRATION

Foreigners are individuals who have had little or no contact with the focal group. Contact with peoples from different environments can expose individuals to pathogens for which local immune systems are ill-equipped. Indeed, the history of migration shows the virulence of pathogens when entering new populations (Diamond, 1997; Dobson & Carter, 1996; Ewald, 1994). Moreover, foreigners will often be unfamiliar with local hygiene practices, placing residents at risk. Studies show that desires for distance from foreigners and preferences for ingroups are most pronounced in those who feel most vulnerable to disease (Faulkner et al., 2004; Navarrete et al., 2007).

The coalitional reasoning discussed above also applies to prejudices toward foreigners. Whereas ingroup relationships require a balance of cooperation and conflict, there is, by definition, little cooperation with true foreigners who are likely to be seen mainly as competitors. Throughout evolutionary history, interactions with foreigners were conflictual. For most nonhuman primates, intergroup encounters are violent (e.g., Southwick, Siddiqi, Farooqui, & Pal, 1974; Wilson & Wrangham, 2003), and ethnographic studies of human hunter-gatherers similarly show violence between groups (e.g., Chagnon, 1992; Eibl-Eibesfeldt, 1974; Ferguson, 1984; Haas, 1990; Kelly, 1995; Robarchek, 1990). Because males were ancestrally more likely to encounter outgroup individuals (e.g., Goodall, 1986; Hasegawa, 1990), males are expected to exhibit greater group-on-group violence (Carpenter, 1974; Chagnon, 1988; Cheney, 1986; Wilson & Wrangham, 2003). In line with this idea, men perceive intergroup situations as more threatening (Pemberton, Insko, & Schopler, 1996) and hold stronger intergroup prejudices (e.g., Sidanius, Cling, & Pratto, 1991). Moreover, people are especially slow to extinguish learned fearful reactions to outgroup men (Navarrete et al., 2009). In all, there exist strong prejudices against members of outgroup coalitions that are especially held by, and directed towards, men.

This helps explain why immigrants often elicit strong antipathies and sometimes violence from local populations. They are seen as posing *multiple* threats—to health, resources, physical safety, and values. Importantly, however, not all immigrants are viewed with equal hostility. Those who are *subjectively* foreign—displaying cues for unfamiliarity—receive greater antipathy (Schaller & Abeysinghe, 2006). In contrast, immigrants who look physically familiar, speak the local language, and act according to local customs are viewed as less threatening. Moreover, in line with the flexibility of threat-management systems, we expect those who arrive during times of relative prosperity will encounter less vulnerable residents and receive less hostility as a result.

This perspective also suggests why immigrant groups elicit less antipathy in subsequent generations. The offspring of immigrants learn the local language, adopt local cultural practices, and live according to local values, and so no longer exhibit these cues for threats. The Irish arriving in the United States in the 1840s were viewed as violent, disease-ridden, resource-grabbing, and allegiant to the Catholic pope, and were stigmatized greatly for it. Today, nearly 200 years later, to be Irish is rarely seen as threatening—and Americans across the ethnic spectrum celebrate St. Patrick's Day.

Of course, foreign groups are often able to get along, at least temporarily. Within societies, alliances form so individuals can more effectively pursue common interests, and this happens at the level of foreign coalitions as well. Moreover, there may be circumstances in which individuals actually become "xenophilic"—in which they prefer outgroup to ingroup members. For instance, in some social species, including humans, females have historically left their home groups to find mates from other groups. The evolutionary logic of female exogamy pertains to incest avoidance, and may help explain why female strangers are stigmatized less than male strangers, and why females are more open to foreigners than are males. Favorable ties might also develop between foreign groups based on trade for rare goods, access to territory, and other mutually beneficial opportunities. That said, the basic evolved inclination is for people to be quite wary of foreigners in their own midst.

REDUCING AND CONFRONTING PREJUDICES

To suggest that contemporary prejudices are rooted in an evolved psychology is not to suggest that they are unchangeable. To the contrary. As we've seen, threat-management systems operate in functionally flexible ways, and certain prejudices emerge under some specifiable circumstances and do not emerge under others. Many people in many cultures strongly condemn and oppose prejudice and this anti-prejudice behavior likely also has a basis in human evolved psychology. Evolutionary approaches can inform efforts to reduce harmful prejudices.

The main principle emerging from a threat-management approach is that by reducing vulnerability to particular threats, one can reduce the related prejudices.

For example, by changing the geographical frame of reference used by Sinhalese Sri Lankans to estimate their numbers—shifting the perception of being outnumbered by the Tamil to outnumbering them instead—Schaller and Abeysinghe (2006) reduced their prejudices (at least temporarily) and made them more favorable toward peaceful resolutions. Similarly, by providing disease-concerned individuals with hand wipes or flu shots, Huang and colleagues reduced (at least temporarily) their prejudices against immigrants, obese people, and people with physical disabilities (Huang, Sedlovskaya, Ackerman, & Bargh, 2011).

A second critical principle is that different interventions will be required to combat different prejudices. In Huang et al. (2011), reported above, infection-reducing interventions did not reduce all prejudices, but rather prejudices related to contagious disease, and only for individuals who felt most vulnerable to infectious disease. The threat-based approach helps explain why certain interventions succeed and others do not (see Schaller & Neuberg, 2012, for a more comprehensive discussion).

A third idea motivated by an evolutionary approach is that people likely possess adaptations designed to counter the prejudices they confront. That is, just as the capacity for prejudice is a human universal, so is the psychological ability to oppose prejudice. Humans not only oppress and enslave members of rival groups, but some members of dominant groups work to empower and liberate lower-status groups. For example, with the Slavery Abolition Act of 1833, members of a dominant group emancipated oppressed groups throughout the British Empire. A psychological theory of prejudice should account for both the motive to discriminate as well as the motive to oppose discrimination.

One possible explanation derives from the fundamental instability of coalitions. To strengthen their position inside a coalition, individuals can create cross-cutting alliances with individuals outside of their coalition. Coalition members are not immune to infighting and cross-cutting alliances can provide an advantage for disputes within the coalition. Humans might have cognitive adaptations for identifying potential cross-cutting allies, and this could help to explain people's efforts to promote the welfare of individuals in oppressed groups.

Another possibility is that humans have anti-prejudice adaptations designed to diffuse escalating alliance-building. When each individual pursues a prejudiced side-taking strategy, this expands the number of coalitions and subsequent alliance-based obligations, which can lead to expanding and explosive disputes. If, instead, bystanders to others' disputes coordinate on an impartial side-taking strategy, these disputes can be contained. Indeed, moral cognition appears well designed to perform exactly this function (DeScioli & Kurzban, 2013). Moral cognition computes the wrongness of people's actions, providing a basis for side-taking that is independent of their identities, including coalition membership. Moral side-taking involves computing wrongness magnitudes for the actions taken by both sides of a dispute, and siding against the individual who performed the action with the greatest wrongness magnitude. Importantly, moral side-taking strategies do not displace prejudiced side-taking, but rather add to the repertoire of human strategies for choosing sides. An individual's choice of strategy will depend on computations of the costs and benefits of each approach. When these values differ across individuals, they will pursue different strategies, potentially explaining individual and cultural variation in prejudice and anti-prejudice behavior.

CONCLUSION

The harms of malicious prejudices have plagued human societies throughout history and continue to do so today. From an evolutionary perspective, several prominent approaches to understanding prejudice have key limitations. These accounts posit particular psychological needs or tendencies underlying prejudice, such as group categorization, social identities, self-esteem, authoritarian values, the fear of death, or justification of group standing (e.g., Adorno, Frenkel-Brunswik, Levinson, & Sanford, 1950; Fein & Spencer, 1997; Jost & Banaji, 1994; Schimel et al., 1999; Tajfel, 1969; Tajfel & Turner, 1986). These accounts inevitably lead to questions about *why* humans have these psychological traits and why they cause these particular behaviors. Moreover, the evidence reviewed in this chapter shows levels of flexibility and complexity in human prejudices, stereotypes, and forms of discrimination that go far beyond what can be predicted by traditional theories.

The evolutionary approach suggests, instead, that the psychological systems underlying prejudices are highly sophisticated computational systems designed to track ancestrally relevant threats (e.g., violence, disease) and opportunities (e.g., cooperation, alliances), and to deploy prejudice—and anti-prejudice—behaviors to manage these threats and opportunities and thereby improve individual fitness. This approach generates nuanced hypotheses, supported by empirical research, well outside the reach of traditional theories.

Critically, the hypothesis that prejudices are designed to benefit the individual does not, in any way, diminish the harms that prejudices cause victims and societies. It is crucial to emphasize, especially for lay audiences, the importance of avoiding the naturalistic fallacy that evolved traits are benign, to be encouraged, or somehow less condemnable. Evolution's products include any number of unseemly and cost-inflicting adaptations, from the viper's poison-injecting fangs to the moose's impaling antlers to human jealousy and homicidal motives (Buss, 2006). The possibility that prejudices are evolved adaptations, if anything, should heighten our concern about these damaging behaviors because they reflect not merely naïve, unschooled biases but instead the operation of evolved, flexible, selfish, and largely unconscious strategies. To outwit such an imposing foe requires theories that are prepared for evolution's most clever and Machiavellian designs.

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CHAPTER 29

Leadership in War: Evolution, Cognition, and the Military Intelligence Hypothesis

DOMINIC D. P. JOHNSON

> It was not the legions which crossed the Rubicon, but Caesar.
>
> —Napoleon Bonaparte

INTRODUCTION

In 401 B.C., Cyrus the Younger launched an expedition into Persia against his rival and brother, Artaxerxes II. At the battle of Cunaxa, Cyrus was killed, and in the ensuing peace negotiations, his second in command, along with all the other generals and many lower-level commanders, were tricked and murdered. Famously, the remaining army of Greek soldiers—"the Ten Thousand"—was left stranded in the middle of hostile territory, hundreds of miles from home, and, most notably, leaderless. Their remarkable march to freedom, fighting as they went, was recounted for history by a soldier named Xenophon (4th century B.C./1989). According to legend, the key to their success was the leadership that emerged organically out of a desperate situation. Leaders, including Xenophon, were "elected" by the troops, and many decisions were made democratically. Against all the odds, the Ten Thousand made it home after a year of long-distance travel and war.

Leadership is a subject that has fascinated people for millennia (Hogan & Kaiser, 2005; King, Johnson, & van Vugt, 2009; Tecza & Johnson, in press; van Vugt, 2006). This should be no surprise, considering that we are one of the great apes—and social mammals more generally—all of which are characterized by strong dominance hierarchies (Mazur, 2005; van Vugt & Tybur, Chapter 32, this volume). When examining leadership in our own societies, we often look to leaders of the past for inspiration. Xenophon's story is remarkable because it bucks the trend of top-down hierarchical leadership that is so familiar to us from contemporary and historical societies, especially in military contexts. Indeed, it hints that democratic leadership was a critical ingredient of their survival against the odds. Most striking of all, perhaps, the idea of the "marching republic" is appealing because small-scale hunter-gatherer societies, like those in which modern humans evolved during the Pleistocene epoch, were also supposedly egalitarian and did not have dominant leaders. But they did have lethal intergroup conflict.[1] Xenophon may therefore symbolize important aspects of the origins of human leadership in war.

THE NATURAL HISTORY OF LEADERSHIP IN WAR

To begin, what is the evolutionary context for leadership and war? What are the broader patterns of coordination and conflict among other animals, among our primate relatives, and among early human societies? And in what respects are human leadership and war unique?

Leadership and War in Nature

Many of our physiological and psychological mechanisms go much further back than the Pleistocene era, and are found in all primates, all mammals, and many other vertebrates. These fundamental phenomena can have relevance to war and leadership, even if they evolved for other reasons. Examples include our fight-or-flight response, dominance hierarchies, and herding behavior. Such ancient traits undoubtedly *affect* leadership and followership in war, but they are not adaptations *for* war. A different question is whether there are unique leadership and followership traits that *evolved specifically to deal with war*—or at least with intergroup conflict more generally.

Collective movement is evident in a range of species, including lower-order ones such as ants, locusts, fish, birds, and antelope (Couzin, Krause, Franks, & Levin, 2005; King et al., 2009). But there is little evidence that such traits represent leadership in any strict sense (much of it appears to be self-organizing, individual behavior), nor that they are specialized for fighting. Most animals fight, and many fights occur between groups, but these are not really organized or led. Some animals do engage in something approaching war, in terms of synchronous lethal violence against other groups—notably ants, lions, and wolves (Wrangham, 1999a). Such conflicts, specifically, can be initiated by certain individuals with the most at stake. Others follow. For example, in group-on-group encounters, female lions with cubs—those with the most to lose—tend to lead approaches towards intruders (McComb, Packer, & Pusey, 1994). But while both leadership and war have precedents in the animal kingdom, they are rudimentary, and the combination—*war leadership*—seems absent.

Leadership and War in Primates

One of the most prominent characteristics of all primate groups is a strong social hierarchy, and these show signs of nascent leadership—even or especially in conflict.

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[1] For the purposes of this chapter, I roughly follow the definition of *war* as "organized, deadly violence by members of one group against members of another" (Ferguson, 2012, p. 2232), and *leadership* as "a process of social influence to attain shared goals" (van Vugt & Ahuja, 2011, p. 24), with some reservations about war being "organized" and goals being "shared."

For example, male chimpanzees may form coalitions to oust the alpha male, while alpha males themselves tend to side with the weak when fights break out, which preserves the status quo (de Waal, 1998). However, these are within-group contexts. Is there any evidence of leadership in between-group conflict? Many primates have noisy and vigorous intergroup fights, but they are not usually led or lethal (Manson & Wrangham, 1991). Chimpanzees are unique among primates for deadly intergroup conflict, in which small parties carry out raids on members of neighboring groups (Wilson et al., 2014; Wrangham, 1999a). Although these attacks appear to be deliberate (moving stealthily into bordering territory), it is not clear from the limited data which individuals, if any, "lead" or initiate lethal raids. There is some indication that higher-ranking males and/or those with more at stake (in status or offspring) are more likely to initiate approaches to intruders, territorial border patrols, and raids (Boehm, 2001, pp. 27–29; Gilby, Wilson, & Pusey, 2013; Wilson, Hauser, & Wrangham, 2001). Still, even if this is confirmed, it does not differ from other contexts, where high-ranking individuals may make the first move in foraging or hunting, but cannot compel others to follow. While dominance hierarchies and intergroup aggression clearly have deep roots among our mammalian ancestors, if we want to examine *leadership in war* we have to turn to humans themselves.

LEADERSHIP AND WAR IN SMALL-SCALE HUMAN SOCIETIES

The nonhuman animal examples are interesting because they suggest (a) you do not need leadership for collective action and (b) lethal intergroup aggression is not unique to humans. However, while commonalities are important, the animal analogues also highlight what is *different* about human leadership—especially in war (Table 29.1). Two overarching attributes in particular set us apart. First, human leadership is unique because of sophisticated *cognition*: For example, theory of mind, language, forward planning, and strategizing can be brought to bear by both leaders and followers. Second, human leadership is unique because of sophisticated *social organization*: For example, large groups, divisions of labor, chains of command, and intergroup alliances all broaden the scope of leadership and followership. Both sets of characteristics enable and extend the practice of war as well as increasing the necessity and utility of leadership. Indeed, Ferguson finds that "war by tribal peoples displays a gradient of more sophisticated organization and practice linked to increasing social complexity and political hierarchy" (Ferguson, 2012, p. 2232). Leadership—both individual and structural—is therefore heavily implicated in the evolution of war, even if it came late in the game in human evolution more generally.

War Leadership in Subsistence Economies Let's look first at the context of leadership in general. Our best model for human evolution during the Pleistocene epoch is represented by hunter-gatherer societies—seminomadic kinship bands of a few dozen people. A considerable literature concurs that they are remarkably egalitarian, with equal rights, little or no private property, and no clear leaders (Boehm, 2001; Lee & Daly, 2004). Although there is variation, hunter-gatherers are at least much *more* egalitarian than our primate forebears or the larger chiefdoms, kingdoms, and civilizations that came later. Among the common traits of small-scale hunter-gatherers are that "Leadership is less formal and more subject to constraints of popular opinion than in village societies governed by headmen and chiefs. Leadership in band societies tends to be by example,

Table 29.1
Key Similarities and Differences in War Leadership Across Contexts

	Animals	Primates	Small-Scale Societies	Chiefdoms	History	Today
Dedicated war leaders	No	No	No	Yes	Yes	Yes
Voluntary participation	Yes	Yes	Yes	Variable	Variable	Variable
Benefits to leaders	Yes	Yes	Yes	Yes	Yes	Variable
Benefits to warriors	Yes	Yes	Yes	Variable	Variable	Variable
Costs for leaders	Yes	Yes	Yes	Variable	Variable	Variable
Costs for warriors	Yes	Yes	Yes	Yes	Yes	Yes
Sexes involved	Both	Mainly males	Males	Males	Males	Mainly males
Size of armies	Few[a]	Tens	Tens to hundreds	Hundreds to thousands	Tens of thousands	Millions
Military institutions	No	No	No	Yes	Yes	Yes

[a] Although ant battles can involve hundreds of individuals.

not by fiat. The leader can persuade but not command" (Lee & Daly, 2004, p. 4). For example, the !Kung of the Kalahari and the Hadza of Tanzania had "either no leaders at all, or temporary leaders whose authority was severely constrained" (Gowdy, 2004, p. 391).

Of course, dominance relationships and power struggles do exist. Indeed, leadership of some form or other may be a human universal (Brown, 1991; van Vugt, 2006). But small-scale societies have social mechanisms for keeping overly domineering individuals in check, and restricting authority to specific domains of expertise (Boehm, 2001). As Tim Ingold put it, "To eliminate distinctions of power . . . is not the same as eliminating power itself. Despite their egalitarianism, hunter-gatherers generally attribute great importance to power and its effects. For them, power is not power *over*, nor are its effects coercive in nature. Rather, power takes the form of the physical strength, skill, or wisdom that draws people into relations clustered around individuals renowned for one or more of these qualities" (Ingold, 2004, p. 404). In the evolutionary psychology literature, this phenomenon has focused attention on the role of status, prestige, and coordination, rather than dominance (Henrich & Gil-White, 2001; Price & van Vugt, 2014; van Vugt & Tybur, Chapter 32, this volume). Ingold has concerns about the concept of "prestige," because it "suggests a competitiveness and ostentation which are wholly foreign to the tenor of hunter-gatherer life," but nevertheless recognizes that it serves to "bring out the point that power works by attraction rather than coercion. Bands do have leaders [or, at least, instances of leadership], but the relationship between leader and follower is based not on domination but on trust" (Ingold, 2004, p. 404).

Such leadership, however informal or weak, may translate into the realm of conflict and war as well. Just as good hunters may be consulted on hunting matters or lead foraging expeditions, so skillful fighters are often consulted on intergroup conflicts or lead raids (Boehm, 2001). Raiding is generally voluntary, and often widely discussed, even though individuals with greater experience or motivation may make the case for offensive action, suggest a strategy, and take the lead. But in hunter-gatherers there are still no real war leaders.

Even among larger tribal societies, Boehm notes that some "have panels of elders who attempt to resolve feuds, but any such resolution is totally voluntary for the parties concerned. There is no centralized coercive power to stop internecine conflict, just as there is no centralized power to make decisions of war and peace" (Boehm, 2001, p. 97). Instead, tribes tend to make decisions by consensus. Ferguson's review of the literature also found that "with some exceptions, tribal warfare relies on consensus and voluntary participation" (Ferguson, 2012, p. 2233). For example, among the Mae Enga of Highland New Guinea, long and inclusive meetings are held to debate whether or not to launch any major attack on a rival group, with everyone permitted to speak. "Big Men" do not interfere, except to summarize and confirm the consensus decision (Meggitt, 1977).

Planning is one thing. Fighting is another. While one can take time and consult others at length in deciding what to do, where, when, how, and so on, "in the thick of combat it is difficult for the entire group to talk over its next move" (Boehm, 2001, p. 97). Of course, this is a familiar problem of combat leadership throughout military history (van Creveld, 1985). Though difficult, leadership in battle is nevertheless attempted in small-scale societies just as it is in modern war. The Meru of Kenya would conduct "carefully planned" raids on cattle, "moving and attacking in specialized formations. The raid organizer was in command, though if courses of action were disputed, men could switch loyalties to other leaders" (Ferguson, 2012, p. 2232). Among the Mae Enga, during battles themselves, experienced "fight leaders" played an important role, switching between leading attacks at the front line and directing the action from the sidelines (Meggitt, 1977, p. 68). When multiple groups ally to fight together, strategies are planned in advance, and a "supreme chieftain" may be assigned to coordinate them in battle (though not always effectively).

Ferguson (2012, p. 2237) notes that because warriors' participation is voluntary and they can vote with their feet, in "the absence of the power to punish for behavior in battle," leaders are constrained in what they can expect and achieve. Others also emphasize the problem of enforcement in coalitionary conflict—which, given the risk of injury or death, represents the mother of all collective action problems (Tooby & Cosmides, 1988). However, punishment or other social consequences may be present even if not obvious or direct. For example, Mathew and Boyd (2011) found that among the Turkana of East Africa, cowardice and desertion in warfare could result in sanctions, physical punishment, or fines by the wider group. Indeed, they argue that without this system of punishment, collective action for war would not be possible. Still, if and when the risks are sufficiently low and the benefits are sufficiently high, punishment may not be necessary for individuals to be motivated to participate (Chagnon, 1988; Johnson & MacKay, 2015; Manson & Wrangham, 1991; Tooby & Cosmides, 1988).

There is a considerable literature on the ethnography of small-scale societies, but while war is a common topic of discussion and analysis, the role of war leadership is much harder to find. Where it does arise, insights are often combined for hunter-gatherers, horticulturalists, and pastoralists (even though the socio-ecological context can be quite different). In lieu of any established literature or theory on war leadership in small-scale societies, below I list a set of common characteristics that tend to recur among reviews of indigenous warfare (e.g., Ferguson, 2012; Gat, 2006; Keeley, 1996; LeBlanc & Register, 2003; Otterbein, 1989; Turney-High, 1949; Wrangham & Peterson, 1996):

- War leaders are not powerful and sometimes not even evident.
- War leaders coexist with others who lead or hold influence in other domains of activity.
- War leaders depend on prestige, status, oratory, and leading by example to win support.
- Participation is voluntary (although there may be strong expectations or social consequences).
- Ambitious warriors often do their own thing and mount their own raids.
- Raids may be led by offended parties, rather than leaders (e.g., to avenge kin or a prior theft).
- War leaders often play an important role in seeding or cementing alliances (through intermarriages, feasts, and negotiations).
- War leaders tend to personally benefit from their activities within and surrounding war (e.g., from booty, land, resources, elimination of rivals, status, and women).

Although this may appear a somewhat ad-hoc collection of features of war leadership in small-scale societies, the common denominators are that (a) war leadership is present but limited, (b) war leaders usually (but not always) participate in fighting, (c) warriors are not easy to control, and (d) war leaders depend on, and benefit from, prestige and status—like Xenophon.

War Leadership in the Transition to Chiefdoms and Beyond While limited in small-scale subsistence societies, war leadership quickly became important and specialized as societies increased in complexity. How leadership and war covary across different types of society can be explored using the Standard Cross-Cultural Sample of 186 indigenous societies around the world (Murdock & White, 1969), which has variables indexing war, political organization, and leadership (Ross, 1983a; Tuden & Marshall, 1972). Key findings are that (a) 53% of societies had no political organization beyond the immediate community (so-called stateless societies), while 29% had a single authoritative leader (Tuden & Marshall, 1972); (b) increasing political complexity and hierarchy (indications of the role of leadership in general) are correlated with social and economic complexity, larger societies, and higher levels of "external" (outgroup) warfare (Ember, 1962; Roes & Raymond, 2003; Ross, 1983b); but (c) external warfare was *not* correlated with the concentration, specialization, or centralization of political power—that is, more war is associated with greater leadership structures, but it did not make for more authoritarian leaders (Ross, 1983a).

While these findings reveal broad patterns across all types of societies, the dynamics of how war leadership changes as human societies develop may be more important. The situation changed considerably as soon as we moved out of small, mostly subsistence groups into larger, hierarchical and ranked chiefdoms. In fact, war and war leadership may have played a direct role in this very transformation. Scholars of early warfare suggest that the transition from egalitarian to hierarchical societies was driven in large part by war leaders gaining prominence and holding on to their power after, or between wars (Ferguson, 2012; LeBlanc & Register, 2003). We saw that among small-scale societies, leadership is expressly limited by domain of activity, and "people cannot extend such situational authority into generalized control over others" (Endicott, 2004, p. 416). However, war leaders may have become a special case because, unlike leaders in other domains, they had an opportunity to make use of their power, resources, loyal warriors, and alliances (as well as, often, physical strength and a record of victories) to consolidate their position and pass on the benefits to kin (Boehm, 2001; Gat, 2006; LeBlanc & Register, 2003). The process may have taken many generations and hinged on additional conditions, such as sendentarism and divisions of labor, but it is war leaders, rather than other types of leaders, that seemed to emerge as kings of the mountain. However important or unimportant war was among Pleistocene hunter-gatherers, therefore, war leaders may have played a disproportionate role in the subsequent development of human social and cultural organization.

While debates persist about the extent of war or leadership in small-scale societies, by the emergence of chiefdoms no one doubts the importance of either. Leadership is not absolute and even in "structural" leadership positions (e.g., inherited ones), power can still be limited. For example, Ferguson concludes that "such leaders have considerable say in war decisions. But most chiefs exercise influence, rather than power" (Ferguson, 2012, p. 2237). Nevertheless, by the time of chiefdoms we were in the era of intensive warfare, dedicated warriors, and strong, sometimes coercive, war leaders—features that would only reach new heights as societies developed into kingdoms, civilizations, and empires. This, of course, sounds familiar in the context of much of subsequent history.

Interestingly, therefore, egalitarianism is an anomaly in the broad history of evolution. Most social mammals, including primates, are despotic. An individual or coalition will dominate all others. Humans shifted away from this ancestral pattern into egalitarianism, but have since fallen back into it. Our evolutionary foray into egalitarianism may have been very important, because if it lasted for most of the Pleistocene epoch, then our cognition, behavior, and social organization may have adapted to it. However, as soon as agriculture was invented, strong hierarchies were back and humans became despotic for all of history (Betzig, 1986; Diamond, 1998). Only in the past few decades have democracy spread and monarchies and dictatorships fallen, although even now this process has not been universally completed or universally successful. Corruption is rampant around the world, including in many Western democracies, and even among the least corrupt, individuals still vie for power and status despite democratic oversight and institutions that resist it (Ludwig, 2002; Robertson, 2012; Shenkman, 1999).

THE LEGACY OF EVOLUTION FOR WAR LEADERSHIP TODAY

Thomas Carlyle proclaimed that "The history of the world is but the biography of great men." One could approximately paraphrase that as the biography of great war leaders. Biblical, preclassical, Greek, Roman, medieval and modern history is largely about the men who led, fought, and conquered empires. This is no doubt an exaggeration. However, to the extent that it is true, war leadership in history becomes an important subject of study for us—as evolutionary scientists—because of the role of evolutionary legacy in human behavior. While historians have for centuries recounted and revised our understanding of war, there are many features that, despite the political, economic and social complexities, suggest the timeless workings of certain traits of human nature and, therefore, an explanatory role for evolutionary psychology—and not least, the struggles for power, nepotism among kin, intergroup conflict, territorial aggression, and a range of cognitive biases (Betzig, 1986; Gat, 2009; Johnson & Toft, 2014; Tetlock, 1998; Thayer, 2004). An area ripe for new research is therefore evolutionary perspectives on historical war leadership (Johnson, 2004; Mazur, 2005; McDermott, 2007; Rosen, 2004), which can shed light on (a) universal features of war leadership across the ages and (b) problems of mismatch in which evolved traits are counterproductive for leaders in modern war (van Vugt, Johnson, Kaiser, & O'Gorman, 2008). But to explore the influence of evolutionary legacy on contemporary war, we need to pay attention to commonalities and differences with the wars of our past.

The Military Horizon: What Is Different About Modern War?

Modern war is usefully contrasted with war in our past by what Turney-High (1949) called the "military horizon." He outlined various features that distinguished "primitive" from modern warfare, notably its low levels of manpower, resources, training, command and control, weapons, specialization, and tactics. Although one can debate the details, there was a line crossed at some point in human history in which war became a militarized endeavor with large numbers of professional soldiers under rigid command structures. Today, all of these characteristics are very different from combat among small-scale societies. The scale, complexity, hierarchy, technology, communications, and objectives make military leadership, as well as war, a very different type of activity (Gat, 2006; van Creveld, 1985). However, not everything is different.

For one thing, although modern armies are vast, a recurrent feature across time is the role of small units "at the sharp end" of any fighting, which are preserved today at the level of the platoon—a couple of dozen men. These are closely bonded teams who live, train, and fight together, and who must rely on each other to kill and avoid being killed (Rielly, 2000). And, of course, these units have a leader who faces the same essential challenge: leading a small group of men by example, earning their respect, and keeping them motivated in the face of lethal aggression. At low levels, therefore, the social context of war may be almost identical to how it always has been.

Second, great attention is paid to advances in military technology and weapons, but such innovations by and large become an advantage for both sides. There may be a lag in who gets weapons first, but in general, opponents catch up with each other in an arms race, which means they stay in the same relative position, just as in evolutionary arms races (Cohen, 2007; Dawkins & Krebs, 1979; Rosen, 1991). Consequently, the real competitive edge often comes not from technology but from age-old *human* factors: strategy, morale, discipline, and, not least, leadership. Even nuclear weapons turned out to represent a largely psychological challenge in the high-stakes game of deterrence and bluff (Freedman, 2003; Schelling, 1960). Despite the remarkable advances in technology, human factors in general and military leadership in particular remain crucial elements of war, and can be decisive factors in victory and defeat (Cohen, 2002; Rosen, 1991).

So neither scale nor technology—two of modern war's most distinctive features—undermines the importance of leadership in war across the ages. But what makes a good leader? Sun Tzu and Carl von Clausewitz, widely regarded as the two greatest strategic thinkers of all time, agreed on many things, but they disagreed about the possibilities and prerequisites of leadership (Handel, 2001; Sun Tzu, 2009; von Clausewitz, 1832/1976). An evolutionary perspective generates some surprising new insight into these differences (Table 29.2).

Table 29.2
Differences Between Sun Tzu and Clausewitzian Views on War and Leadership

	Importance according to	
	Sun Tzu	Clausewitz
Intelligence	Vital	Overrated
Deception	Critical	Unimportant
Surprise	Critical	Unimportant
Control	High	Low
Outcomes	Predictable	Unpredictable
	⇓	⇓
Ideal military leader	Rational, calculating	Intuitive geniuses
Evolutionary analog	Raids	Battles
Application	Primitive/ancient warfare	Modern/recent warfare

What is striking from an evolutionary perspective is that the key features important to Sun Tzu—deception, surprise, and predictability of outcomes—are closely aligned with *raids* in *primitive* warfare (e.g., see Wrangham 1999a, 1999b). By contrast, Clausewitz's emphasis on unpredictability and confusion is much more closely aligned with *battles* and *modern* warfare. This is interesting in itself, because it suggests fundamental differences between ancient and modern war, and eastern and western strategy (Sun Tzu was writing in China around 500 B.C., Clausewitz in Prussia in the 1800s). But most remarkable of all is the implications for leadership. Not coincidentally, Sun Tzu envisages the ideal leader as calculating, rational, and able to weigh decisions based on prior intelligence and force strengths. Clausewitz, by contrast, is skeptical of the effectiveness of surprise and stresses the problems of unpredictability and "friction" (when interacting parts do not perform as expected), leading him to suggest that intuitive "geniuses" are required to make good judgments in the fog of war—Napoleon being the archetype (who had remarkable mental and multitasking abilities, van Creveld, 1985). The point here is that ancestral war may have favored Sun Tzu-style leaders, who were effective in mounting the asymmetric surprise raids of the Pleistocene era, but came ill-equipped for the problems of modern war captured by Clausewitz—large, complex, slow-moving armies that clashed in chaotic open battles of annihilation.

PSYCHOLOGICAL BIASES: JUDGMENT AND DECISION-MAKING BIASES IN WAR LEADERSHIP

A major research area in political science and international relations is the role of psychology in decision making—especially in crises and wars (Levy, 1983; McDermott, 2004a; Post & George, 2004; Sears, Huddy, & Jervis, 2003; Tetlock, 1998; Vertzberger, 1990). Robert Jervis's (1976) landmark book *Perceptions and Misperceptions in International Politics* drew on the "cognitive revolution" in psychology to offer new accounts of a range of puzzles in diplomacy, deterrence, and conflict. While this literature has mainly relied on social psychology and behavioral economics, there is a gathering interest in the evolutionary origins of judgment and decision-making

Table 29.3
Some Key Psychological Biases Affecting Leadership in War

Bias	Effect	Example	References
Prospect Theory	Risk-proneness when facing losses	Cuban Missile Crisis	Haas, 2001; Levi and Whyte, 1997
In-group/out-group bias	Devaluation and dehumanization of out-groups	Rwandan genocide	Fiske, 2002; Staub and Bar-Tal, 2003
Overconfidence	Overestimation of benefits or probability of victory	World War I	Blainey, 1973; Johnson and Tierney, 2011
Cognitive dissonance	Forcing data to match beliefs	2003 Iraq War	Cooper, 2007; Festinger, 1957
Fundamental attribution error	Assuming others' actions are malicious	Cold War	Gilbert and Malone, 1995; Larson, 1997
Analogizing	Tendency to fit new problems to past events	Vietnam	Khong, 1992; May, 1973

Note. (1) All such biases can affect leaders up and down the hierarchy, including political leaders (deciding whether or not to go to war), military leaders (deciding how to fight a war), and bureaucratic leaders (deciding how to resource and run a war), and (2) these biases may have been adaptive in the past, but they are likely to be maladaptive today, due to a mismatch between their original triggers and function and the modern social and physical contexts in which they arise (leading to failure rather than success).

biases, which often leads to novel predictions (Johnson & Toft, 2014; Lopez, McDermott, & Petersen, 2011; McDermott, Fowler, & Smirnov, 2008; Rosen, 2004; Thayer, 2004). While there are many cognitive and motivational biases that are of relevance to leadership and war (to be found, for example, in Kagel & Roth, 1995; Kahneman, 2011; Sears et al., 2003; van Vugt & Ahuja, 2011), here I have summarized some key examples in Table 29.3, and expand in the text on just three "big ones" that (a) have been implicated as influencing leaders' decisions about war and (b) are argued to have evolutionary foundations.

Prospect Theory A key psychological phenomenon affecting decision making about conflict is prospect theory. In decisions involving uncertain outcomes, people are risk-averse when choosing among potential positive outcomes (the "domain of gains"), but risk-prone when choosing among potential negative outcomes (the "domain of losses"). In essence, people tend to gamble more when facing the prospect of losses (Kahneman & Tversky, 1979; McDermott, 1998).

Prospect theory has been used to explain key historical events such as Japan's decision for war in 1941, the Cuban Missile Crisis of 1962, and the tendency to escalate wars rather than accept defeat, such as in Vietnam (Haas, 2001; Levi & Whyte, 1997; Levy, 2000, 2003; McDermott, 1998, 2004b; Taliaferro, 2004).

Of particular interest for us is that the preferences underlying prospect theory may have an evolutionary origin (McDermott et al., 2008). When resources are plentiful and dangers scarce, organisms should avoid risky decisions, just as standard economic models of expected utility would predict. However, when starvation or other dangers threaten survival, selection can favor whatever risk-taking is necessary to give the animal a chance of life rather than certain death. This does not necessarily maximize expected payoffs (e.g., food). But it maximizes Darwinian fitness. An evolutionary perspective therefore suggests novel predictions for when and why we may expect to see risky decision-making among leaders about, or during, war.

Ingroup/Outgroup Bias Of the long list of psychological biases in human judgment and decision making, one of the most pervasive and powerful is the "ingroup/outgroup" bias. A mass of empirical evidence demonstrates that people (a) rapidly identify with their ingroups (even when they are strangers assigned into arbitrary groups), (b) systematically overvalue their own group's performance and qualities, and (c) systematically devalue the performance and qualities of other groups (Fiske, 2002; Fiske & Taylor, 2007; Hewstone, Rubin, & Willis, 2002; Tajfel, 1974).

Ingroup/outgroup bias has been implicated in a range of aspects of war, including genocides such as in Bosnia and Rwanda (Staub & Bar-Tal, 2003), perceptions of enemies such as the United States and the USSR during the Cold War (Larson, 1997; Silverstein, 1989), and influential theories about why states are intrinsically hostile to each other (Jervis, 1976; Wendt, 1999).

Again this bias appears to have an evolutionary origin (Haselton & Nettle, 2006; Sidanius & Kurzban, 2003, see also Kurzban & Neuberg, 2005). In human evolution, familiar and kin-based ingroups provided security, resources, and social exchange, while contact with outgroups risked exploitation, injury, or death. Attachment to the ingroup and avoidance of outgroups was therefore likely to be strongly favored by natural selection. Again, an evolutionary perspective suggests novel predictions about when and why we may expect to see intergroup biases among leaders encouraging or affecting war.

Overconfidence All mentally healthy people, especially men, show a systematic bias towards overconfidence in a wide range of domains. In particular, people tend to (1) overestimate their capabilities, (2) overestimate their control over events, and (3) underestimate their vulnerability to risk—three widely replicated phenomena collectively known as "positive illusions" (Sharot, 2011; Taylor & Brown, 1994).

Overconfidence has long been identified as a cause of war by both historians and political scientists, encouraging overambition, reckless diplomacy, overestimation of one's strength, and underestimation of the enemy and the costs of war (Ganguly, 2001; Howard, 1983; Johnson, 2004; Johnson et al., 2006; Johnson, McDermott, Cowden, & Tingley, 2012; Lebow, 1981; Stoessinger, 1998; White, 1968). Two landmark books on the causes of war—separated by 25 years of work on the subject—both highlighted overconfidence (or "false optimism") as a recurrent and powerful phenomenon on the eve of war throughout history (Blainey, 1973; Van Evera, 1999). For example, overconfidence is argued to have contributed to European states' expectations of a quick victory in 1914 (Johnson & Tierney, 2011), U.S. expectations in Vietnam (Tuchman, 1984), and the Bush administrations' discounting of the challenges of postwar reconstruction in Iraq (Woodward, 2005). Jack Levy concluded that "Of all forms of misperceptions, the one most likely to play a critical role in the processes leading to war is the underestimation of the adversary's capabilities" (Levy, 1983, p. 83).

Once again, recent work suggests an evolutionary origin for overconfidence (Johnson, 2004; Johnson & Fowler, 2011; Nettle, 2004). Overconfidence can be adaptive because it increases ambition, resolve, persistence, deterrence, and the credibility of bluffing, generating a self-fulfilling prophecy in which exaggerated confidence actually increases the probability of success (Nettle, 2004; Taylor & Brown, 1994; Trivers,

Table 29.4
Evolutionary Hypotheses on War Leadership

Hypothesis	Implications	Evidence	References
Humans have evolved traits for *war* leadership	Evolved traits for military leadership	Nascent	The Military Intelligence Hypothesis (this chapter)
Humans have evolved traits for leadership (that may carry over into war)	Evolved traits for leadership	Growing	van Vugt and Ahuja, 2011
Humans have evolved traits for coalitions (that may carry over into leadership)	Evolved traits for warriors	Strong	Tooby and Cosmides, 1988
Humans have evolved traits that influence contemporary war leadership	Evolved traits for life in general (including psychological biases); with liabilities for people in leadership positions	Strong	Rosen, 2004

2011). Some authors have specifically suggested that overconfidence is adaptive in war because of the importance of resolve, bluffing, and exploiting opportunities (Johnson, Weidmann, & Cederman, 2011; Wrangham, 1999b). Intriguingly, van Vugt (2006) highlights the empirical association of leadership with boldness, risk-taking, and seizing the initiative to solve problems of coordination, especially when there are large potential gains and high levels of uncertainty. In our evolutionary model, overconfidence was more likely to evolve precisely when the stakes and uncertainty are high (Johnson & Fowler, 2011). Some level of emboldened confidence may, therefore, be an essential ingredient of successful leadership, as both psychologists and military commentators have noted (Baumeister, 1989; von Clausewitz, 1832/1976). Once again, an evolutionary perspective generates a range of new and testable predictions about when and why we may expect to see overconfidence among leaders before or during war.

ARE THERE EVOLVED TRAITS FOR WAR LEADERSHIP?

Above we explored various general traits of evolved psychology that can affect modern war and leadership. This leaves the more speculative but 6-million-dollar question of whether we also have traits that are, in fact, specifically evolved adaptations *for* war leadership (Table 29.4). I say "speculative" because (a) even the idea that we have evolved traits for *leadership* of any kind is still a new area of investigation (Price & van Vugt, 2014; van Vugt, 2006; van Vugt & Ahuja, 2011); (b) as we saw earlier, war leadership is sporadic and limited in small-scale human societies, so it is not obvious whether we should expect specific evolved traits for *war leadership per se*; and (c) there is very little experimental work that has tested this possibility.

Although there has been considerable research on evolutionary adaptations for dominance, status, coalitions, aggression, and fighting (Buss, 1996; Buss & Shackelford, 1997; Daly & Wilson, 1988; Duntley & Buss, 2011; Henrich & Gil-White, 2001; Kurzban, Tooby, & Cosmides, 2001; Lopez et al., 2011; Mazur, 2005; Tooby & Cosmides, 1988, 2010; van Vugt & Tybur, Chapter 32, this volume; Wrangham, 1999a), there is hardly anything on evolved traits associated explicitly with war leadership. One problem is that much of evolutionary psychology is about universal traits that were adaptive for, and hence manifest themselves in, all people. Since, by definition, only some people can be leaders (in fact, only a tiny minority), leadership traits may be constrained to evolve by some form of frequency-dependent selection—traits that do well as long as not too many people have or express them (van Vugt, 2006). And indeed, some authors have noted that leaders are overrepresented by people with certain personality types or even personality disorders (Ghaemi, 2011; Ludwig, 2002; Nettle, 2001). An alternative is that we all have leadership (and followership) traits, but they are differentially expressed according to the situation or environment (Price & van Vugt, 2014; Spisak, O'Brien, Nicholson, & van Vugt, 2015). These two possibilities—the trait-versus-state debate in the leadership literature—are both plausible but in need of further investigation from an evolutionary perspective (van Vugt, 2006; van Vugt & Ahuja, 2011), especially in the context of leadership in war.

We do have some intriguing studies to build on, however. One of the most striking results to emerge from the evolutionary psychology literature in recent years is how brute physical features can predict preferences and behavior. For example, experiments and empirical studies have shown that, in general, people favor leaders who are male, older, trustworthy, taller, and from one's own group (Todorov, Mandisodza, Goren, & Hall, 2005; van Vugt & Ahuja, 2011; van Vugt & Spisak, 2008). However, this can depend on context. In a manipulation study of morphed faces, people preferred certain leadership traits (such as greater age and being male) more in circumstances of intergroup threat and war than in other types of scenarios (Spisak, 2012; Spisak, Dekker, Krüger, & van Vugt, 2012). This concurs with real-world observations that in times of crisis, people may prefer or accept more aggressive and authoritarian leaders (Boehm, 2001; McCann, 1992). However, these studies come down to an understanding of *followership*, rather than leadership, or at least "cognitive models" of the kind of leaders people want in a given setting. We are not yet sure how such leaders would decide or act, and whether or not they would be successful as a result.

A few studies get at traits more directly relevant to leadership, or at least to more dominant individuals. For example, Aaron Sell and colleagues found that men's muscle mass can predict their beliefs in the utility of force—both in the context of everyday life and in foreign policy (Sell, Hone, & Pound, 2012; Sell, Tooby, & Cosmides, 2009). Stronger men are more likely to resort to and endorse fighting, which makes evolutionary sense given their greater ability to extract resources and attract, coerce, or deter others. In studies of leaders themselves, facial features associated with dominance have been found to predict the later attainment of military rank among U.S. military cadets (Mueller & Mazur, 1996) and achievement drive among U.S. presidents (Lewis, Lefevre, & Bates, 2012).

Clearly, there are intriguing findings suggesting a role for dominance in both leadership and conflict, as well as strong hints that prestige and social coordination are as or more important (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Price & van Vugt, 2014; van Vugt, 2006; van Vugt & Tybur, Chapter 32, this volume). But much work needs to be done to verify whether any such traits are adaptations for leadership in war. The final section, however, proposes that there is at least one evolved trait that is likely to be associated explicitly with war leadership, and it lies not in brawn, but in brainpower.

THE MILITARY INTELLIGENCE HYPOTHESIS

War is a complex, lethal activity, and all else equal, the side that is better prepared, organized, and coordinated—that is, better led—is more likely to win. Here I propose the "Military Intelligence Hypothesis" (MIH), which is that (a) intergroup conflict poses cognitively demanding adaptive problems, (b) solving these problems was important for fitness, and (c) this contributed to the evolution of human intelligence. The brain, in other words, has been honed in part to the myriad ways to kill and avoid being killed (see also Duntley & Buss, 2011; Thayer, 2004). The Military Intelligence Hypothesis is thus a kind of "*anti*-social brain hypothesis," in contrast to Humphrey and Dunbar's "social brain hypothesis" (Dunbar, 2003; Humphrey, 1986), in which human cognition was influenced by the adaptive challenge not (only) of intragroup competition and cooperation, but rather of intergroup conflict. The evolution and metabolic expense of our disproportionately large brain has proven a significant puzzle for science, but an important, if unfashionable, piece of this puzzle may be the unforgiving problem of surviving and thriving in an environment of lethal intergroup warfare.

Cognitive advances would help any individual, whether leader or soldier, but they apply most strongly to war leadership because the real purchase of this military intelligence is in organizing multiple individuals to act cleverly together (via coordination by a leader), not individuals acting cleverly themselves (via uncoordinated independent actions). In combat, a disciplined whole is strikingly more powerful than the sum of its parts (Johnson & MacKay, 2015).

Supporting Evidence

The MIH is consistent with cross-species comparisons. Lethal intergroup conflict is rare in the animal world, but where it occurs, it tends to be restricted to social mammals of high intelligence—most notably chimpanzees among primates, and wolves among carnivores (Manson & Wrangham, 1991; Wrangham, 1999a; ants are an interesting exception). The mere formation of *coalitions* is restricted to higher-intelligence animals, such as primates, canids, and dolphins (Harcourt & de Waal, 1992). From a broad comparative point of view, therefore, it may be no coincidence that humans have both remarkable levels of intelligence and remarkable levels of war. But the argument is not that the luxuries of intelligence begat war. Rather, the demands of war begat (or boosted) intelligence.

The MIH also concords with archeological evidence. A study of 175 hominid skulls from across the Pleistocene epoch found that variance in cranial capacity was best predicted by measures of population density, suggesting that while several factors may have contributed, brain evolution was primarily driven by competition with other humans (Bailey & Geary, 2009). Other studies have found that population pressure (population density controlled for available resources) correlates with the level of warfare (Kelly, 2013). It may also be no coincidence that the cognitively sophisticated *Homo sapiens* rapidly replaced long-established Neanderthals in both the Levant and Europe (Gat, 1999).

The Cognitive Challenges of War

The primary focus of the MIH is the cognitive demands of strategy—the complex challenge of planning what to do in interaction with an unpredictable and deadly

Table 29.5
Domains of Intergroup Conflict That Demand Sophisticated Cognition (in alphabetical order)

Domain	Significance	Cognitive Demands
Alliances	Gaining and maintaining third-party supporters	Perspective taking, theory of mind
Cooperation	Mobilizing and maintaining warriors	Cheater detection, enforcement
Coordination	Aligning interests and goals of warriors and supporters	Initiative, problem-solving
Deception	Achieving surprise, masking intentions	Bluffing, acting, concealment
Diplomacy	Extracting gains while averting costs	Bargaining, perspective-taking, patience
Intelligence	Anticipating enemy strengths, weaknesses, and intentions	Collecting, understanding, and integrating information
Persuasion	Mustering support	Reasoning, moralizing, rhetoric, oratory
Strategy	Planning, deploying, and utilizing forces	Dealing with uncertainty, interactions, rapid decision making, cunning, prediction
Weapons	Staying ahead of the arms race	Designing, making, and using tools

opponent. However, the demands of war leadership are much more far-reaching than this, and include a range of cognitively demanding tasks (Table 29.5). Of course, many of the traits listed are adaptive in interpersonal and within-group interactions (not just war), so they are also consistent with the social brain hypothesis. However, there are three reasons why the application of even these traits may be of special importance in war.

First, the problems of war are *harder*. Since war tends to be against out-groups rather than the in-group, it poses special adaptive challenges including, for example, predicting the behavior of people you do not know, which is harder than predicting the behavior of people you do. One also has to deal with limited information about their strengths, resources, reserves, or alliance arrangements. "Knowing the enemy" is a classic challenge of war.

Second, the problems of war have *higher stakes*. Not only does war threaten unusual levels of costs and lethality, it also offers the possibility of bountiful gains (booty, land, resources, elimination of rivals, status, and women). For all participants—victors and vanquished alike—fitness consequences are significant. Therefore, even if war was infrequent in our evolutionary history, it may have exerted a strong selection pressure on ways to exploit or avoid it.

Third, the problems of war are *pervasive*, even in times of peace. Because of the ever-present threat of intergroup conflict, even when (or precisely because) war is not actually occurring, there are numerous tasks and challenges that require cognitive sophistication and have significant implications for Darwinian fitness. These include building fortifications, social organization, forming alliances, signaling, deterrence, strategizing, allocating resources, preparations for war, stockpiling, training, designing and making weapons, gathering intelligence, and contingency planning. Groups (and individuals within them) that were poorly organized, prepared, or trained for war would have been more likely to suffer at the hands of rivals in a better state of readiness. We may therefore expect additional selection pressures on military intelligence arising from a host of peacetime activities that nevertheless stem from war—and indeed, influence its outcome.

An Extension of Coalitionary Psychology

The MIH might seem to overemphasize the role of war in the evolution of human intelligence. However, (a) it is not mutually exclusive of other factors driving human intelligence; (b) the high level of death rates from war in ethnographic and archaeological populations (c.15%; Bowles, 2009) suggest that adaptations affecting success in war would be under strong selection pressure; and (c) it is, in fact, a logical extension of a previous argument for the role of human intelligence in war made by John Tooby and Leda Cosmides. Tooby and Cosmides (1988) noted, in a widely cited but never published paper, that coalitional aggression is remarkable not only for its importance among humans, but for its rarity among other animals. Numerous species, such as elephant seals, deer, or gorillas, have a single male that dominates all reproduction in the group. If lesser males ganged together, they could easily depose the alpha and split the spoils. But they never do. Tooby and Cosmides suggest the reason is that forming a coalition demands sophisticated cognitive mechanisms to achieve and sustain the necessary levels of cooperation. Since most other animals do not have such mental sophistication, the great opportunities of coalitions and alliances are foreclosed to them (as we saw above, coalitions are found only among a select few other species, all of which have higher intelligence—such as chimpanzees, wolves, and dolphins). This led Tooby and Cosmides to suggest that humans have evolved distinctive psychological traits for forming coalitions (Kurzban et al., 2001; Tooby & Cosmides, 2010; van der Dennen, 1995; Wrangham, 1999a).

What were these traits? For coalitionary aggression to make sense given the inherent risks to life and limb, two features must be in place: (1) some reasonable probability of net gains and (2) the detection and sanction of free riders. Tooby and Cosmides (1988) argued that in the Pleistocene setting of asymmetric raids, the large gains and low costs should easily tilt the balance in favor of war (as do Johnson & MacKay, 2015; Manson & Wrangham, 1991; Wrangham, 1999a). The bigger problem remains in identifying shirkers and enforcing cooperation: Who takes on these policing costs? They suggest this may have been solved by certain individuals having higher stakes in war, or enforcement being delegated to others. Although it is hard to see exactly how this might play out among a coalitionary group of equal individuals (as they envisioned the problem), it is easy to see how leadership can plug the gaps here. Leaders are likely to have higher stakes in the outcome, as well as lower costs of enforcement (given physical power, authority, status, kin ties, or allies).

Tooby and Cosmides identified a crucial problem in the great benefits of coalitionary aggression and yet the significant evolutionary obstacles of achieving it. But leadership may have helped to cross the canyon of this big collective action problem to reach the fertile fields of war. Taken together, the multiple advantages of intelligence for effective war leadership, the high death rates due to intergroup conflict, and the cognitive challenges of coalitionary warfare suggest that war itself may have contributed to the enlargement and sophistication of the human brain.

CONCLUSIONS

The importance of war in human evolutionary history remains controversial, but it seems likely that it exerted significant selection pressure on human social organization, behavior, and cognition. Although there are variations in the form and frequency of warfare among small-scale societies, there are also remarkably consistent patterns, which suggest a common adaptive problem and common solutions to solve it. One important solution is likely to have been coordination and leadership—without these, victory comes hard and death comes easily. But even if war leaders were only transitory or weak in our evolutionary past, evolutionary psychology still has much to say about leadership in modern war. This chapter has addressed two very different strands of insight: (1) humans have a range of evolved dispositions and biases (many of which are described elsewhere in this volume), that can have large and important effects on leaders in their decisions for war and how they fight them (just as they can affect any other kinds of decision), and (2) humans may have evolved leadership and followership traits, some of which could be explicit adaptations to intergroup conflict and war. A significant one is hypothesized to be intelligence itself.

What are the lessons for contemporary war? Wars in recent centuries tended to involve the clashes of large, institutionalized armies of states and empires. In the 21st century, war is more commonly proving to be asymmetric conflicts against ad-hoc, loosely organized, often nonstate actors (Kilcullen, 2010; Strachan & Scheipers, 2011). These smaller sides are not without leaders, but they are much more decentralized. New research—from an evolutionary perspective—argues that this gives them an edge in terms of greater flexibility and faster adaptation than the slow, lumbering machinery of Western military organizations (Johnson, 2009; Sagarin et al., 2010). In Iraq and Afghanistan, where Western troops were faced with a novel military challenge against indistinct foes wearing civilian clothes and using unconventional methods, established doctrines quickly failed. Moreover, within a large and complex organization such as the U.S. Army, change was not easy to accomplish and even harder to institutionalize. Instead, there became a premium on another solution—individual leaders on the ground who showed themselves to be flexible within the constraints of the military machine. General Petraeus, among other senior officers, called for a new generation of "adaptive leaders" (Wong, 2004). As Petreaus explained: "There is no substitute for flexible, adaptable leaders. The key to all that we did in Iraq was leaders—especially young leaders—who repeatedly rose to the occasion and took on tasks for which they'd had little or no training" (Broadwell, 2009). Human factors and leadership remain as important to contemporary warfare as they did for Xenophon and the Ten Thousand, and perhaps for warriors of all human societies since time immemorial.

Strategic theorists since Sun Tzu and Clausewitz have consistently emphasized the difficulty of leadership in war—it is a domain of unrivalled contingency, uncertainty, and confusion. As a result, Lawrence Freedman cautions that "it must never be forgotten that strategy is an art and not a science" (Freedman, 2007, p. 369). However, if war was important in human evolutionary history, natural selection is likely to have favored cognitive and behavioral strategies that helped to coordinate and kill—and avoid being killed—whatever the difficulties. One of the most important tools of all, both then and now, is effective leadership. Combined with the many insights on evolved psychological biases that affect war leaders just as they affect everyone else, evolutionary psychology offers a scientific framework to help us understand the role of leadership even in the "art" of war.

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PART VI

CULTURE AND COORDINATION

DANIEL CONROY-BEAM and DAVID M. BUSS

The importance of groups is underscored by the need for two sections on the psychology of group living. Chapters in this section focus on adaptations that emerge as features of our species' groupish nature. Living in groups offers our species a bounty of benefits and costs, but also exposes us to a raft of new problems. These include coordinating belief and action, accumulating and transmitting knowledge, and knowing and exploiting oneself, other people, and group strengths. From these problems emerge morality, reputation, prejudice, and perhaps culture itself—topics that compose a cutting edge of evolutionary psychology. The chapters in this section represent large advances into previously little-touched psychological territory and are likely to become pillars within the broader foundation of evolutionary psychology.

No treatment of evolutionary psychology would be complete without a detailed examination of *cultural evolution*—the processes by which cultural variants are invented, selectively jettisoned, and selectively retained, resulting in cumulative change over time in ideas, inventions, values, beliefs, artifacts, and institutions. Maciej Chudek, Michael Muthukrishna, and Joe Henrich take up this daunting challenge with a superb chapter on the processes by which cultural evolution takes place (Chapter 30). They argue that cultures do indeed evolve in ways that do not rely on genes and strict replicators. The evolution of the huge human capacity for social learning, and hence cultural learning, they argue, enabled our species to cross a critical threshold to become a truly cultural species. They articulate some of the evolved psychological adaptations on which cultural evolution relies, such as conformist transmission and credibility enhancing displays. They end with a discussion of gene-culture coevolution. This critical chapter provides a conceptual roadmap for the future of the uniquely human components of "the cultural animal" that is us.

Humans have also been called "the moral animal," and for good reason. Rob Kurzban and Peter DeScioli provide an outstanding original chapter on morality (Chapter 31). It focuses on moral judgment—how people judge the actions of others to be right or wrong. The complex cognitive psychology of moral judgment is inexorably linked with moral emotions, particularly moralistic anger and moralistic disgust.

These emotions, in turn, often motivate punishment of those deemed to have morally transgressed. Importantly, Kurzban and DeScioli hypothesize that moral judgments serve a critical and underappreciated adaptive function—to guide coalitional side-taking in times of social conflict. The moral side-taking hypothesis generates a raft of novel predictions, and is likely to produce a sea change in thinking about morality in the next decade.

If morality provides one solution to the problem of within-group alliance and coordination, adaptations for hierarchy provide another. Mark van Vugt and Joshua Tybur (Chapter 32) provide an excellent chapter on status hierarchies, arguing that their complexity can be understood only by deep knowledge of the multiple psychological adaptations involved. They use evolutionary game theory as one tool to explore these adaptations, and then turn to the links between status and hormones, physique, verbal and nonverbal indicators, and emotions such as anxiety, shame, rage, and depression. They then explore sex differences in status striving and other elements of male and female psychology of status. They end with the evolutionary psychology of leadership, offering the "service for prestige" hypothesis to explain the mutual adaptive benefits afforded to both leaders and those who are led. Since status hierarchies are universal and reproductively relevant resources are inextricably linked with position within status hierarchies, this chapter opens up new and largely unexplored territory for discoveries in this domain.

One such domain is that of reputation, explored in depth by Pat Barclay (Chapter 33). Although humans are not the only species in which individuals hold reputations, our unique capacity for language renders reputation exceptionally important. As with status hierarchies, humans are likely to possess multiple adaptations for dealing with reputation. These include cultivating one's own reputation, influencing or manipulating the reputations of others in what has sometimes been called "information warfare," and even skepticism about the value of the information depending on its source. Although "gossip" is sometimes seen as a trivial and idle way of spending time, Barclay argues that it is a critical form of manipulating reputations. Humans develop reputations as cooperators (ability and willingness to confer benefits) as well as aggressors (cost-inflicting proclivities). Barclay's chapter also opens up new territory by posting key adaptationist landmarks for future intrepid researchers who explore the critically important, but largely overlooked, domain of social reputation.

Cristine Legare and Rachel Watson-Jones follow with a terrific chapter on ritual (Chapter 34)—one unique way in which humans across cultures solve the coordination problem. They argue that rituals serve vital functions—identifying group members, ensuring commitment to the group, facilitating cooperation within the group, increasing cohesion within the group, and critically, coordinating group or coalitional action. They draw on a unique combination of empirical studies from samples of children and adults, offering a developmental as well as an evolutionary perspective on the origins of ritual. Along the way, they provide key insights ranging from ethnographic anthropological studies to experimental studies of the effects of ostracism on ritual, overimitation, and conformity in children. This chapter paves the way for future psychologists in a discipline that has overlooked the importance of ritual.

Ara Norenzayan (Chapter 35) provides an insightful evolutionary psychological analysis of the evolution of religion. He argues that religion, a culturally universal phenomenon in varying forms, is best understood as a synthetic combination of by-products of a suite of cognitive adaptations along with adaptations themselves, such as costly signaling in the service of cooperation. Religions themselves have evolved, he argues, not through standard Darwinian selection, but rather through cultural evolution as a partial solution to the problem of large-scale cooperation among hundreds, thousands, or millions of individuals. Norenzayan's theory of religion, particularly the emergence of "Big Gods" as a cultural solution to the problem of large-scale cooperation, has the signal virtue of synthesizing adaptationist, by-product, and cultural evolutionary perspectives.

Steven Pinker ends the section on a strong note with his incisive contribution to the ongoing debate surrounding group selection (Chapter 36). The title of his essay—The False Allure of Group Selection—provides more than a hint about his skepticism of group selection as an explanatory scheme. He starts by enumerating the many different senses in which scholars currently use "group selection," including as a distinct form of selection, any behavior that involves groups, and a redescription of genic selection using a different accounting system that defines practically any social interaction, however fleeting, as a "group." He argues cogently that these many uses of "group selection" create large-scale confusion in which anything that loosely involves groups or group living is attributed to the causal process of "group selection." Some theorists are on record as disagreeing with Pinker's arguments, but his proposed solution must be taken seriously: "I offer a simple solution: Stop using the term *group selection* as a loose synonym for the evolution of group living, group competition, group norms, group practices, social networks, culture, selflessness, kindness, empathy, altruism, morality, clannishness, tribalism, or coalitional aggression." Pinker's essay should be required reading for everyone in the evolutionary sciences.

CHAPTER 30

Cultural Evolution

MACIEJ CHUDEK, MICHAEL MUTHUKRISHNA, and JOE HENRICH

YOU AND I are very unusual beasts. Our ancestors, mere African primates, spread across the globe long before the origins of agriculture, the first cities, or industrial technologies. More ecologically successful than any mammal, human foragers colonized most terrestrial ecosystems, from the frozen tundra of the Arctic to the arid deserts of Australia. Yet, despite our massive ecological success, we are physically weak, slow, and relatively bad at climbing trees; any adult chimp can kick our butts and any big cat can easily chase us down. We can't distinguish edible from poisonous plants, and our gut can't detoxify poisons. We can't survive without cooked food, but we aren't innately able to make fire (or cook). Our babies are born dangerously premature, with skulls that haven't yet fused. Our females stop reproduction long before they die (menopause), yet remain sexually receptive throughout their cycle. Perhaps most surprisingly, our kind are not very bright, and our success as a species is not due to our intelligence (Henrich, forthcoming).

Skeptical? Imagine we took you and 19 friends and pitted you against a troop of 20 capuchin monkeys from Costa Rica, without equipment. We parachute both teams into the Ituri Forest in central Africa. After 6 months, we return and count survivors. Who would you bet on? Well, do you know how to make arrows, nets, and shelters? Do you know which plants are toxic (many are)? You can start a fire without matches, right?

Chances are your team would lose, despite your oversized crania and vaulted intelligence. But, if not for figuring out how to survive as foragers—which our ancestors managed to do across a staggering variety of environments—what's that big brain *for*, anyway?

In fact, the human half of this experiment has played out many times. Hapless European explorers accidentally stranded in unfamiliar environments have typically floundered, and often died. History provides cases from the Arctic, tropical forests in South America and Africa, Australian deserts, and along the coasts of North America (Henrich, forthcoming). Forced to live as hunter-gatherers, these Europeans couldn't find food or distinguish poisonous from edible plants. They couldn't successfully hunt, locate water, avoid danger, make fire, or fashion tools, shelter, or watercraft. Meanwhile, foraging populations had inhabited these same environments for centuries, routinely overcoming such "challenges" (what they call "daily life").

Examples of such ill-fated ventures in the 19th century include the Franklin Expedition (Boyd, Richerson, & Henrich, 2011), where every member of the best-equipped expedition in the history of British polar exploration perished in a land in which local foragers had thrived for almost a millennium, or Burke and Wills's foray into the Australian outback (Henrich & McElreath, 2003), in which, despite their extensive preparations and equipment, they died because they did not know the local aboriginal techniques for detoxifying plants. You might also consider watching the film *Van Diemen's Land* (2009), which vividly depicts the travails of Alexander Pearce and seven other Europeans. In 1822, these men escaped a prison camp on the Australian island of Tasmania. Unlike the hostile conditions faced by Franklin, whose ship froze in the Arctic, or Burke and Wills, lost in the desolate deserts of central Australia, these men spent a mere three months in a verdant forest, equipped with a steel axe. Yet they found only two ways to feed themselves: stealing from local Aboriginal foragers, who had inhabited this ecology for at least 35,000 years (Cosgrove et al., 2010), and eating each other.

How does all this floundering by educated, technologically sophisticated explorers square with the massive ecological success of our species? How is it that we are so frail as individuals, so helpless when dropped into a novel ecology, and yet our ancestors, wielding merely stone tools, swept across almost the entire planet?

The reason we are such unusual animals is that we are an *evolved cultural species*. Unlike all other species, we are addicted to culture. You and I rely on a body of cultural know-how that is transmitted from one person to another, and accumulates over generations. Stripped of this nongenetic information, we are rather pathetic compared to other species (Boyd et al., 2011; Henrich, forthcoming).

We need an evolutionary explanation for the existence and behavior of a cultural species. Over the past three decades, the scientific enterprise of developing this explanation has advanced rapidly. In this chapter, we will try to bring you up to speed on our emerging understanding of the field of cultural evolution: how a species evolves to be cultural, how culture itself evolves, and how cultural evolution interacts with, and sometimes drives, genetic evolution.

A cultural species is one that has evolved to socially transmit complex behavior-shaping information between generations. A key threshold for defining a cultural species is *cumulative cultural evolution*: the point at which these transmitted behaviors accumulate enough that they are more complex, sophisticated, and well adapted than anything a single asocial or noncultural individual could devise alone in his or her lifetime, regardless of how individually intelligent that person is (Boyd & Richerson, 1996). No individual today, no matter how smart, could recreate the world we live in. Socially accumulated cultural adaptations have been so central to our species that they have driven subsequent genetic adaptations (Laland, Odling-Smee, & Myles, 2010; Richerson, Boyd, & Henrich, 2010).

As evolutionary researchers, if we want to understand a species that has crossed the threshold into cumulative cultural evolution, we need—in addition to ecology, evolution, and psychology—a theory of how cultural information itself changes over time (evolves). We need theoretically sound and empirically verified answers to questions such as:

1. Can culture evolve? Does the notion of evolution even apply to something so very different from genes?
2. How did a cultural species evolve? How could a species similar to extant, nonhuman apes come to possess such highly adaptive, but nongenetic, behavioral repertoires, and why haven't other species done the same?
3. What kind of psychological adaptations does a cultural species need? How do they influence cultural evolution?
4. How does culture itself evolve? How do these cultural repertoires adapt and accumulate over generations?
5. How do genes adapt to cultural evolution? Have culturally evolved products like tools, fire, languages, and knowledge about plants and animals shaped our genetic evolution and our evolved psychological adaptations?

Let's dive right in to the answers.

CAN CULTURE EVOLVE? DOESN'T EVOLUTION REQUIRE GENES OR REPLICATORS?

It's now clear that neither evolution nor adaptation requires discrete traits, "replicators," low mutation rates, vertical transmission, or random variation (Henrich & Boyd, 2002; Henrich, Boyd, & Richerson, 2008). Genes evolve, but it doesn't follow that all evolving things must be gene-like. Genetic evolution is just one way information can change and accumulate. A large body of formal mathematical models now illustrates how culture can evolve, and when and how this is like—and unlike—genetic evolution.

Evolutionary adaptation has three basic requirements: (1) individuals vary, (2) this variability is heritable (information transmission occurs), and (3) some variants are more likely to survive and spread than others. Genes have these characteristics, so they evolve and adapt. Culture also meets all three requirements, but in different ways. Like bacterial genes, cultural information spreads horizontally, not just from parent to child. Formal models of cultural evolution begin from simple descriptions of how individuals acquire behaviors—by learning from others, learning individually (e.g., trial and error), or by genetically encoded responses ("evoked culture"). Then, using mathematical techniques drawn from population genetics, epidemiology, statistics, and communications, they explore how the distribution of phenotypes—behaviors, motivations, beliefs, and so on—changes over time.

There's no analogy with genes. These models are built for culture, given what we know about human learning. Even the earliest models focused on the differences between cultural and genetic evolution: the transmission of continuous traits (like how long to make your spear), "horizontal" learning from peers, or "oblique" learning from older nonparents (Cavalli-Sforza & Feldman, 1973). Of the 38 different models in Boyd and Richerson (1985), roughly half explore cultural traits as continuous (not discrete) with transmission fidelity modeled as a parameter (so, no assumption of "replication"), and many also considered the influence of cognitive biases in learning and the impact of individual learning on cultural and gene–culture evolution.

To get a handle on these formal models, consider an example. Suppose a young hunter wants to figure out the best length for his arrows. He (or she) watches the three most successful hunters in the community, notes the lengths of their arrows, and then averages them.

Did anything replicate? No, but that's not a necessary or useful concept for cultural evolution.

Was something inherited? Yes, the learner didn't invent an arrow or pick an arrow length *de novo*; these were inherited from others by social learning. The phenotypes (arrow lengths) of the new generation will be correlated with those of their "cultural parents" (those they learned from).

Was there selection? Yes, the learner constrained the space of possible arrow lengths by choosing the three most successful hunters. This is selective cultural transmission.

Will there always be variability for selection to act on? Yes, even in this very simple model, as long as there are fluctuations in hunting success and individuals are imperfect copiers, arrow lengths will vary and learners will selectively imitate just some of them.

Will there be adaptive evolution? Yes, under many conditions. If everyone learns this way and if there is an optimal arrow length for hunting, eventually arrow lengths will converge to it. This kind of adaptation—the process of phenotypes (e.g., behaviors and technologies) becoming better suited to their environment—doesn't require genetic change or intelligence. It happens without anyone constructing a mental model of aerodynamics or performing cost-benefit analyses of the effectiveness of different arrows on various prey types.

Later we discuss emerging research on how cultural information evolves as it travels the landscape of the adapted minds of our cultural species. To really understand this, though, we'll need to start by understanding the cognitive adaptations that make cultural evolution possible in the first place.

HOW DID WE EVOLVE TO BE A CULTURAL SPECIES?

Many people still think that "evolutionary" or "biological" explanations oppose "cultural" explanations—"Nature versus Nurture." However, this approach shows how cultural explanations are merely one type of evolutionary explanation. In 1985, Boyd and Richerson extended the Darwinian umbrella to cover "cultural" explanations by asking, Under what conditions does natural selection favor social learning over individual exploration or genetic adaptation? How might natural selection shape psychology to most effectively acquire ideas, beliefs, values, motivations, and practices from others? Under this expanded umbrella, explanations involving social learning ("cultural explanations") can interface with noncultural hypotheses within one epistemological framework. Recognizing that social learning is part of the explanation of a phenomenon doesn't mean that genetically evolved aspects of psychology aren't also important parts of the explanation.

As neuroscience now makes inescapably clear, both genes and culture shape our brains. Growing up in different societies, learning and navigating different culturally evolved social norms, institutions, and technologies, results in different neurological and hormonal reactions (Han et al., 2013; Kitayama & Uskul, 2011; Na & Kitayama, 2012; Nisbett & Cohen, 1996), that propel different perceptions, judgments, motivations, and behaviors. Cultural evolution shapes our biology in the short term by influencing our development and our genes in the longer term. There's much more to our biology than our genes (Henrich, forthcoming).

HOW AND WHEN DID CAPACITIES FOR CULTURE EVOLVE? WHEN IS CULTURAL LEARNING GENETICALLY ADAPTIVE?

A great deal of theoretical work explores whether and when cultural learning improves genetic fitness. Will selection favor rare cultural learners in a population of mostly asocial learners? It often will: Culture is adaptive when asocial learning is hard and environments fluctuate a lot, but not too much.

While the mathematical reasoning that supports this answer is sometimes subtle (Aoki & Feldman, 2014; Boyd & Richerson, 1985; Hoppitt & Laland, 2013; Nakahashi, Wakano, & Henrich, 2012), the logic of the conclusion is easy to appreciate. If asocial, individual learning (e.g., trial and error) is easy and effective, then metabolic energy and attention spent carefully observing others (cultural learning) is wasted. If environments don't vary much, genes that adapt directly to the environment can produce adaptive behavior more efficiently than ones that build metabolically expensive brains capable of carefully observing others, inferring their goals, copying their actions, and so on. If, on the other hand, environments vary so much that each generation faces dramatically different challenges, then your parents' generation's behaviors, strategies, and practices just aren't worth copying, and asocial learning or genetic programming is the best bet.

These theoretical insights fit well with empirical observations of human behavior. We are more influenced by others' behavior when individual experimentation is difficult, costly, or produces ambiguous results (Caldwell & Millen, 2010; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). Even infants socially reference adults more when confronted with more ambiguous stimuli (Kim & Kwak, 2011). Evolutionary models have allowed us to build theories of human learning.

Why did humans in particular become a cultural species, and why only in the past few million years (Henrich, forthcoming; Henrich & Tennie, under review)? One explanation suggested by these models is that only recently did (a) environments become too unpredictable for genes to track them, (b) fitness-relevant challenges become too hard to be easily, asocially reconquered by each individual, and (c) a species have the cognitive preadaptations to kick-start high-fidelity cultural learning. Consistent with this, ice-core evidence shows that the rate at which global climates (and consequently hominid habitats) fluctuated increased dramatically over the 5 million years since our lineage split from chimpanzees (Potts, 1998; Richerson & Boyd, 2000; cf. Shultz, Nelson, & Dunbar, 2012).

In terms of establishing when humans became cultural, the evidence is scarce, but archaeological findings show that for more than at least 1.8 million years, we have relied on technologies that are hard to invent and master asocially (for review of the evidence, see Henrich, forthcoming). Our hominid ancestors relied on expertly produced Acheulean stone tools, which are hard to reinvent alone (Stout & Chaminade, 2012). Contemporary, healthy, well-educated adults, with a completed example of a stone tool in hand and facing no time constraints, cannot produce stone tools like expert Acheulean stone tool makers did and contemporary experts still do (Geribàs, Mosquera, & Vergès, 2010). In the few remaining societies that use stone tools today, acquiring expertise requires many years of apprenticeship and social learning (Stout et al., 2002). This suggests that by 1.8 million years ago, our lineage already relied on social learning.

Theory and observation both suggest that as global climates began to increasingly fluctuate over the past 5 million years, selection drove many species to rely more on socially learned information. Ours, however, was the first to rely so heavily on social learning, and to do it so faithfully and consistently that we crossed the threshold to cumulative cultural evolution and became a cultural species. Why it was our species that crossed the threshold is just beginning to get scholarly attention, though some researchers argue the key lies in the social organization (e.g., pair bonding) and group sizes of our ancient ancestors (Burkart, Hrdy, & van Schaik, 2009; Chapais, 2008; Henrich, forthcoming).

THE PSYCHOLOGY OF A CULTURAL SPECIES

Building from this theoretical bedrock, scholars have honed in on the details of how natural selection shapes the psychology of a cultural species. These investigations weave formal evolutionary theory with careful empiricism to establish what cues cultural learners use to figure out who to learn from (model biases) and what to pay attention to (content biases).

Some people are just better at certain things, and natural selection favors cultural learners who imitate better models. By studying how children and infants learn, we can test hypotheses about which cultural learning biases were adaptive for our ancestors.

Skill, Success, and Prestige

When learners can easily spot skilled models (that guy's spear goes further), selection should favor a bias for learning from them (for a review, see Chudek, Heller, Birch, & Henrich, 2012). Supporting this evolutionary logic, children preferentially imitate more skillful models when learning object names, artifact functions, and even causal properties. They do this (a) even when the more skilled individual is a stranger rather than a familiar teacher from their preschool, (b) even a week later, (c) even when the more skillful model acts in bizarre and unconventional ways (Scofield, Gilpin, Pierucci, & Morgan, 2013) or has an unfamiliar accent (Corriveau, Kinzler, & Harris, 2013), and (d) even when they have witnessed the skillful model being intentionally deceitful (Liu, Vanderbilt, & Heyman, 2013). Even infants are more likely to imitate a previously competent over a previously incompetent adult (Chow, Poulin-Dubois, & Lewis, 2008; Zmyj, Buttelmann, Carpenter, & Daum, 2010). In novel environments, infants are more likely to seek social cues from novel, competent strangers than their own mother (Kim & Kwak, 2011; Stenberg, 2009)

Young children also preferentially learn from more confident individuals (see review in Chudek, Brosseau, Birch, & Henrich, 2013). Interestingly, children who speak languages with obligate evidential markers—grammatical indicators of the source of information (e.g., Turkish)—respond more to skill cues at a younger age (Lucas, Lewis, Pala, Wong, & Berridge, 2013), suggesting that cultural information itself can shape cultural learning biases.

But sometimes skill differences aren't easy to assess. Even today it's hard to know whether fad diets improve or worsen your health; even with decades of research, it's still not clear what the optimal diet contains, though many people believe they know. Imagine how much murkier these choices were for our prehistoric ancestors. Even when skill is opaque, learners can make good choices by tracking success (Henrich & Gil-White, 2001): Imitate whomever has more positive life outcomes—more wives, more wealth, more friends, and so on. Consistent with this, young children seem to prefer individuals who experience entirely random positive outcomes (Olson, Dunham, Dweck, Spelke, & Banaji, 2008).

Assessing success differences can be difficult, can be costly, or can take a long time, but children need to make learning decisions right now! Luckily, you can also imitate your peers' learning choices ("prestige bias"). For an in-depth exploration of these ideas, see Henrich & Gil-White (2001). These insights explain why when children see strangers paying more attention to someone, they're more likely to learn from them (see review of evidence in Chudek et al., 2012), and when adults need to design a virtual stone arrowhead for hunting, they preferentially imitate both prestigious models (those others have paid attention to) and successful models (those whose stone tools reaped better payoffs), particularly when they themselves were struggling with the challenge (Atkisson, O'Brien, & Mesoudi, 2012).

Self-Similarity, Age, Sex, and Ethnicity

Of course, it's not just about picking the most skilled model; there are also better models for you in particular. A 3-year-old might be more likely to acquire behaviors adapted to his or her personal ecology—the skills it takes to be a successful 3-year-old—from a 4-year-old than by trying to imitate a 50-year-old. Young children do prefer learning from similar or slightly older-aged peers in a variety of domains (see review in Shutts, Banaji, & Spelke, 2010). Even 14- to 18-month-old infants seem to have better recall for actions when they are modeled by 3-year-olds than by adults (Ryalls, Gul, & Ryalls, 2000). It is also well established that children have strong same-sex biases in their learning preferences (Shutts et al., 2010; Wolf, 1973). Adults, meanwhile, seem more susceptible to social influence by those who share their existing beliefs (Hilmert, Kulik, & Christenfeld, 2006).

The existence of an evolving cultural corpus can also give rise to ethnicities—that is, symbolically marked groups (McElreath, Boyd, & Richerson, 2003). Once your fitness depends on culturally transmitted strategies for interaction, and all your peers' fitnesses do too, local norms can become critically important (Chudek & Henrich, 2011), and it makes sense to use arbitrary signals (like accent, dress style, tattoos, body mutilation, etc.) to preferentially identify, interact with, and learn from coethnics. In fact, any interaction governed by social norms (Henrich & Henrich, 2007) can spontaneously generate just these kinds of ethnic correlations between an arbitrary signal (e.g., dialect) and their behaviors (Efferson, Lalive, & Fehr, 2008). Recent developmental psychology has shown that children and infants pay careful attention to others' accents and prefer interacting with and learning from people with familiar ones (see review in Kinzler, Corriveau, & Harris, 2011).

Conformist Transmission

Most people today have lived through the historically bizarre phenomenon of "going to school." Though we grew up in very different parts of the world, at around age 5 most of us found ourselves faced with compulsory attendance in a microsociety of same-aged, mostly unrelated peers—each an evolved cultural learner, and each trying to make sense of the world and making countless choices about what to wear, how to behave, whom to affiliate with, and how to invest their time. So, chances are, you already have some pretty good firsthand experience of conformist transmission (people preferentially adopting the most common behavior) and even anticonformity (preferentially avoiding it).

The simplest null models of cultural evolution assume that—in a given domain, say, how early to wake up—learners carefully observe the beliefs and behaviors of their peers or parents and then pick one at random. These models imply that the probability of someone choosing a cultural variant is just the frequency of that variant in the preceding generation. A natural next step is to ask: Does it sometimes pay to be more or less likely to adopt a cultural variant than its population frequency? If it does, human psychology might be adapted to, all else being equal, conform or anticonform. A widespread conformist bias has profound implications for the long-term, large-scale patterns of cultural evolution we'd expect to see in history.

The question of whether and when conformist transmission pays continues to be the focus of nuanced theoretical analyses. While some models suggest that conformist transmission should be pervasive (see review in Nakahashi et al., 2012; Perreault, Moya, & Boyd, 2012), others imply a more limited scope (Eriksson, Enquist, & Ghirlanda, 2007).

Though psychologists have a long history of studying "conformity" in the broad sense, only recently has evidence begun accumulating on conformity in this narrow sense relevant to cultural evolution: how learning probabilities change as a function of the frequency of a cultural variant. Across several studies, researchers have observed that some individuals use conformist learning (Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; Morgan et al., 2012; Toelch, Bruce, Meeus, & Reader, 2010), among a diversity of other strategies, like ignoring frequency information entirely (Efferson, Lalive, Richerson, et al., 2008), copy the strategy whose frequency is increasing the fastest (Toelch et al., 2010), and increasing dependence on social information as the absolute number of demonstrators increases (which is consistent with theory; Perreault et al., 2012).

CREDIBILITY-ENHANCING DISPLAYS (CREDs)

Imagine yourself as a Pleistocene youth. You notice that Big Bruce is a great hunter, is very rich, has many wives, and that everyone pays attention to him. Something makes Bruce successful, but what is it exactly? Is it the spears he uses, where he hunts, what time of day he goes out, how he shaves his head, or the gods he worships? Since it's hard to know, selection can favor copying everything about Bruce. This logic helps explain why even today, sports or music celebrities are able to increase the sale of milk, cologne, or underpants (Chudek et al., 2012).

However, if we blindly imitated prestigious or successful people, they could easily exploit us. Bruce could tell us the secret to success is giving him half of our meat. The Credibility Enhancing Displays hypothesis (CREDs; Henrich, 2009) proposes an evolved defense: We doubt claims that aren't backed up by actions. CREDs help us understand patterns of religious belief transmission: More children become believers when their parents attend weekly services and give money to charity than if they merely profess belief (Lanman, 2012). In experiments, adult participants make costly commitments to new beliefs after witnessing others engaging in costly actions that only make sense in the light of particular underlying beliefs (Willard, Norenzayan, & Henrich, 2015).

DO THESE CULTURAL LEARNING MECHANISMS MATTER IN THE REAL WORLD?

One of the starkest demonstrations of prestige and self-similarity biases—particularly relevant for students of evolutionary psychology—is the *Werther effect* (Phillips, 1974): the phenomenon of copycat suicides. In 1774, the German author Goethe published *The Sorrows of Young Werther*, whose main protagonist, driven to sorrow by unrequited love, shoots himself. The subsequent spate of copycat suicides by young men led authorities to ban the book in Italy, Leipzig, and Copenhagen. Since then, spikes of copycats of well-publicized suicides of famous individuals (Coleman, 2004; Mesoudi, 2009), by similar victims and using similar killing methods, have been documented in the United States, Germany, and Japan. Besides the obvious prestige or success effect, copycats tend to match their models on gender and ethnicity and be somewhat younger. Statistical analyses show that many of these suicides were not individuals who would have committed suicide anyway, since the rate spikes are not followed by relative dips in the months following the celebrity's suicide (see review in Henrich & Henrich, 2007).

At first glance from an evolutionary vantage point, it seems inexplicably maladaptive that people should kill themselves, let alone that they should do so in imitation of strangers who only superficially resemble them. However, these disturbing patterns make more sense when you recognize that humans are an obligate cultural species. We are equipped with a cultural learning psychology that, on average, sifts out better models and more adaptive information and predisposes us to acquire this information, even if the behavior propelled by this information is individually costly in the short term. Sadly, these cognitive mechanisms can tragically misfire.

WHAT TO LEARN (CONTENT-RICH MECHANISMS)

Not all cultural information is equal—it pays to ignore some things and focus on others. Natural selection ought to have attuned people to attend to fitness-relevant forms of information. These include information about animals and plants, kinship, dangers, mating, fire, reputation, social norms, and social groupings. In fact, many of the psychological adaptations studied by mainstream evolutionary psychology provide the rich cognitive architecture and shape the acquisition of cultural information, creating what we call content biases.

For example, children not only keenly attend to information about animals, but they are selective in what they store in memory. Barrett and his collaborators have demonstrated that children across societies are particularly savvy learners of social information about dangerous animals (Barrett & Broesch, 2012)—we're especially likely to remember when someone tells us that an animal is dangerous, and when children make mistakes they tend to err on the side of assuming animals are dangerous (Barrett & Broesch, 2012; Broesch, Henrich, & Barrett, 2014).

The information is then structured cognitively into hierarchical taxonomies, and information gleaned about one animal or one species is probabilistically extended to other species by category-based induction. If you learn that a particular pet parrot has hollow bones, you readily infer that all parrots have hollow bones, and that perhaps all birds have hollow bones. The combination of cultural learning and this folkbiological cognition provides adults in small-scale societies with an immense body of valuable and adaptive knowledge. However, without cultural input, this cognitive machinery corrodes and begins to malfunction, as it does in urban Western populations (Atran, Medin, & Ross, 2004; Medin & Atran, 2004).

Similarly, recent investigations of infants' responses to plants suggests that even at around 1 year of age we recognize plants as something special that should be approached cautiously (Wertz & Wynn, 2014) and have a special sensitivity to information about whether they are edible (Wertz & Wynn, in press). Infants, who seem to immediately put almost anything in their mouths, will pause when encountering a plant and wait to see if anyone else tastes or eats it (a CRED) before putting it in their own mouth.

Here's a small sampling of work in other content domains of cultural learning:

> *Reputation information:* Mesoudi, Whiten, and Dunbar (2006) have demonstrated that gossipy information—about others misdeeds and affairs—gets transmitted more faithfully through laboratory social networks.
>
> *Fire:* Fessler (2006) has drawn on diverse evidence to argue that children's psychology may be calibrated for attending to and learning about fire.
>
> *Norms:* Tomasello and his colleagues have experimentally demonstrated that young children are particularly attuned to notice others' behavioral regularities and interpret them as injunctive social norms, spontaneously enforcing them on a "norm-violating" behaving puppet (Schmidt, Rakoczy, & Tomasello, 2011; Schmidt & Tomasello, 2012).

By focusing on content mechanisms, cultural evolution can interface in important ways with mainstream evolutionary psychology. For example, much work on human mating preferences has shown reliable patterns across societies as well as interesting cross-population variation and historical change over time (Buss, Shackelford, Kirkpatrick, & Larsen, 2001; Henrich, Heine, & Norenzayan, 2010). Consistent with this, increasing evidence now shows how humans use the forms of biased cultural learning discussed above not only in assigning mate values to individuals but also in assigning mate vales to attributes, like hair style or dress (see review in Henrich, forthcoming; Little, Jones, DeBruine, & Caldwell, 2011; Zaki, Schirmer, & Mitchell, 2011). Of course, this doesn't imply that mate preferences are merely culturally learned, since there ample and reliable preferences across diverse societies and mate preference variation may be due to factors besides cultural learning. It does, however, begin to suggest how an evolutionary psychology that fully incorporates cultural evolution can provide a more complete account of human nature and diversity.

Finally, one important and emerging area of work is the evolution of teaching, which is the flip side of cultural transmission (Fogarty, Strimling, & Laland, 2011). Evolutionary approaches to teaching have already begun to generate important insights in small-scale societies (Kline, Boyd, & Henrich, 2013).

CULTURAL EVOLUTION

So far we've explored scientific terrain that should be familiar to someone reading a handbook of evolutionary psychology. We've asked how natural selection might have adapted our modern minds for navigating a particularly important challenge our ancestors faced—the challenge of cultural learning. Now we take an exciting step further by asking: Given our evolved psychology, how does culture itself evolve? How can we, as researchers, describe, model, test, and understand the ways in which the information we transmit between individuals and between generations changes over decades, centuries, and millennia?

CULTURAL EVOLUTION BUILDS ADAPTATIONS

Cultural adaptations are all around us, but they can be hard to see, let alone understand. In a few cases, such as the metric system, our cultural corpus was honed by smart minds making deliberate choices. For the most part, though, the behaviors we acquire—how we tie our shoes, give directions, and even divide the color spectrum (Deutscher, 2011)—have been dynamically shaped by many millions of evolved, biased minds learning, forgetting, applying, and transmitting information over generations. These dynamics play out on scales far larger than our individual lives, and so, like genetic evolution, are difficult to perceive with the naked eye.

There are, however, rare and valuable moments when the consequences of these processes are cast into stark relief. For instance, when anthropologists study small-scale societies through the lens of modern science, they see culturally acquired practices extraordinarily well adapted to local environmental challenges, yet the people themselves merely claim it's just "our custom" (Henrich, 2002; Henrich & Henrich, 2010). How can we explain this? Must we assume that each culture's history is peppered with long-lost savant shamans, who secretly, consciously crafted these traditions?

We needn't, which is good given the many flaws in human reasoning (Henrich, forthcoming). Mechanisms such as the success bias, prestige bias, conformist bias, CREDs, content biases, and intergroup competition allow cultural information to improve and aggregate over generations, without anyone ever needing to understand why or how it is happening, or why a given cultural practice or tradition is effective.

CULTURAL EVOLUTION SHAPES PREFERENCES AND THINKING

Don't make the mistake of thinking that culture is a passive thing—merely a message that is distorted by our biased minds as it is whispered between generations. Culture isn't just shaped by our minds; our minds are shaped by culture.

Consider this case: Like other primates, humans are born with a taste aversion to spicy chili peppers. However, despite this aversive content bias, many populations in the New World have incorporated chilies and other strong spices as essential ingredients in their cuisine. Billing and Sherman (1998) conducted an extensive survey of the recipes from across the world, along with a survey of the antimicrobial properties of different spices. They found a strong relationship: Societies in climates that posed the greatest pathogen risk due to food spoilage also had the greatest preponderance of antimicrobial spices in their food.

How did these societies come to have such conveniently adaptive culinary tastes? It is implausible that individuals recognized that the bad taste of plant toxins was outweighed by their value in fighting disease and decided to overcome their innate aversions and incorporate spices into their diets. Most individuals just try different foods and imitate others' dietary choices as children. What tastes good is a combination of genetics (sweet items provide glucose) and culture (chili peppers provide antimicrobial defense despite genetic predispositions against them). But how does culture override our genetically encoded preferences?

Experiments show that children readily adopt the food choices and preferences held by their peers (Birch, 1987; Duncker, 1938), and exercise those preferences in both their private food rankings and public behavior. Consistent with this, evidence from neuroscience indicates that seeing cultural models prefer something actually makes a learner enjoy it or desire it more himself, even if he is alone (Zaki et al., 2011). The available evidence indicates that cultural learning alters our brains to change our preferences for, or tastes in, wine, men, and music (see review in Henrich, forthcoming, Chapter 16).

These cultural adaptations, modifications of our tastes in this case, are the long-term outcomes of population-level evolutionary processes, guided by the adaptive learning biases we described above. When many people across many generations are more inclined to learn from their slightly healthier and more successful peers, the entire population's dietary preferences and culinary repertoire will gradually become more adaptive. The same processes sometimes shape food taboos. Henrich and Henrich (2010) fill out the details of this process by examining how an adaptive repertoire of fish taboos, which protect pregnant women from dangerous marine toxins, has accumulated to address a local environmental challenge in Fiji.

In addition to preferences, ample evidence from diverse societies documents variation across populations in seemingly basic psychological domains (Henrich, Heine, et al., 2010). Across cultures, people differ in susceptibility to visual illusions, notions of fairness, motivations to punish, morality, endowment effects, spatial and folkbiological reasoning, conformity, IQ, underwater vision, and analytic thinking. In some cases, these psychological differences may arise from jukebox-like adaptive responses to distinct environmental cues, but the strength of these cues is almost always shaped by culturally constructed environments, including both institutions and technologies. Cultural evolution provides an evolutionarily grounded approach to building theories about how and why these (nongenetic) psychological differences emerge and are maintained (Henrich, Ensminger, et al., 2010; Hruschka & Henrich, 2013; Leibbrandt, Gneezy, & List, 2013; Nisbett & Cohen, 1996).

Documenting societal differences needn't be just an exercise in butterfly collecting (for this, see cultural psychology); in the light of cultural evolution, patterns of cultural differences can be theorized within a Darwinian framework.

SOCIALITY INFLUENCES CULTURAL EVOLUTION

The sociality of a population—its size and interconnectedness—also influences the process of cumulative cultural evolution. Larger populations tend to have more complex technology and culture (Edinborough, 2009; Kline & Boyd, 2010; Powell, Shennan, & Thomas, 2009). When populations shrink, cultural and technological complexity seems to also decline (Boyd et al., 2011; Henrich, 2004). Models of cultural evolution (Aoki, Lehmann, & Feldman, 2011; Kobayashi & Aoki, 2012; Lehmann, Aoki, & Feldman, 2011; Powell et al., 2009) explain why.

Each society has a distribution of skills—some individuals, like Bruce, are better at making bows than others. Prestige and success biases lead people to copy Bruce. On average, most imitators don't become as good as Bruce, but the larger the population, the higher the chance that one or two may be better. In a more interconnected population, people are more likely to have access to better models, learning from the best and integrating insights and techniques from more individuals. If populations shrink, the number of people better than Bruce decreases, and even with adaptive learning biases, on average, accumulated know-how or technical sophistication may be lost over generations. Recently, two teams have confirmed these predicted relationships using laboratory experiments (Derex, Beugin, Godelle, & Raymond, 2013; Muthukrishna, Shulman, Vasilescu, & Henrich, 2013). Psychology-style laboratory experiments can teach us about long-term cultural evolution.

CULTURAL MALADAPTATION

Our transition to cumulative cultural evolution has allowed us to live in an astonishing array of environments and become Earth's dominant species. But just as genetic evolution doesn't always lead to perfect solutions—from runaway selection (peacock tails), to the previously adaptive (sickle cells), to the vestigial (wisdom teeth)—so too can cultural evolution lead to cultural maladaptations.

Runaway cultural evolution can occur when naïve learners preferentially learn from prestigious individuals, identified by an arbitrary marker, leading to an arms race for more potent versions of the marker. Boyd and Richerson (1985) give the example of tattooing in Polynesia. Without the benefits of a modern tattoo parlor, tattooing in Polynesia was painful and somewhat dangerous, such that only about a foot of the body could be tattooed in one sitting. The recovery from each sitting involved 8 to 12 days of local inflammation and fever, which sometimes proved fatal. Tattooing was also very expensive, taking 6 months for the initial tattoo and requiring the supply of food and shelter for the artist and his family for the duration. Why would such a maladaptive practice evolve?

Being both expensive and dangerous, tattoos became a marker of prestige, and tattooed individuals were more likely to be imitated by others, including their preference for tattooing and tattooed cultural models. As people competed for prestige, tattoos became larger and more elaborate, increasing their danger and cost in a runaway process, where individuals spent more and more resources they could otherwise use for food, shelter, and other immediately adaptive benefits. Similar processes may explain why poorer people spend money on luxury goods, and knock-offs, well beyond what they can afford.

Our norm psychology (Chudek & Henrich, 2011)—our tendency to recognize, internalize, and copy norms—cannot readily distinguish between adaptive, neutral, or even maladaptive norms. Mechanisms like reputation, signaling, and costly punishment can sustain any costly behavior independent of whether the behavior contributes to others or the group. Indeed, many nonadaptive traditions have stabilized in some cultures—from New Guineans eating the brains of their dead relatives and developing the fatal brain disease kuru to some Africans and Middle Easterners removing the clitori of their girls (Durham, 1991; Edgerton, 1992).

How cultural evolution produces and maintains maladaptive practices is a rich area for future research. Early insights include why ineffective medical treatments spread (they are used for longer periods, so have more chance to be imitated even though they are abandoned more frequently [Tanaka, Kendal, & Laland, 2009]); how lifetime celibacy, reliance on prayer over modern medicine, or suicidal warfare spread (Henrich, 2009); and the network structures that make maladaptive practices more likely (Yeaman, Schick, & Lehmann, 2012).

INTERGROUP COMPETITION SHAPES CULTURAL EVOLUTION

We have discussed learning biases, such as prestige, success, and conformity biases that allow individual-level choices to shape population-level outcomes. However, sometimes cultural differences between competing populations can have their own potent influences on cultural evolution. Such processes are usually called *cultural group selection*, and may have particularly important consequences for understanding the emergence of our sense of morality and prosocial motivations.

Many biologists are skeptical of "genetic group selection," and many psychologists are rather confused by the highly technical and mathematical nature of the debates (see Henrich, 2012). Here's a necessarily too-brief introduction. Natural selection operating within groups usually eliminates genes that cause individuals to behave cooperatively (i.e., paying costs to benefit other group members). Even if a cooperative group outcompetes others in the short term, cooperative individuals are at a disadvantage *within* their group. This disadvantage usually dominates because even small rates of migration quickly make interacting groups genetically similar, sapping the genetic importance of intergroup competition. This is why biologists are skeptical of genetic group selection.

Cultural group selection is an entirely different story. Unlike genetic evolution, it has a variety of mechanisms that sustain trait variation between populations. These relate to language barriers, conformity bias, prestige, ethnocentric biases, reputation, CREDs, punishment, and norm psychology, just for a start. This persistent between-group variation means that intergroup competition, when it occurs, favors some ideas, norms, values, institutions, and practices over others. Since the children of migrants adopt the cultural traits of their community yet still carry their parents' genes, cultural group selection is plausible under many circumstances where genetic group selection is not. Cultural evolution and intergroup competition can also generate purely within-group selection pressures on genes, favoring psychological mechanisms for prosociality, norm compliance, and shame (Chudek & Henrich, 2011; Chudek, Zhao, & Henrich, 2013).

Empirical work by Bell, Richerson, and McElreath (2009) confirms these theoretical expectations: Globally, the amount of cultural variation among groups is much greater than the amount of genetic variation among groups. This is precisely the evidence that convinces evolutionary theorists that cultural group selection could very well be a major force in cultural evolution.

The importance of intergroup competition in shaping cultural evolution is further supported by a rich combination of experimental work, field studies, historical cases, and archaeological research. For recent reviews, see Richerson and Boyd (2005), Richerson et al. (2014), and Henrich (forthcoming).

THE CULTURAL EVOLUTION OF RELIGION

Religion is an evolutionary puzzle. Supernatural beliefs, devotions, and rituals are universal, but variable, and often demand costly commitments to beliefs and practices that violate logical consistency and intuitive expectations (Atran & Norenzayan, 2004; Boyer, 2001). From an evolutionary perspective, a purely genetic account would be hard-pressed to explain these costly and often fitness-reducing beliefs and practices. However, our species has (at least) two lines of inheritance—genetic and cultural—and the mechanisms of cultural evolution we've discussed can begin to unravel this evolutionary enigma.

The cultural evolution of religion involves (a) content biases, (b) CREDs, and (c) cultural group selection (Atran & Henrich, 2010; Norenzayan, 2013). First, our theory of mind abilities, which may have evolved for high-fidelity cultural learning, favor beliefs in supernatural agents (Atran & Norenzayan, 2004). Cognitive scientists have argued that religious agents, such as spirits, are "minimally counterintuitive" and thus more easily remembered and retransmitted (Norenzayan, Atran, Faulkner, & Schaller, 2006)—a content bias. So, you can't explain religion without reference to reliably developing features of mind.

However, nothing in this (so far) purely content-based approach explains why some people believe in and are committed to a particular supernatural agent or agents while others are not. Folktales may spread widely because they are minimally counterintuitive, but people need not be deeply committed to those folktales. Similarly, Christians may come to entirely acquire the concept of Shiva or Zeus, but not come to believe in either (Gervais, Willard, Norenzayan, & Henrich, 2011). A proper theory needs to explain the existence of faith or committed belief. CREDs provide one solution to this puzzle (Henrich, 2009). Watching Mom, Dad, and members of one's community engage in costly displays of self-sacrifice (animal sacrifices, fasting, prayer time, charitable giving, celibacy, time-consuming rituals such as church services, etc.) deepens observers' commitment to the beliefs underlying these practices. Gods who demand costly sacrifices from believers are transmitted more effectively because learners, seeing those costly sacrifices, will themselves come to deepen their faith.

Finally, why are gods in the modern world frequently concerned with rewarding and punishing people for (im)moral behavior? Why are the gods of hunter-gatherers typically weak, whimsical, and not morally concerned? The final puzzle piece is intergroup competition. Supernatural beliefs and rituals that galvanize cooperation and favor success in intergroup competition preferentially proliferate over centuries. The rise of big moralizing gods (such as Yahweh and Allah) may have been pivotal for the evolution of larger societies of anonymous but prosocial individuals compared to the smaller and often nonmoralizing deities typical of small-scale societies (Atran & Henrich, 2010; Norenzayan, 2013). A large body of experiments now supports that belief in religions with big moralizing gods, but not other religions or atheism, promotes prosocial behavior with strangers who are coreligionists (Atkinson & Bourrat, 2011; Norenzayan & Shariff, 2008). Cultural group selection helps us understand the variation in religions over space and time.

CULTURE-GENE COEVOLUTION

There's now little doubt that cultural evolution has shaped genetic evolution, especially over the past 10,000 years. Specific genes in the genome have been identified that show evidence of positive selection as a consequence of cultural practices. Examples of genes selected by pressures created by cultural evolution include genes for milk drinking (lactase persistence; gene LCT), alcohol processing (alcohol dehydrogenase, ADH), and blue eyes (HERC2), not to mention a host of genes related to brain growth, dietary diversity, and pathogen resistance (Laland et al., 2010; Richerson et al., 2010).

Building on this, some researchers have argued that cultural evolution has been driving genetic changes in the human lineage for hundreds of thousands or even millions of years, back to the origins of the genus Homo (Henrich & McElreath, 2003; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007). Variously termed the Cultural Brain Hypothesis or Cultural Intelligence Hypothesis, the idea is this: By generating an ever-expanding body of cultural know-how, including knowledge and skills related to tool making, animal tracking, plant processing, fire making, cooking, and shelter construction, cultural evolution created the key selection pressures driving recent human evolution and ignited an autocatalytic interaction between genes and culture that drove the rapid expansion of human brains in a relatively short period of evolutionary time. Once culture began to accumulate, selection would have increasingly favored brains equipped to acquire, organize, store, and retransmit the available cultural information. However, as brains got bigger and better at cultural learning, cultural evolution would have responded by expanding the pool of adaptive information available to the learner. The better learners got, the faster culture evolved and the larger the pool of cultural information grew. The cultural brain hypothesis claims that big brains are *for* cultural learning, not generalized intelligence, individual problem solving, or Machiavellian deception and strategizing.

The importance of culture may have implications beyond the autocatalytic culture-gene coevolutionary spiral of the human lineage. Researchers have also considered how social learning may have shaped primate brains, group size, sociality, and life history (van Schaik & Burkart, 2011; van Schaik, Isler, & Burkart, 2012). Theoretical models of these hypothesized gene-culture coevolutionary processes successfully reproduce the empirical patterns of relationships between brain size, group size, and juvenile periods observed in primates (Muthukrishna, Chudek, & Henrich, 2015).

Gene-culture coevolution neatly sets humans within the primate order while at the same time explains our unique evolutionary trajectory.

CONCLUSION

Understanding humans from an evolutionary perspective isn't easy. Not only do we have countless psychological adaptations and peculiarities, honed to environments long vanished, but we are an evolved cultural species, the inheritors of two different and very complex systems of evolving information. Like most discoveries in our information age, the evolutionary science of our cultural species hasn't emerged *sui generis* from the mind of a great thinker. Rather, it has and continues to coalesce at the intersection of an ever-ballooning body of work by biologists, anthropologists, and economists from many different backgrounds. Psychologists play a key role in this important episode of discovery, as the many citations above attest. In our view, this approach unites and synthesizes exciting lines of research in developmental psychology, social psychology, cultural psychology, and evolutionary psychology under a broad Darwinian umbrella. The emerging science of cultural evolution is building an understanding of our species from its origin to the present day, from the genetic evolutionary emergence of cultural learning in our species to the many fascinating phenomena produced by cultural evolution around us today, such as religions with big moralizing gods, markets, normative monogamy, ethnicity, castes, and technological change.

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CHAPTER 31

Morality

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INTRODUCTION

IN THE PRIOR version of the chapter on morality in this *Handbook*, Krebs (2005) took his task to be to "explain how mechanisms that give rise to moral and immoral behaviors can evolve" (p. 747). In this version of the *Handbook*, reflecting changes in scholarship surrounding morality over the past decade, we seek to explain not moral *behaviors*, but rather the evolved function of mechanisms that give rise to moral *judgments*, *beliefs*, and *motives.*

This crucial distinction is subtle and readily overlooked. One research question asks: What explains behaviors that are widely judged as morally right, such as altruism, honesty, and fairness? A second, very different, research question asks: What explains why humans judge any behaviors *at all* to be moral or immoral?

In focusing on moral behavior, Krebs followed in distinguished footsteps. Darwin (1871), in his two chapters on morality, developed an explanation for *altruistic behavior*, proposing that sympathy was the "foundation stone" of morality, motivating people to help others. Darwin built his account on group selection, the idea that moral behavior was selected because it facilitated success in between-group competition, an idea that waned (Williams, 1966) and waxed (Haidt, 2012) in subsequent years.

Research in moral psychology over the past two decades, especially proposals by scholars such as Shweder, Rozin, and Haidt (e.g., Haidt, Koller, & Dias, 1993; Shweder, Mahapatra, & Miller, 1987), has expanded the discussion beyond what Darwin, Krebs, and others took to be the quintessential puzzle in moral psychology: why humans deliver benefits to one another. Haidt, for example, emphasized that cross-culturally, moral issues include not only altruism but also sexual practices, intuitions about purity, and deference to authority, among other spheres of life.

In turn, this expansion has led to new explanations for "moral" behavior. Haidt (2012), for example, invoked kin selection (Hamilton, 1964), reciprocal altruism (Trivers, 1971), and pathogen avoidance to explain the array of behaviors that encompass morality. Importantly, these explanations continue to focus on moral behavior. Kin selection theory explains why people have systems designed to deliver

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benefits to close relatives. Reciprocity theories (Axelrod & Hamilton, 1981; Fehr, Fischbacher, & Gächter, 2002; Nowak & Sigmund, 2005; Trivers, 1971) explain why people have systems designed to aid those who have previously helped themselves (or others, in the case of indirect reciprocity). Theories of pathogen avoidance explain why people have mechanisms designed to cause them to avoid exposure to bacteria and viruses.

Although these theories do an excellent job of explaining many kinds of moral behavior, it is important to note what these theories do not explain. Although the selective advantage of avoiding pathogens, for instance, explains why individuals avoid decaying animals, it emphatically does not explain, *in itself*, why one individual can come to believe that other individuals should be punished for exposure to pathogens. Whereas many organisms have adaptations designed to resist pathogens, humans *judge* others for engaging in behaviors that they themselves avoid, *believe* that such behaviors are "wrong," and (in at least some cases) are *motivated to harm* (i.e., punish) people who engage in such behaviors.

The balance of this chapter is aimed at explaining these features of human psychology. Far from leading to a disconnect with the previous *Handbook* chapter and related theories, explanations of judgment, beliefs, and motives dovetail felicitously with prior accounts. To the extent that people's beliefs about what is wrong and should be punished are explained, an additional explanation is provided for why people choose not to engage in behaviors so judged: to avoid the punishment others are motivated to mete out.

MORAL PHENOMENA: CUTTING MORALITY AT THE JOINTS

Throughout history, moral beliefs have motivated people to imprison, torture, and execute other people for behaviors such as premarital sex, witchcraft, endorsing religious beliefs, and scientific research. Morality continues to motivate hate crimes, mass incarceration, and terrorism (Atran, 2010). Moral condemnation of abortion kills 47,000 women per year and inflicts injuries on millions by causing societies to outlaw safe abortions (World Health Organization, 2011). In the United States in 2012, law enforcement reported 1,318 hate crimes motivated by anti-homosexuality attitudes (Federal Bureau of Investigation, 2012). Moral condemnation of drugs has had "devastating consequences for individuals and societies around the world," including mass incarceration and funding organized crime (Global Commission on Drug Policy, 2011). On a smaller scale, people's moral judgments can interfere with close personal relationships, as when moral righteousness undermines compromises among friends.

These destructive moral phenomena are distinctively human. In contrast, many behaviors commonly judged as morally right, such as altruism, parental care, honest communication, monogamous mating, respect for property, and restraint of aggression are widely observed in nonhuman animal species (Davies, Krebs, & West, 2012). Importantly, members of these species do not make explicit moral judgments, communicate moral rules, debate which rules are best, punish violators, or espouse impartial judgment. There are then, across taxa, many causes of behaviors commonly judged "moral," even in the absence of moral judgments and systems of moral rules.

Moreover, the human capacity for moral judgments does not necessarily systematically lead to moral behavior (Kurzban, 2010). Research on moral hypocrisy shows that people often engage in behavior that they themselves judge to be morally wrong

(Batson & Thompson, 2001). In one set of experiments, most participants made someone else do an unpleasant task rather than do it themselves even though they said it was morally best to use a coin flip to decide (Batson & Thompson, 2001). Similarly, developmental research has found that children's moral judgment of other people's lies was unrelated to their own lying behavior (Talwar, Lee, Bala, & Lindsay, 2002). In short, there is a double dissociation between moral behavior and moral judgment that potentially points to different evolved functions, and, further, suggests that it is moral judgment that is most distinctive and least understood.

Researchers can, of course, define "morality" in many ways. However, we are not certain of the value of defining "morality" as all behaviors that humans might moralize: altruism, reciprocity, fairness, honesty, monogamy, fighting, parenting, black magic, supernatural beliefs, cryopreservation, cigarette smoking, and on and on. Similarly, extremely broad definitions such as prosocial or non-zero-sum behavior essentially include all social behavior and equate morality to sociality, making these two terms redundant. We therefore favor a narrower scientific definition, following moral philosophers such as Kant (1785/1993) or Moore (1903), who draw a sharp distinction between moral judgment and the behaviors that are morally judged. Evolved moral adaptations, on this view, are the cognitive programs that compute moral values for a diversity of actions, but are not the systems that produce the actions themselves.

For the remainder of this chapter, we use the term "morality" to refer to the observation that people, cross-culturally, judge some behaviors as "wrong" as opposed to "right" or "not wrong." Our interest is in explaining this "moral sense," as James Q. Wilson (1993) put it: people's experience of others' behavior as falling along a moral continuum. The balance of this section reviews the empirical features of moral beliefs and judgments that a theory of morality must explain.

BEYOND HARM AND ALTRUISM

A critical advance in the study of morality was the idea that moral judgment does not focus only on preventing harm and promoting altruism. This is clear from the anthropological record, which shows a stunning diversity of rules about sex, food, violence, communication, property, trade, witchcraft, supernatural beliefs, and more. For instance, recently there has been debate in Iran about whether it is immoral to own a dog, currently a punishable offense (Fassihi, 2011).

Shweder, Much, Mahapatra, and Park (1997) interviewed participants from Bhubaneswar, India, about perceived moral violations such as a woman who ate rice with her husband and his elder brother, a son who addressed his father by his first name, or a widow who ate fish twice in a week. When asked why these and 30 other behaviors were morally wrong, participants' justifications referred not only to harm, but also to hierarchy, duty, divinity, purity, and other concerns.

Further, Haidt (2001) showed that even when people claim that consideration of harm drives their moral judgments, these claims are often *post hoc* justifications rather than the genuine causes of judgments. Haidt presented participants with harmless moral offenses and asked them why the offenses were morally wrong. Many participants referred to particular harms. Researchers then asked participants to imagine that these harms were hypothetically ruled out. When all harms were removed, many participants maintained their moral judgments even when unable to explain why, a phenomenon termed *moral dumbfounding*. Tetlock (2000) used a similar procedure and found the same results: Many participants continued to condemn practices such as markets for body organs even after potential harms were eliminated to their satisfaction. Related work shows that the harshness of moral judgments for violations (such as eating dogs, cleaning a toilet with a flag, etc.) is not predicted by participants' own assessments of harm (Haidt et al., 1993; Haidt & Hersh, 2001).

Haidt's (2012) *moral foundations theory* attempts to account for the diversity of moral rules. Haidt motivates each foundation—fairness, loyalty, authority, sanctity, and, of course, harm—with a different adaptive problem: parental care, reciprocity, coalitions, hierarchies, and contaminants, respectively.

A good theory of morality needs to account for diversity in the content of moral rules. At the same time, a good theory should also account for the many common features of moral cognition that cut across moral domains. Why, for instance, are violations in different domains all judged "wrong," rather than each only having its own specific label as uncaring, unfair, disloyal, disobedient, or impure? Across domains, wrongness is associated with accusations, guilt, condemnation, gossip, punishment, and impartiality. These common properties can be seen in the process of *moralization*—when amoral actions are transformed into moral violations (Rozin, 1999). Rozin (1999) argues that moralization of behaviors such as smoking or eating meat are associated with a suite of psychological features including prohibition, outrage, censure, overjustification, internalization, and facilitated social learning.

Nonconsequentialism

Explanations of moral judgments must, obviously, account for the broad empirical patterns of such judgments. Arguably one of the most important patterns is that moral judgments are often *nonconsequentialist* (cf. Sinnott-Armstrong, 2006). That is, as an empirical matter, people's judgments of whether a behavior is wrong do *not* depend *only* on their beliefs about the (actual, direct, and intended) consequences of the action (Hauser, 2006). Specifically, moral judgment is deontic, sensitive to the action chosen by the actor, rather than only the intended consequences.

The most common empirical example is judgments about the Trolley Problem, a vignette used to probe people's moral intuitions (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001; Mikhail, 2007). In the Footbridge case, a runaway trolley will kill five innocents on the track unless a man with a large backpack is pushed off of a footbridge onto the tracks, killing the man but stopping the trolley. If people's moral intuitions were consequentialist, then people would judge pushing the man with the backpack as morally good, since the consequences of pushing lead to one death instead of five. Cross-culturally, in sharp contrast, a vast majority of subjects judge pushing to be wrong (Hauser, 2006). Similar evidence of nonconsequentialism is found in research on taboo tradeoffs (Tetlock, 2003) and protected values (Baron & Spranca, 1997); results of research in these areas show that moral cognition is particularly attuned to prohibited actions rather than only consequences.

These observations of nonconsequentialism are important because they contradict prominent explanations for moral judgment. Altruism models, for example, predict a primary focus on consequences. For instance, kin selected systems should be expected to guide behavior towards good (i.e., inclusive fitness maximizing) consequences.

And, indeed, many organisms routinely harm or kill one close relative (sibling, offspring) in order to benefit more than one other close relative (Mock, 2004). In sharp contrast, 84% of people said it's wrong to push one brother to save five brothers (Kurzban, DeScioli, & Fein, 2012), even though many participants (47%) said they would push anyway, despite it being wrong. If moral judgments were designed by kin selection, then people should judge pushing to be virtuous, rather than wrong. Nonconsequentialist judgments point to a different class of explanation. Moral judgment systems focus on *how actions are completed* as opposed to *the consequences they bring about*. This points to the possibility that they are solving a *coordination problem*, as discussed below (DeScioli & Kurzban, 2013).

JUDGMENTS ARE COMPLEX, IMPLICIT, AND VARIABLE

Although some view moral judgments as products of simple heuristics (Baron, 1994; Gigerenzer, 2007; Sunstein, 2005), other researchers have found that moral judgments are complex, responding to many features of behavior and context. Returning to the Trolley Problem, discussed above, Mikhail (2007) found that moral judgments depend systematically on particular structural features of the behavior. In the Footbridge case, for instance, the person with the backpack is used as a means to an end—stopping the trolley. In the Switch case, however, the man's death is a side effect, and most participants judge killing one to save five by diverting the train to be morally permissible. Moral judgments track this distinction between means and side effects across a variety of moral offenses (DeScioli, Asao, & Kurzban, 2012).

Another important distinction that has received substantial attention is the act/omission distinction. Somewhat puzzlingly, people reliably evaluate an outcome as less wrong if it comes about as a result of inaction as opposed to action, holding both the outcome and intentions constant. For instance, withholding the antidote from someone is judged less wrong than poisoning someone, even when the intent in both cases is the person's death (Cushman, Young, & Hauser, 2006). This effect too occurs across a variety of moral domains; for instance, participants judge cannibalism to be more morally wrong if it is done through an action as opposed to inaction (i.e., not spitting out food after finding out that it is human flesh; DeScioli, Asao, & Kurzban, 2012).

Although moral judgments track these dimensions of behavior, participants are often unable to articulate the relevant factors behind their differing moral judgments (Haidt, 2012). Indeed, Haidt and others have argued that moral psychological judgments are frequently—though not always—implicit and intuitive as opposed to conscious and explicit. The source of moral judgments, then, is at least sometimes located in nonconscious systems, including emotional systems. These considerations have led Mikhail (2007), among others, to compare moral judgment to natural language insofar as such judgments involve complex and unconscious computations.

Finally, a key feature of moral judgments is that the actions that are moralized vary tremendously across time and across cultures (Haidt, 2012; Rozin, 1999; Shweder et al., 1987). This variability is perhaps most transparent in cases in which two different cultures moralize opposite behaviors. For instance, Western readers are familiar with property rights regimes in which the person who takes a resource is the perpetrator: *Taking* is moralized. However, in some moral regimes, in which property rights prioritize needs over who acquired the goods, *refusing to give* is moralized. For example, Fiske (1992) discussed *communal sharing* relationships in which individuals are expected to share resources with those in greater need. More generally, moralized categories of behavior in one culture often seem very peculiar to members of other cultures. Food taboos, clothing restrictions, and sexual mores offer many examples.

In short, while there are some cross-cultural similarities in moral rules—unprovoked intentional harm is frequently moralized—there is also a tremendous amount of variability.

PUNISHMENT

Moral judgments, once made, are accompanied by a cascade of emotions and motivations; in particular, moral infractions evoke anger and disgust (Rozin, Lowery, Imada, & Haidt, 1999), and, generally, the intuition that the actor should be punished (Robinson & Kurzban, 2007; Wiessner, 2005). The desire for punishment provides a clue to the function of moral judgments. For example, if moral judgments were built simply for choosing interaction partners (Baumard, André, & Sperber, 2013), then it is unclear why people would seek punishment rather than simple avoidance of perpetrators.

Further, the motive to impose costs is important because the motive itself could potentially carry costs. Because harming others provokes subsequent retaliation by the person harmed and their allies (e.g., Knauft, 1987), the motive to do so must, presumably, be offset by some gain to the individual.

Three other well-documented features of the motive to punish are potentially important. First, while the desire that perpetrators be punished is very common, people do not necessarily want to mete out the punishment themselves. Laboratory evidence indicates that when behavior is kept carefully anonymous, people do not engage in much costly punishment (Kurzban & DeScioli, 2013), suggesting the absence of a motive to punish per se, absent reputational benefits (Kurzban, DeScioli, & O'Brien, 2007). This distinguishes moralistic punishment from revenge in which people seek to punish those who have imposed harm on them (rather than for violating a moral rule against someone else) (McCullough, Kurzban, & Tabak, 2013).

Second, there is tremendous cross-cultural variability in how infractions are punished, ranging from informal sanctions (Hess & Hagen, 2002; Kaplan & Hill, 1985; Wiessner, 2005) to the intricate, culturally elaborated police and justice systems in industrialized societies. Third, and perhaps related, whereas the particular behaviors that are punished—and how much they are punished—vary tremendously, there is widespread agreement about the relative severity of many moral violations and, consequently, the severity of punishment they merit (Robinson & Kurzban, 2007).

IMPARTIALITY

A signal feature of evolved social behavior is *favoritism*, whether with respect to kin (Hamilton, 1964), prior interactants (Trivers, 1971), coalitions members (Harcourt & de Waal, 1992), coethnics (Gil-White, 2001), and so forth. Favoritism allows organisms to direct social efforts toward partners who bring them greater benefits.

One feature of moral psychology, impartiality, presents a puzzle in this context. By *impartiality* we mean that a person is *impartial* to the extent that the person's judgment of another's moral wrongness is applied independent of the actor's identity (e.g., kinship, ingroup, ethnicity). Impartiality, then, refers to ignoring the very criteria that altruism systems commonly use to guide preferential behavior (see also Shaw, 2013).

The empirical data do not, of course, support the extreme claim that *everyone* is *always* impartial in their moral judgments of others' actions. The data do, however, support the narrower, weaker claim that people are sometimes impartial. That is, people will sometimes damage their valuable relationships when the violation of a moral rule is at stake. One study found, for instance, that more than half of American soldiers would report a member of their unit—generally extremely loyal groups—for committing violence against foreign civilians (Morgan, 2007).

Evidence from the laboratory is similarly suggestive. Lieberman and Linke (2007), in one of the few studies looking at the relationship between preexisting social ties and moral judgments, found that people's wrongness judgments did not depend on group membership or even kinship relations; kin were judged as harshly as strangers, though kin were seen as deserving less punishment.

Generally, impartiality as a communally valued aspect of moral judgment—illustrated by Lady Justice's blindfold—is both a puzzle and clue surrounding moral judgments. Set against the backdrop of adaptations for treating others *differently* depending on relationships—including loyalty, reciprocity, and nepotism—moral impartiality stands out as an important property to explain.

MORAL JUDGMENTS COORDINATE IN CONFLICTS

The empirical patterns in moral judgment suggest that the underlying psychological mechanisms do not function to benefit kin, solidify groups, avoid pathogens, and so on. Instead, we argue that these patterns are best explained by a different function: choosing sides in disputes (DeScioli & Kurzban, 2009, 2013).

In human social life, people have conflicts over status, resources, and mates. Bystanders to these conflicts often must choose sides, particularly when both sides request support. In nonhuman animals, with a few exceptions, the adaptive problem of choosing sides does not exist. In some cases, this is simply because conflicts are never greater than dyadic is size: In many animal species, individuals do not team up (Harcourt, 1992). In other species, when bystanders intervene they always side with kin (e.g., baboons; Seyfarth & Cheney, 2012), so difficult side-taking decisions do not commonly occur. More rarely, individuals in some species support nonkin, including chimps, macaques, and dolphins (Connor, 2007; de Waal, 1982; Schülke, Bhagavatula, Vigilant, & Ostner, 2010).

Human conflicts often escalate beyond two individuals. Bystanders are sometimes loyal to long-term friends, but they also change sides, being flexible in their coalitions (Kurzban, Tooby, & Cosmides, 2001). So, when conflicts emerge, observers to the conflict—which we hereafter refer to as "third parties"—might choose to intervene on one side or the other, in which case they must use some criterion for choosing sides.

One way that third parties might choose is based on dominance, taking the side of the more dominant individual involved in the conflict. We refer to this as a bandwagon strategy. Under such a choice regime, the most dominant individual would win all conflicts and would have a monopoly on power, as in linear dominance hierarchies (e.g., Holekamp, Sakai, & Lundrigan, 2007). Although some human social groups are rigidly hierarchical, with a despot at the top, most are not (Boehm, 1999).

A second way that humans might choose sides is based on the strength of preexisting relationships, backing the disputant who is closer in kinship, friendship, or group membership. This is choosing sides based on partiality or favoritism. As an empirical matter, people frequently show favoritism, but, crucially, they do not always do so. Departure from partiality, even if rare, is interesting given the central role that it plays in theories of altruism. Instead, third parties sometimes choose sides with a stranger against a friend, a friend against family, or with a foreigner against a compatriot. This sometimes happens, for instance, when the closer individual perpetrated unprovoked intentional harm on a more distant individual.

Choosing sides based on alliances can lead to costly escalated fighting (Snyder, 1984). Imagine a world in which conflicts emerge periodically and each third party always chooses the closer person to support. Any two individuals will tend to have their own family and friends to support them. The result is that fights will tend to be evenly matched. A key finding from the literature on animal contests is that evenly matched disputes are most likely to escalate because neither side is so outmatched that it is clearly best to back down (Arnott & Elwood, 2009; Davies et al., 2012; Enquist & Leimar, 1983; Mesterton-Gibbons, Gavrilets, Gravner, & Akçay, 2011; Parker, 1974). Due to these costs of escalation, other ways of choosing sides might be able to invade by reducing these costs.

In order to avoid escalated fighting, bystanders can try to choose the same side as everyone else—that is, to coordinate their side-taking decisions. Coordination problems occur in a wide variety of social contexts, such as avoiding collisions on the road, carrying furniture with housemates, meeting up at the same location, or negotiating a price for a trade, and this class of problems has been intensively studied (Camerer, 2003; Schelling, 1960; Thomas, DeScioli, Haque, & Pinker, 2014).

One way to accomplish coordination is for everyone to make their decisions contingent on a public signal (Schelling, 1960). This coordination strategy is referred to as a *correlated equilibrium* (Aumann, 1974). The most frequently used example of a correlated equilibrium is a traffic light. While any color of light could be used to mean "go" or "stop," once this equilibrium has been selected, each individual driver does best by using the colors to make decisions. In coordination games, when other players are expected to make decisions based on an otherwise arbitrary signal, each player's interest is to make decisions contingent on that signal, maintaining the equilibrium.

DeScioli and Kurzban (2013) proposed that moral contents serve this coordination function for bystanders choosing sides in conflicts. Moral cognition assigns moral wrongness to a set of actions and motivates people to debate and agree on which actions are morally wrong and on their wrongness magnitudes. When disputes arise, the moral side-taking strategy is to choose sides against the individual who has taken the action with the greatest moral wrongness. This decision rule might lead an observer to side against a friend or relative, but this cost must be set against the benefit of siding with other third parties.

This strategy works when third parties agree before conflicts break out—either explicitly or implicitly—how they will all make their choice should a conflict arise. A key point is that, just as in the traffic light case, *if* potential third parties agree in advance, *then* a given third party pays a big cost for deviating from this prior agreement because their side will be vastly outnumbered by nondeviating third parties. (Such third parties might nonetheless choose to support a friend or relative; the ultimate decision depends on all of the relevant costs and benefits.)

Importantly, moral side-taking is only one coordination equilibrium among others, including bandwagon and alliance strategies. Each third party's best strategy depends on how other people choose sides, which can explain why morality is diminished in human groups that prioritize hierarchy (e.g., fascist regimes) or loyalty (e.g., ethnic conflict). For example, in extremely hierarchical societies, people routinely violate moral rules when they are directed by authorities to perform immoral acts such as murder or genocide. Related, in ethnic conflicts, people engage in otherwise immoral behaviors such as murder or rape, given the support of their coethnics for doing so. In these social contexts, the motives to adhere to moral rules and to condemn moral violators are diminished because bystanders have coordinated on power or loyalty as the primary basis for choosing sides.

Further, because the function of moral beliefs is *coordination* as opposed to, say, cooperation, *there is no particular reason that the consequences of actions must be central to moral beliefs*. If everyone else is going to judge the person doing action X as "wrong," then similarly judging action X to be wrong can be the best strategy even when doing X makes everyone involved better off. (Indeed, there are many examples; see section titled "Conflict and Agreement Over Moral Contents," further on.) Related, just like traffic lights, what people agree in advance is "wrong" can be nearly anything and still successfully perform a coordination function. Just as many different combinations of phonemes can mean "cow" (i.e., the animal), it doesn't matter *which* combination means that particular animal as long as everyone has (roughly) the same belief about what the word "cow" refers to.

Note that this proposal explains *beliefs* as opposed to behavior. Observing a person behave in a way that violates a preexisting moral rule—don't steal—evokes the belief (judgment) that the action is "wrong" and the person ought to be sided against.

COORDINATION EXPLAINS MORAL PHENOMENA

COMPONENTS OF MORAL REPRESENTATIONS

Joining the same side as other third parties requires *prediction*. The dynamic coordination model proposes that moral judgment—the representations (beliefs) that spontaneously arise to categorize particular actions as "wrong"—function to predict the side other observers will choose.

One key aspect of these representations is that they include (at least) two agents, a *perpetrator*—the agent who committed the "wrong" action—and a *victim*—the agent who was wronged (Gray & Wegner, 2009; Gray, Young, & Waytz, 2012). These representations are necessary to guide behavior against the perpetrator and in support of the victim. The prototypical role of a victim leads to some unusual cases, such as suicide in which the same agent is both perpetrator and victim; indeed, people seem to invent victims as needed once they have made a wrongness judgment (DeScioli, Gilbert, & Kurzban, 2012).

Moral judgments, then, serve as a prediction about others' side-taking behavior and, in addition, guide behavior toward making the same choice. The concurrent motivation that the perpetrator be punished satisfies another functional requirement, signaling to other third parties that one is taking sides against and supports aggression toward the perpetrator. This idea might explain why some people seem eager to announce their moral condemnation of others' actions, ranging from expressions of anger or disgust to public comments in various social media to public demonstrations of outrage (Tooby & Cosmides, 2010). Beyond these signals, communicating the willingness to punish the perpetrator—by, for instance, actually doing so—is an even more reliable signal of support. Moralistic punishment, then, can be understood as a costly signal that facilitates third-party coordination.

IMPARTIALITY AND NONCONSEQUENTIALISM

Viewing moral judgments as coordination devices explains impartiality. To the extent that judgment depends on relationships to a perpetrator or victim, coordinating with other third parties—who will have different loyalties—is undermined. To function effectively, moral judgments must align with other people's moral judgments. This requires individuals to make judgments based on the disputants' actions per se instead of the individual's relationships to the disputants. To use the traffic light example, there is no advantage to believing that a red traffic light signals "go," even if you prefer to continue driving through a red light, because coordination requires all drivers to agree, independent of their personal preferences. This entailment, an unbiased perception of actions, is the essence of impartiality. This is not to say that people will always behave impartially after evaluating others' acts; as discussed above related to research by Lieberman and Linke (2007), observers might evaluate acts as equally wrong when committed by friends and strangers, but still respond differently in the two cases, supporting punishment for strangers but not for friends and relatives. Third parties are expected to weigh the benefits of impartiality against the costs to their relationships. Consistent with this idea, Petersen (2013) found that people with fewer friends, and hence lower costs for impartiality, are more prone to moralization.

The coordination function explains nonconsequentialist judgments because coordination requires building the same representation as others build *regardless of how consequences affect others' judgments*. To the extent that people's judgments are driven by features of the behavior other than consequences—as the array of Trolley Problem results illustrates—people are best off aligning their own judgments similarly. This does not preclude the possibility that intended consequences can also affect moral judgments. Indeed, they do in many cases (Robinson & Darley, 1995). However, because specifying what is "wrong" is designed for coordination (as opposed to reducing harm), intended harm need not be the sole criterion for judging wrongness as, indeed, it is not (e.g., Haidt, 2012; Mikhail, 2007; Tetlock, 2003).

Related, to be effective at resolving conflicts, a group's vocabulary of moral rules—those behaviors judged as "wrong"—should include most actions that might initiate conflict. These actions include those pertaining to harm, property, contracts, sex, status, and so on. This requirement helps to explain why changing technologies inevitably lead to new moral rules being minted, such as rules and laws governing electronic property rights or Internet surveillance.

CONFLICT AND AGREEMENT OVER MORAL CONTENTS

Although different moral rules might work equally well for coordinating side-taking, moral rules might have very different consequences for different people within a social group. For example, if some individuals have a mating strategy of pursuing multiple mates, then they are disadvantaged by moral rules against promiscuity or polygamy, relative to monogamous maters. To make local rules work to an individual's benefit, moral cognition might include adaptations for advocating moral rules that are in the individual's interest, leading to fights and debates over moral rules (Kurzban, Dukes, & Weeden, 2010; Tooby & Cosmides, 2010; Weeden, 2003; Weeden & Kurzban, 2014).

History is replete with illustrative examples. Robinson and Acemoglu (2012) argue that a particular kind of contract called the *commenda* in medieval Venice made some people rich and influential. Once established, such people banned the use of the *commenda* to prevent others from rising to compete with their power. Scholarship in criminal law has long recognized this process; the "conflict model" suggests there is "an on-going struggle between vested interest groups which seek to have their particular values legitimated and supported by the coercive power of the state" (Thomas, Cage, & Foster, 1976, p. 110).

An obvious modern example is digital music. Musicians are better off when duplication of their products is moralized and punished; consumers are in the reverse position. These incentives readily explain why Metallica and recording companies filed suit against Napster, the (now defunct) peer-to-peer file-sharing service.

Conflicts are not always obvious. Weeden (2003), for example, proposed that conflicts over the morality of abortion are really proxy battles over sexual strategies. People pursuing a more short-term mating strategy (Buss, 2006) are obstructed when practices facilitating promiscuity are moralized, banned, and punished. Applying this logic to abortion, Weeden (2003) found that people pursuing a strategy weighted toward mating effort and away from parenting effort were more likely to be pro-choice; people pursuing monogamous strategies, reciprocally, were more likely to be pro-life. Although people justify their moral views with reference to freedoms or religious texts, life history variables are, Weeden argues, driving people's positions on abortion.

Moral side-taking does not always lead to conflict but can also cause agreement about which actions are immoral because some rules affect everyone more or less the same. Rules that punish intended physical harm, for instance, protect everyone who can be physically harmed—that is, everyone—and therefore lead to roughly equivalent benefits to all. Everything else equal, the least conflict should be expected over these rules, which DeScioli & Kurzban (2013) refer to as Rawlsian because of their equal effects. Indeed, reflecting the Rawlsian nature of some rules, there are many cross-cultural commonalities in moral contents—such as rules surrounding unprovoked intentional killing (Mikhail, 2009).

This mix of conflict and agreement is expected to generate themes and variations in moral rules across cultures. Where there is conflict, variation is substantial and potentially influenced by the number of people affected and their ability to coordinate to advocate for their interests. Where there is agreement, cross-cultural themes emerge with some moral rules showing widespread adoption.

The dynamic coordination model described above makes few predictions about which cultures will adopt which moral rules. Because there are arbitrarily large numbers of equilibria, additional theory is needed to account for variation. One such account is from Haidt and colleagues' Moral Foundations Theory (MFT; Haidt, 2012), which proposes that disagreements over moral contents can be usefully divided into disagreements over the weight placed on six basic content areas of morality (harm/care, fairness/reciprocity, ingroup/loyalty, authority/respect, purity/sanctity, liberty/oppression). In the United States, for example, Democrats value notions of autonomy, individual rights, and fairness while Republicans place greater weight on purity (e.g., Graham, Haidt, & Nosek, 2009).

According to MFT, members of different groups try to bring about moral regimes within their society that reflect their emphasis on the respective foundations. In turn, these different emphases aid groups in coalescing around these common moral commitments (Haidt, 2012). MFT views moral commitments less as strategic and more as alternative sets of norms around which to build coalitions and alliances reflecting differences in emphasis on the different moral foundations.

Note that if the dynamic coordination explanation for beliefs and motives is correct, then moral conformity is also partially explained. As Boyd and Richerson (1992) showed, in a world in which agents punish (i.e., impose costs on) those who X, there will be selection for choosing not to X, to avoid such punishment. In a social world in which betraying trust is punished, people are predicted not to betray trust absent sufficiently large offsetting incentives. Trustworthiness, then, can be partially explained by the presence of beliefs that such betrayals are "wrong" and motives to punish those who betray.

By viewing moral rules as points in a large equilibrium space—echoing work on cultural evolution (Boyd & Richerson, 2005)—the dynamic coordination model links research in moral psychology to work in cultural evolution. If moral rules are for coordination of side-taking decisions (as opposed to cooperation), it is far less surprising to find that groups have equilibrated at welfare-destroying rules, as they so often have historically (Diamond, 2005; Robinson & Acemoglu, 2012). Related, because groups compete with one another, those groups with "bad" (i.e., aggregate welfare-destroying) rules will, on average, be at a disadvantage to groups with "good" rules. This dynamic explains why good rules are common, and should be expected to become even more so over time.

MORAL EMOTIONS

Historically, because the study of morality concentrated on prosocial behavior, researchers focused on "moral emotions" such as empathy, sympathy, and guilt. This dates at least as far back as Adam Smith's (1759) *Theory of Moral Sentiments*, with its focus on sympathy, echoed by Darwin more than a century later. This emphasis continues to some extent in modern approaches. Haidt (2003), for instance, plots the moral emotions on the axes of the prosociality of the associated behavior on the one hand and the person's own interests on the other.

In contrast, research on moral condemnation, the primary topic here, focuses instead on two emotions associated with judging others' actions: anger and disgust (Hutcherson & Gross, 2011).

ANGER

Observing a moral violation often triggers anger and outrage (Rozin et al., 1999). In general, the emotion of anger motivates and prepares an individual for aggression. This raises the question of why moral judgment is closely connected to anger and aggression.

Outside of the moral realm, people get angry when they, their allies, or relatives have been harmed (Fessler, 2010; Srivastava, Espinoza, & Fedorikhin, 2009). The functional logic of this response to harm is straightforward. Anger serves as a *deterrent* (McCullough, Kurzban, & Tabak, 2013; Tooby & Cosmides, 2008) or a mechanism for *recalibration* (Sell, Tooby, & Cosmides, 2009). If B knows A will reply to harm with retaliation, B will be less likely to harm A in order to avoid these subsequent costs (McCullough et al., 2013). The related *recalibration* function entails using the threat of harm to make other people engage in less harmful (or more beneficial) actions in the future. (See Sell et al., 2009, for a discussion.)

However, people also get angry when someone violates a moral rule, even when no harm has been done (DeScioli & Kurzban, 2009; Haidt, 2012; Rozin et al., 1999). Moreover, this occurs even when the violation does not directly affect the individual or their allies. This suggests that human anger expanded to include an additional input, not only harm but also someone else's choice of a morally prohibited action. Similar to basic anger, moral anger motivates aggression toward the perpetrator. However, the motivation might not be to aggress against the perpetrator per se, but rather to support others' aggression against the perpetrator. According to the dynamic coordination model described above, the behavior motivated by anger at moral violations signals that the person has judged an action as wrong and will side against the perpetrator. Under the proper conditions, it will further lead to imposing costs on the perpetrator (Kurzban et al., 2007).

The close connection between moral judgment and anger does not fit well with altruism models, which instead predict reliance on empathy. In fact, moral outrage reduces empathy toward perpetrators (Decety, Echols, & Correll, 2010). One reasonable possibility is that this reduction facilitates support for harming the violator. The reduction of empathy can be profound, as illustrated by historical examples of public support for draconian punishments of harmless offenses such executions for holding different supernatural beliefs (Levy, 1993) or for illicit sexual behavior (Appiah, 2010). Whereas these observations conflict with altruism models, they fit the side-taking model in which aggression toward the perpetrator plays a key role.

DISGUST

Following Tybur, Lieberman, Kurzban, and DeScioli (2013), we distinguish two issues surrounding moral disgust. The first issue is the question of why many behaviors that elicit disgust, such as incest and eating particular foods, are, cross-culturally, frequently moralized. The second issue is why morally wrong acts that are not "disgusting" in the traditional sense—stealing candy from a baby—recruit the language of disgust.

We follow previous work holding that core disgust functions to avoid hidden risks such as pathogens and inbreeding costs (Tybur, et al., 2013). In this light, the moralization of disgusting acts seems especially vexing. Moralizing actions disincentivizes them. However, disgusting actions are typically things people don't want to do anyway. Because disgusting actions are generally harmful to fitness, people are motivated to avoid them, and would, presumably, do so even if they were not moralized in their social group.

Haidt (2007, 2012) proposed one answer to this question—that the moralization of disgusting behaviors serves to "bind" people into cooperative groups. He proposes that human in groups "circle around sacred values" (p. 31), arguing that moralizing actions, including disgusting actions, unite and unify.

A second possible answer to this puzzle, proposed by Tybur et al. (2013), rests on the possibility that the moral rules that are observed across cultures depend on who is willing to fight to support (or oppose) them, as discussed above. Generally, people only oppose rules preventing them from doing things they want to do. So, because people, by and large, don't want to do actions they view as disgusting, there should be the least resistance to rules that moralize disgusting actions, possibly explaining their prevalence.

As an empirical matter, eliciting disgust does seem to affect moral judgments. Participants who smell a disgusting odor, for instance, judge acts more morally wrong than controls (Schnall, Haidt, Clore, & Jordan, 2008). A parallel result has been obtained for taste (Eskine, Kacinik, & Prinz, 2011). Particularly intriguing, the cues that lead to sexual aversion toward opposite-sex siblings also predict the extent to which one judges one's opposition to incest by others (Lieberman, Tooby, & Cosmides, 2003, 2007).

The second question is why morally wrong actions are frequently described using the language of disgust. As an empirical matter, people do indicate that wrongful actions that have nothing to do with pathogens or sex, such as theft from a blind person, are "disgusting." Related, when subjects are asked to nominate actions that caused them to be "disgusted," they nominate times when a moral rule was violated (Curtis & Biran, 2001; Haidt, McCauley, & Rozin, 1994; Haidt, Rozin, McCauley, & Imada, 1997; Tybur, Lieberman, & Griskevicius, 2009).

Why this is the case remains the subject of debate. Hutcherson and Gross (2011), for instance, proposed that moral disgust functions to "mark" people who are threatening. This view suggests that labeling others' actions as disgusting will aid in avoiding those actors in the future. In contrast, Tybur and colleagues (2013) propose that using the language of disgust serves a coordination function. They suggest that showing the canonical disgust expression or using disgust metaphors signals to third-party observers that one opposes a particular action or perpetrator, facilitating third-party coordination against that individual. Additional work will be required to distinguish these possibilities for why actions perceived as morally wrong recruit the language of "disgust."

SUMMARY

Emotions have been increasingly incorporated into the study of morality. Research in this area is made more difficult by the fact that feelings of anger and disgust are frequently closely though not perfectly correlated (Russell & Giner-Sorolla, 2013). Empirically, people do frequently report strong affective reactions to moral violations, even in cases in which the violation does not harm themselves or a relative or ally. These emotions, in turn, appear to motivate the administration of—or support of—sanctions imposed on the perpetrator, though the details of the context exert important influences on the decision to do so.

CONCLUSIONS

We began with the observation that scholarship on the evolution of morality can be conveniently divided into two threads that turn on the distinction between *doing* and *believing*. Humans *do* many things that might be labeled "moral." Many altruistic acts are so labeled. A related but distinct question surrounds a particular sort of belief, or mental representation. Many people have the belief that sex between full siblings, for instance, is *wrong* or *immoral*.

Explanations for why people *do things* are likely to be different from explanations for why people *believe things*. The previous incarnation of the morality chapter in this *Handbook* consisted in large measure of explanations for why people *behave* in particular ways. Krebs (2005) referred to explanations such as reciprocity, kin selection, group selection, and so on. Related, Haidt (2012) leans on these explanations to ground Moral Foundations Theory in evolution.

In contrast, we have discussed explanations for moral *beliefs*. Because theories such as reciprocity and kin selection are good for explaining (prosocial) behavior but not as apt for explaining judgments of moral wrongness, additional ideas are needed to supplement these powerful explanations. Thankfully, the past 20 years has seen a fluorescence of research on moral psychology, and new conceptual tools are available to shed light on this perennially vexing issue. Debates continue, however, and it is clear that much work has yet to be done on the function of the cognitive systems that generate moral condemnation, and the panoply of human behaviors that moral condemnation motivates.

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CHAPTER 32

The Evolutionary Foundations of Status Hierarchy

MARK VAN VUGT and JOSHUA M. TYBUR

> Who can say for sure that the deprivation which afflicts him with hunger is more painful than the deprivation which afflicts him with envy of his neighbor's new car.
>
> —J. K. Galbraith

The imperial city of Rome was the largest urban area in the world of its time. Despite being a democracy, Rome had an elaborate system of ranks and social standings visible to all. The Roman dress, the toga, was a status symbol par excellence; only free Roman citizens could wear it. Foreigners, slaves, and even exiled citizens could not wear it in public, and it was taboo for Roman citizens to be seen in public without wearing one. Social status within the citizen class was further demarked by different kinds of togas. On formal occasions, most Roman men and ordinary members of the Senate wore plain white toga virilis, whereas politicians campaigning for public office wore the conspicuously ultrawhite, bleached toga candida. The white toga praetexta had a broad purple stripe on its border, and only priests and magistrates could wear it. Finally, the toga picta, a brightly colored and richly embroidered garment, could only be worn by military commanders on their triumphs through the streets of Rome and by the consuls and emperors on special occasions like the Gladiator Games (Baker, 2010).

Rome was not unique in emphasis of status. All human societies, large or small, wealthy or poor, industrialized or subsistence based, have status hierarchies. The anthropologist Donald Brown (1991) has documented social status as universal across human cultures, and hierarchy is conceptualized as one of the key, universal dimensions of human social relationships in A. P. Fiske's (1992) relational models theory. Even foraging societies that might appear egalitarian at first blush are characterized by status hierarchies and, like the Romans, individuals at higher places in status hierarchies enjoy special benefits. For example, adult males of the Ache, an indigenous

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foraging people in Paraguay, invest large amounts of time and energy into acquiring meat. In a sense, hunting is their job, and meat is their income. The tangible fruits of one individual's labors, though, cannot be stored long term in a manner that could allow the accumulation of capital and the subsequent status increases that real estate moguls, wall street executives, and heads of state enjoy. Instead, meat is shared with other members of the group in a relatively egalitarian manner. This egalitarianism in terms of tangible resources does not prevent the accumulation of status based on hunting performance, though; the best hunters in the band accumulate prestige, which allows them to have more extramarital affairs and sire more children than the average hunter (Hill & Kaplan, 1988). Similar associations between hunting skills and reproductive success have been reported among other hunter-gather societies such as the Ache, Hadza, !Kung, and Tsimane (von Rueden, 2014).

In addition to being common across human cultures, status hierarchies are prevalent in nonhuman social species as well (Ellis, 1995). A widely cited example is the pecking order in chickens. If a group of chickens is placed together for the first time, they will all initially peck each other in competition over food. Before long, though, a simple linear hierarchy emerges within the group where every hen knows its place —A pecks B; A and B peck C; A, B, and C all peck D; and so on —and the pecking order determines which hens gets preferential access to food. Hierarchy also determines access to females in various primate species (to which humans are closely linked). There are positive associations between male rank and reproductive success among chimpanzees, bonobos, gorillas and rhesus macaques, although the strength of the association varies depending upon socioecological conditions such as (a) resource predictability, (b) the ability to monopolize resources, and (c) the ability to form leveling coalitions against dominants (Boehm, 1999; Ellis, 1995).

Given the ubiquitous nature of status hierarchies across human and nonhuman groups, and the fitness-relevant consequences of placement in status hierarchies (e.g., access to food and mates), it is likely that natural selection would have favored psychological mechanisms that are specialized for navigating status hierarchies. This chapter explores these mechanisms in several ways. First, we define the relevant concepts. Second, we discuss the selection pressures that might have favored the evolution of a universal status striving tendency. We do this partially through the logic of a simple game theoretical model. Third, we review some of the proximate mechanisms—including behavioral, morphological, hormonal, and affective systems—through which individuals are able to assess their relative status and likelihood of winning a status challenge, make status gains, and manage status losses, whereby we pay attention to sex differences in status striving. Finally, we investigate the emergence of one specific high-status position in human groups, leadership.

DEFINITIONS

Following Cummins (2005), we define *status* as an individual's standing in the social hierarchy, which determines priority access to resources in competitive situations. We further draw a distinction between status hierarchies based on *dominance* versus *prestige* (Henrich & Gil-White, 2001; note that social psychologists Magee and Galinsky, 2008, use the terms *power* versus *status*, respectively, to refer to these concepts). In dominance hierarchies—which are common among nonhuman primates—individuals achieve priority access to resources through threat, intimidation, and displays of force. Prestige, in contrast, is a freely deferred status granted to individuals because they help other individuals achieve their goals. In return, prestigious individuals (e.g., individuals with valued skills or knowledge) receive priority access to resources (Hill & Kaplan, 1988). Power, a concept recently explored by social psychologists, refers to the ability to influence others' outcomes by virtue of someone's control over resources, often based on position in the hierarchy (Keltner, Gruenfeld, & Anderson, 2003; Magee & Galinsky, 2008). Finally, it is useful to distinguish between *status* hierarchies and *decision-making* hierarchies, although these are often times conflated particularly in humans (van Vugt, 2006). *Leadership* refers to a special position in the decision-making hierarchy where individuals exercise disproportionate influence on group decision making and can gain priority access to resources in return (Price & van Vugt, 2014; van Vugt, 2006).

AN EVOLUTIONARY PSYCHOLOGY PERSPECTIVE ON STATUS

Given that (a) status hierarchies are ubiquitous across observed human societies, both modern and historical, (b) status hierarchies are observed in nonhuman primates, as well as other animals, and (c) an individual's position in status hierarchies has consequences for access to sexual partners and other fitness-relevant resources, humans likely possess evolved psychological mechanisms for status-striving and navigating status hierarchies. These mechanisms (a) motivate individuals to advance their positions in status hierarchies (*status improvement*), (b) convert advantageous status positions into fitness benefits (*status capitalization*), (c) assess and monitor others' positions in status hierarchies (*status assessment*), and (d) manage and cope with changes in status positions in social hierarchies, both gains and losses (*status management*). These mechanisms are instantiated as coordinated interactions among hormonal, cognitive, emotional, and behavioral systems, and they need not be consciously motivated.

An evolutionary psychology approach assumes that the psychological systems of status take the shape of stimulus-response mechanisms that can be seen as conditional ("if-then") decision rules that produce behaviors that were, on average, adaptive in the ancestral environment (Gigerenzer & Goldstein, 1996; Tooby & Cosmides, 2005). A conditional rule such as "Only challenge an individual's status if the likely benefits outweigh the costs" enables individuals to achieve better payoffs than a decision rule to "challenge anyone's status." Multiple selection mechanisms might have shaped this type of modular status psychology. Some evolutionary theories stress individual competition as the basis for status differences, viewing hierarchy as the resultant of individuals pursuing their own interests. Evolutionary biologist George Williams (1966) remarked: "The dominance-subordination hierarchy . . . is not a functional organization. It is the statistical consequence of a compromise made by each individual in its competition for food, mates, and other resources. Each compromise is adaptive but not the statistical summation" (p. 218). Other evolutionary theorists stress the functionality of status differences for both individuals and groups. One may be better off as a low-status member in a group with a stable hierarchy than as a high-status member in an unstable group (Caporael, 1997; Ronay, Greenaway, Anicich, & Galinsky, 2012). Accordingly, social hierarchies in humans may be the product of selection operating at multiple levels (e.g., group and individual; see Wilson, van Vugt & O'Gorman, 2008; compare with Pinker, Chapter 36, this volume).

		Player 2	
		Yield	Dare
Player 1	Yield	2, 2	1, 5*
	Dare	5, 1*	–1, –1

Figure 32.1 Chicken: A Game of Status
Note. Payoffs are for Player 1 and 2, respectively; Yield and Dare constitute alternative game strategies (underpinned by genes); game equilibria are indicated with asterisks.

GAME THEORY AND STATUS

Status striving can be conceptualized as a social strategy that has been selected for by virtue of its role in fostering reproductive success. This can be illustrated by applying insights from evolutionary game theory (Maynard Smith, 1982), which models social interactions as games in which strategies compete with each other in a Darwinian fashion. Evolutionary game theory is like economic game theory, except that the agents are genes, which embody strategies that are pitted against alternative strategies. Strategies, and the genes that lead to their development within individual organisms, spread through a population by virtue of the superior decision rules they produce in fitness relevant situations, whereas inferior strategies are culled from the population.

We can model status interactions as different social strategies in a game of Chicken (Figure 32.1), which parallels the well-known Hawk-Dove game in evolutionary biology. The name "chicken" stems from a game in which two car drivers drive towards each other on a collision course. One must swerve or both may die in a crash; yet if one driver swerves and the other does not, the one who swerved is called the chicken (coward). The principle of the game is therefore that while each player prefers not to yield to the other, the worst possible outcome occurs when both players do not yield. Status interactions have the feature of a Chicken game in which one can assume that players have two available strategies, either to challenge for status (Dare) or to avoid a status confrontation (Yield)—these are akin to the hawk and dove strategies, respectively. A challenger always wins against an avoider and can therefore gain status. Pursuing a Dare strategy is thus effective when there are lots of Yield types around who will accept your status. But as Darers become more common in a population—because they convert resources gained in status competitions into fitness—interactions between them will increase. These interactions result in negative payoffs for both parties (Figure 32.1). In populations with many Darers, individuals who bow out of intense competition can thrive. The Yielders might have to surrender resources to the Darers, but they avoid costly battles, and their interactions with other Yielders are fruitful. Hence, there is a countersurge of Yielder types in the population.

Under certain conditions, the population will reach a mixed equilibrium of Dare and Yield strategies over time, at the point at which each strategy enjoys similar expected reproductive success. This is a classic example of frequency-dependent selection (Buss, 2009; Maynard-Smith, 1982).

Animal research supports the principles of this status game. Consider orangutans, where males differ greatly in size. The flanged males are physically large, and they attract females to their territories by making loud vocal calls. The unflanged males are weaker and smaller, and they do not hold a territory themselves. Their strategy is to avoid the big males and to wait for the opportunity to mate with an unguarded female (Harrison & Chivers, 2007). This explains why these two strategies continue to coexist in the male orangutan populations at particular frequencies. Similar alternative mating strategies, reflecting the Dare and Yield tactics, have been observed in cuttlefish, salmon, and beetles (Hunt & Simmons, 2001).

The Dare-Yield combinations are referred to as the game equilibria. Once interactions settle into an equilibrium state, they are likely to remain there because neither player obtains a better outcome by switching to a different strategy (this is called an "evolutionarily stable strategy" [ESS], or in economics and political science, a Nash equilibrium). This game thus selects for adaptations that exploit equilibrium state of D-Y interactions, potentially giving rise to a stable status hierarchy. The implications of the model for the formation of status hierarchies are multifold. First, the benefit of Dare is higher in an interaction with a Yielder, and a Yielder always defers to a Darer. Second, it is better to Yield in interacting with a Darer (especially if the Darer is likely to win the status competition). Third, the combined payoffs of the D-Y interaction are better than for pairs of either D- or Y-types. Thus, groups composed of Darers and Yielders tend to have better gross payoffs than homogenous groups. In contexts of intergroup competition, this dynamic might favor groups with a mixed assortment of status strategies (for empirical evidence, see Ronay et al., 2012).

The Chicken game analysis offers a potentially valuable lens through which to think about status adaptations and our evolved psychology of status. First, it shows why humans should strive to improve their status, as this determines their differential access to resources (Frank, 1985). Second, it shows how groups can arrive at relatively stable status hierarchies (the game equilibria) instead of facing constant challenges for status. Third, it provides an analytical framework for answering questions that parallel some of the foundational issues within social and personality psychology—for instance, how phenotypic qualities of the individual (a la the "person") interact with the situations they find themselves in (cf. Kenrick & Funder, 1988; Lewin, 1946; Reis, 2008). Individuals lacking the phenotypic qualities to challenge for status, such as those lacking in physical strength or valuable skills, should avoid the costs of status competition.

Fourth, these status strategies should be conditional. Individuals predisposed to challenge for status should switch to a Yield strategy in situations in which they are likely to come up against a more formidable opponent or an opponent that is more committed to compete. The latter explains the home advantage effect documented in studies of animal behavior in which individuals that own territories are likely to fight harder than the ones invading a territory. Fifth, depending upon relative payoffs of low or high status, we expect status confrontations to vary in intensity. The relative benefits of a challenge, for instance, may be greater for men than for women, which could explain the commonly observed sex differences in status striving, risk taking, and dominance (van Vugt, Hogan, & Kaiser, 2008). Finally, the game offers insight into status challenges between groups, where one group lacking the qualities to compete (e.g., through lack in numbers or resources) may yield to another group and a stable between-group hierarchy might emerge. The game analysis forms the foundation of social psychological theories of intergroup processes, explaining why individuals identify more with high-status groups and are motivated to make costs to improve their group standing (Tajfel & Turner, 2004).

This parsimonious game is naturally limited in a number of ways. It is agnostic regarding the nature of the costs inflicted in status challenges (e.g., physical or psychological costs), and it says nothing regarding the proximate mechanisms underlying status interactions—how do individuals signal their phenotypic qualities to each other and what qualities do they signal? Although we assume that such signals have evolved to be honest, in actual status interactions signals may be faked (e.g., lowering your voice pitch during a job talk). Finally, the game is agnostic about whether status battles are based on dominance, prestige, or a combination (e.g., scientists and ultimate fighters compete in very different ways for status).

EVOLVED STATUS MECHANISMS

Status and Hormones

Testosterone Human and nonhuman animal studies suggest that hormones are one of the proximate mechanisms that facilitate the emergence, development, and maintenance of status hierarchies in groups. Levels of the androgen testosterone (T) relate to individuals' relative status in both human and nonhuman samples (Archer, 1996; Ellis, 1995; Sapolsky, 1990), and not due only to shared relationships with third variables such as age, sex, or size. After intrasexual competition—competition within one sex for access to mates—victors on average experience an increase in testosterone, whereas losers experience a decrease in testosterone. This pattern has been observed in direct physical competitions, in nonphysical competitions, in experimental competitions within the lab, and in natural competitions (e.g., wrestling; Gladue, Boechler, & McCaul, 1989; Mazur & Booth, 1998; Mazur, Booth, & Dabbs, 1992). Changes in testosterone also occur vicariously and as a result of status competitions among groups. During the final match of the 1994 FIFA World Cup between Brazil and Italy, researchers found an increase in testosterone levels among fans of the winning team and a decrease in testosterone levels among fans of the losing team (Bernhardt, Dabbs, Fielden, & Lutter, 1998). The relationship between status and testosterone also appears to be bidirectional, with changes in testosterone producing a change in position in the social hierarchy. When biologists administered testosterone to low-ranking cows, for example, the cows' hierarchical positions increased; when testosterone was subsequently withdrawn, the cows' position dropped (Bouissou, 1978).

It is not quite clear how these testosterone changes convert into reproductive outcomes. One possibility is that increasing T motivates individuals to adopt a dare or challenge strategy (cf. Archer, 1996). Evidence linking testosterone and dominant/aggressive behaviors has been found among men in highly intrasexually competitive prison populations and in nonprison populations (Mazur & Booth, 1998). Testosterone might also stimulate individuals to engage in prestige battles. After being administered a small dose of testosterone, participants gave more money in an economic game, compared to a control group receiving a placebo, but only when giving money produced reputation benefits (Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010).

The nature of the relationship between testosterone and status can be illuminated by considering the energetic tradeoffs that testosterone facilitates. Ellison (2003; Ellison & Ellison, 2009), for example, conceptualizes testosterone as regulating male reproductive effort. Higher testosterone levels during development produce "masculine" traits such as a more prominent brow ridge and larger jaw, a deeper-pitched voice, and greater muscle mass. Such masculine traits are useful in dominance competitions, including physical combat, as well as in prestige contests, including mediation in conflicts (von Rueden, 2014). Increases in testosterone following competition victories can be interpreted as general increases in energy allocating to mating effort, then. If testosterone also serves as an input into some of the psychological mechanisms governing mating displays, then these increases in testosterone following success in intrasexual competitions can lead individuals to convert their victories into reproductive opportunities (*status capitalization*).

Engaging in status competition can be costly, both in terms of the energetics associated with testosterone production (e.g., Muehlenbein & Bribiescas, 2005) and in terms of the direct challenges from conspecifics that increased testosterone leads to, fighting other challengers. Given these costs, individuals who pursue an avoid strategy should be more wary of being placed in a high-status position in which they are frequently challenged. Josephs, Sellers, Newman, and Mehta (2006) provide some support for this hypothesis. After rigging a competition, they observed that lower-testosterone individuals placed into a high-status position (i.e., victors in a competition) and high-testosterone individuals placed into a low-status position (i.e., losers in a competition) showed patterns of relatively high arousal, with greater heart rate and worse performance on tests of cognitive performance. In addition, those individuals who experienced increases in testosterone after losing the competition wanted to compete again with the same individual; those individuals who decreased testosterone after losing wanted to avoid another confrontation (Mehta & Josephs, 2006).

Cortisol and Serotonin Testosterone is not the only hormone that regulates positions in status hierarchies. Indeed, cortisol also fluctuates in response to situations or events that might alter positions in status hierarchies. Those situations that lead to transient increases in cortisol are often subjectively experienced as "stressful." Like testosterone, cortisol functions to regulate the allocation of energy to different physiological systems. Unlike testosterone, however, changes in cortisol function to supply the organism with extra bursts of energy by extracting glucose from physiological reserves that are lower priority in emergency situations (Ellison & Ellison, 2009). Adults and children of low socioeconomic status typically show higher cortisol levels than those of higher socioeconomic status, suggesting more frequent exposure to daily stressors (Kapuku, Treiber, & Davis, 2002; Marmot, 2004). Among married couples, the perception of the dominance of one's spouse correlates with blood pressure reactivity during marital interactions (P. C. Brown, Smith, & Benjamin, 1998). Low-ranked managers have higher baseline levels of cortisol than higher-ranked managers in organizations (Sherman et al., 2012). Although the causal direction in these relationships is yet unclear, it is consistent with Sapolsky's (1990) baboon studies showing that lowly ranked baboons experience continuous elevated levels of cortisol. An interpretation of this effect is that cortisol buffers against the stress from experiencing a low status position with an associated lack of resources (see Figure 32.1).

Finally, high status has been linked to elevated levels of serotonin, a neurotransmitter, primarily found in the central nervous system, which is thought to be related to feelings of happiness and well-being. Primate studies have found that as individuals move up the social hierarchy of their group, their serotonin levels increase (Sapolsky, 1990). Experiments with vervet monkeys show that males with high social rank had almost twice as much serotonin in their blood as did the low-ranking monkeys (Raleigh, McGuire, Brammer, & Yuwiler, 1984). A causal link between serotonin and status was established when scientists administered citalopram (a serotonin drug) to 10 healthy volunteers. While taking the drug, these volunteers were rated as significantly more dominant by observers, and they also increased their eye contact when interacting with strangers compared to a placebo group (Tse & Bond, 2002). Not surprising, drugs to fight depression and anxiety in humans (e.g., Prozac) work by increasing serotonin levels in the brain. Serotonin may well be an internal cue of one's status position in a group.

Status and Physique

To the extent that position in status hierarchies and competitions for status, and, ultimately mates, favor physical size and strength, the highest quality individuals would be expected to be bigger, at least for males. (Kokko, Brooks, McNamara, & Houston, 2002, note that physical size is partially influenced by testosterone.) Physical formidability offers obvious advantages during bouts of intrasexual competition, and it strongly predicts status in nonhumans; larger male baboons are ranked higher than smaller male baboons (Johnson, 1987), and larger individuals are more likely to win dyadic challenges in spiders (Taylor, Hasson, & Clark, 2001) and crayfish (Pavey & Fielder, 1996).

In human (males) there are two potential ways that physical size translates into higher status. The first is through a series of physical dominance displays between intrasexual competitors. Larger males would, on average, win against smaller individuals, and larger individuals would rise to the top of hierarchies. Naturally, this need not involve actual physical combat. An individual's stature can be used as *information* regarding that individual's likelihood of success in competition, and confrontations are settled based on this information rather than actual combat, which would decrease costs for all parties involved (status assessment). In this sense, stature can be thought of as a cue to intrasexual competitive ability, and hence a critical piece of information in deciding who should be challenged and who should be deferred to. Recent developmental studies show that even before the end of their first year, human infants expect a physically larger object to prevail over a physically smaller object in a dominance contest (Thomsen, Frankenhuis, Ingold-Smith, & Carey, 2011). Hence, individuals of stature can simply avoid a status competition because they are not being challenged (see Figure 32.1).

The second is through physical size serving as a marker of someone's prestige. Anthropological research suggests that physically stronger individuals may be better at procuring resources for the group, defend the group against hostile outgroups, and settle intragroup disputes (von Rueden, 2014). Furthermore, there is evidence linking stature to health, intelligence, and political influence, which are prestige indicators (Blaker & van Vugt, 2014). Height is positively associated with several variables associated with status, including income (Judge & Cable, 2004), military rank (Mazur, Mazur, & Keating, 1984), and authority in the workplace (Gawley, Perks, & Curtis, 2009). Furthermore, within businesses, individuals in managerial positions are on average taller than individuals in nonmanagerial positions (Egolf & Corder, 1991;

Murray & Schmitz, 2011). Prestigious American science professors tend to be taller than the general public, and even the U.S. presidential elections are won by the taller candidate at a rate greater than chance (McCann, 2001; Stulp, Buunk, Verhulst, & Pollet, 2013). There is also evidence that being tall facilitates an individual's upward social mobility. A study involving pairs of brothers and sisters found that the taller sibling was on average better educated (Bielicki & Waliszko, 1992). Different languages seem to reflect the relationship between stature and status; in various cultures, traditional and modern, leaders and other high-status individuals are often referred to as "Big Men" (van Vugt & Ahuja, 2011).

That people use height as a cue to others' placement in status hierarchies is demonstrated in a recent experiment showing that taller male and female managers are perceived as better leaders (Blaker et al., 2013). Whereas taller males were perceived as both more dominant, more intelligent, and healthier, taller females were only seen as more intelligent. This suggests that stature might lead to status benefits in both sexes, but that it does so via physical formidability more in men than in women.

There are other traits that might allow an individual to leverage physical formidability into status. A handful of studies have reported that fat-free muscle mass—which is estimated by running small electrical current through the body, and can be used as a proxy for physical strength—is positively correlated with wages for both males and females (Böckerman, Johansson, Kiiskinen, & Heliövaara, 2010). Men's physical strength also predicts their quickness to anger and their likelihood of applying aggressive tactics to achieve their goals (Sell, Tooby, & Cosmides, 2009)—thus being quicker to adopt a Dare strategy. Physical size at age 3 predicts aggressiveness and disagreeableness at age 11, which suggests that strategies relating to physical strength are calibrated early in life (Ishikawa, Raine, Lencz, Bihrle, & Lacasse, 2001). Physically stronger men also endorse social norms that are beneficial to strong individuals. For example, Price, Kang, Dunn, and Hopkins (2011) demonstrated that physically stronger men have a stronger preference for social hierarchies and status inequalities. Petersen, Sznycer, Sell, Cosmides, and Tooby (2013) similarly found that upper-body strength predicted men's endorsement of resource redistribution policies that favored them: Poorer men's upper-body strength predicted stronger endorsement of wealth redistribution, whereas wealthier men's upper-body strength predicted weaker endorsement of wealth redistribution.

Other traits that might relate to success in intrasexual competition also convey high status. Facial masculinity—which includes chin prominence, heaviness of brow ridges, and facial muscularity—predicts career development of military officers, with these traits being associated with higher rankings within a military academy and more and quicker career promotions (Mueller & Mazur, 1996). The relationship between facial masculinity and success in hierarchical organizations might result from both the tactics that more facially masculine individuals employ (dominance) and the potential preferences for more facially dominant individuals as leaders (prestige). The latter is supported by evidence that individuals vote for a more facially dominant leader, especially in the context of war (Spisak, Dekker, Krüger, & van Vugt, 2012).

Finally, physical attractiveness predicts a number of positive social outcomes afforded to higher-status individuals, such as having more dates and friends and making more money (Roszell, Kennedy, & Grabb, 1989). In a study of college fraternities and sororities, more physically attractive individuals were perceived as more prominent and occupied high-status roles in these student organizations more often (Anderson, John, Keltner, & Kring, 2001; Kalick, 1988). However, physical attractiveness was more strongly predictive of social status in men than in women, suggesting that attractive women may have an edge in competition for mates but not necessarily in challenges for positions of leadership.

VERBAL AND NONVERBAL INDICATORS OF STATUS

In addition to leveraging physical capital into higher status, humans also employ various behavioral tactics to convey their status (although whether they do this deliberately remains to be seen). Consider a handshake. Shaking hands is a ubiquitous manner of introduction in the Western world, especially between men who meet for the first time. Something as simple as grip strength during a handshake might be an efficient manner of learning about another man's status. Socially dominant and extraverted individuals have firmer handshakes (Stewart, Dustin, Barrick, & Darnold, 2008). High-status individuals are also more likely to have an open, relaxed posture, show less emotional expressivity in their face, and are less likely to laugh, especially in interacting with low-status individuals (Ketelaar et al., 2012). In a lab study, participants who viewed individuals engage in subtly rude and norm-violating behaviors rated these individuals as more decisive, strong, powerful, and in control (van Kleef, Homan, Finkenauer, Gündemir, & Stamkou, 2011). In a review of the literature on nonverbal behavioral interactions, Argyle (1994) concludes that dominant individuals stand at full height with an expanded chest, hold a firmer gaze, speak in a low-pitched voice, and gesture more.

A lower voice pitch can also provide information about an individual's status as it is related to physical size and higher testosterone. Lower voice pitches are linked to status and occupational success (Puts, Hodges, Cárdenas, & Gaulin, 2007). Indeed, in a recent study on CEOs of companies registered on the American Stock Exchange showed that CEOs with lower voices make more money, with a 25% decrease in voice pitch being associated with a $187,000 increase in annual salary (Mayew, Parsons, & Venkatachalam, 2013). Men also lower their voice pitch when they are addressing another man who is lower in status, suggesting that voice pitch might be used to assert dominance in lieu of physical competition (Puts, Gaulin, & Verdolini, 2006). Finally, verbal expressions may differ between high- and low-status individuals. People are seen as more prominent and prestigious when they speak more clearly, louder, more confidently, and more directly, whereas those who speak more softly and pepper their comments with nervous giggles are seen as lower in status (S. T. Fiske, 2010). Moreover, high-status individuals often initiate conversations, shift discussions to their own areas of competence, and are more likely to interrupt other speakers in the conversation (Godfrey, Jones, & Lord, 1986; Mast, 2002). Finally, displays of emotions convey status differences. Group members who express anger are perceived to be of higher status than those who appear sad (Tiedens, 2001).

STATUS CHANGES AND EMOTIONS

Humans have likely evolved a suite of different emotional systems to negotiate positional changes in status hierarchies (Tooby & Cosmides, 2008). When individuals emerge victorious in a status competition (lower left cell of Figure 32.1), they experience happiness, elation, and pride (Cheng, Tracy, & Henrich, 2010; Tracy & Robins, 2007). In contrast, a status loss (upper right cell of Figure 32.1) produces an increase in feelings of social anxiety, shame, rage, and depression (Gilbert, 1990). Moreover, identical behaviors can elicit starkly different affective sensations depending on the status consequences of the behavior.

Consider public speaking. As many readers of this chapter have experienced themselves, giving a research presentation to a group of undergraduate students results in less anxiety than giving the same talk to a mix of peers and more prestigious individuals at an international conference. Presumably, this difference in anxiety reflects the different status consequences of a good versus poor performance to the two groups, with poor performances in front of undergraduates not affecting status as much as a poor performance in front of a group of scholarly peers. Anxiety, or even the prospect of feeling anxious, might reflect the type of functional forecasting and simulation discussed by Tooby and Cosmides (2008). That is, simulating the aversive effects of actual status losses (i.e., experiencing anxiety) might lead individuals to either avoid situations in which they are likely to lose status or invest extra effort into winning such competitions. Similarly, people feel shame if they experience a loss in reputation, for example, after a moral transgression (Giner-Sorolla & Espinosa, 2011; Haidt, 2003; Tracy & Robins, 2006). On the other hand, when people lose a status competition that they feel they should have won, they may feel rage, which might motivate them to seek a rematch or revenge. Finally, after experiencing a prolonged loss of status (e.g., unemployment), people may feel depressed, which motivates them to temporarily avoid any status competition until they have gained enough resources to participate in status competitions. Depression symptoms indeed stop after people find a new job or start a new relationship, at which point they might have the capital to reenter the fray of status competition (Gilbert, 1990).

Other emotions could similarly guide behavior after status contests depending on the outcome of the competition, the individual's status, and the status of their competitor (Figure 32.1). After winning a status contest, a high-status individual might experience either pity or contempt for the low-status person, depending presumably on how the loser responds to his or her defeat, or the manner in which the loser challenged the winner before the competition. In contrast, depending upon the reactions of the winner, low-status individuals might display admiration when they feel they have legitimately lost the battle, and they might feel envy to motivate greater efforts during the next bout of competition.

SEX DIFFERENCES IN STATUS STRIVING

Like all mammals, men and women differ in their reproductive potential. Women invest more heavily in offspring (e.g., via the time and energy invested in gestation and lactation), and the number of years that they can conceive is constrained relative to men. Comparatively, men have lower minimal obligate investment in offspring, they can sire more offspring (with another partner) after a single act of conception, and they are reproductively viable for a longer period of their lives (Trivers, 1972). As a result, the ceiling of reproductive output is higher for men, and men's reproductive output tends to be more variable than female reproductive output (Bateman, 1948; Brown, Laland, & Borgerhoff Mulder, 2009). These differences in minimal obligate investment form the theoretical foundation for sex differences in mating strategies (e.g., Sexual Strategies Theory; Buss & Schmitt, 1993) and myriad related sex differences ranging from aggression (Archer, 1996; Wilson & Daly, 1985) to experiences of disgust toward unwanted sexual advances (Tybur, Lieberman, Kurzban, & DeScioli, 2013). These sex differences also imply that there might be evolved sex differences in psychological status systems.

Male reproductive output is more variable than female reproductive output, but which males produce more offspring? As we discussed earlier, higher-status males sire more offspring across several species (Ellis, 1995). An extreme example comes from the northern elephant seals living off the west coast of the United States and Mexico. Males compete for dominance before the breeding season starts, and the winners get exclusive access to females, whereas the losers are excluded from mating during the breeding season (Blaker & van Vugt, 2014). Employing the game-theoretical model presented earlier (Figure 32.1), this means that the relative payoffs for Dare versus Yield will be greater for male same-sex interactions than for female same-sex interactions. The implication is that there is a stronger incentive for males to compete for status than for females because of the larger reproductive gains involved.

The relationship between male status and reproductive success also appears in humans. It was particularly strong in early complex societies, such as the Aztec, Inca, and Mesopotamian civilizations (Betzig, 1993). In these societies, access to women was strictly regulated, with higher-status men enjoying greater access to women than lower-status men. In the more egalitarian hunter-gatherer societies, the reproductive skew was arguably less pronounced, but the best hunters and political leaders nevertheless enjoyed more sexual affairs. Indeed, among contemporary Tsimane—a foraging people in the Bolivian lowlands in which pair bonding is normative—higher-status men (both dominant and prestigious men) have more extramarital sexual affairs than lower-status men (von Rueden, Gurven, & Kaplan, 2011). The same applies to modern industrialized societies. Perusse (1993) investigated the relationship between the position of male employees and their sexual opportunities. The self-report data showed that employees with more senior positions had more sexual liaisons. Young male members of street gangs are reported to have more sexual affairs and greater status among their peers than nongang members of the similar age (Palmer & Tilley, 1995). American World War II soldiers who returned home as war heroes—recipients of the Congressional Medal of Honor—had more children than other veterans who did not receive this award (Rusch, Leunissen, & van Vugt, 2014). This tendency for males to convert their high status into reproductive success is common enough to be labeled with a specific term: the Bathsheba syndrome (D. C. Ludwig & Longenecker, 1993).

STATUS, MATING, AND MEN'S PSYCHOLOGY

Given the stakes of the outcomes of status competitions, men are expected to use more costly tactics to advance their own status goals. These tactics often involve dominance displays (e.g., physical fights; Archer, 2009), and they are often used in response to otherwise trivial threats—threats that only concern status rather than safety or tangible resources (M. Wilson & Daly, 1985). Further, aggressive responses to status threats appear to be used more by men when other men—other intrasexual competitors—are present to witness the outcome of the competition (Griskevicius et al., 2009). Additionally, men gain status by participating in coalitional fights against other men of rival groups. Men contribute more to their groups in settings of intergroup competition than in the absence of intergroup competition, whereas women do not (van Vugt, de Cremer, & Janssen, 2007). Men also report more aggressive intergroup encounters than women, and they are more likely to support and participate in between-group violence (the male warrior effect; van Vugt et al., 2007). Finally, men score higher on social dominance orientation, which measures the extent to which people prefer status differences and unequal resource access between groups in society (Pratto, Sidanius, Stallworth, & Malle, 1994). The direction of this sex difference is invariant across cultures, even appearing in relatively egalitarian societies such as Sweden and the Netherlands. Intergroup aggression may be a preferred tactic for especially low-status males to elevate their status via combat, and therefore increase their access to resources (Chagnon, 1990; McDonald, Navarrete & van Vugt, 2012; Navarrete, McDonald, Molina, & Sidanius, 2010).

Men may also apply prestige tactics to attract sexual mates. When groups of male participants were playing a public-good game in a laboratory study and were being watched by an attractive woman, they donated more to the group fund than when there was no audience or when the audience was a man (van Vugt & Iredale, 2013). Additionally, men donate more to street beggars when in the presence of female company rather than male company or alone (Iredale, van Vugt, & Dunbar, 2008). Finally, when men and women were primed with romantic motives and were then asked about their helping decisions, men endorsed engaging in heroic, status-enhancing forms of helping (e.g., jumping into water to help someone who is drowning; Griskevicius et al., 2007). In contrast, women endorsed more conventional, low-risk helping (e.g., volunteer work) after a romantic prime. In a virtual environment, men cross a scary rope bridge faster when observed by female bystanders compared to male bystanders (Frankenhuis, Dotsch, Karremans, & Wigboldus, 2010). Finally, men who are more committed to their current partner self-reportedly take fewer risks than men who are less committed to their partner (Frankenhuis & Karremans, 2012).

STATUS AND WOMEN'S PSYCHOLOGY

If men's status conveys information regarding benefits to women (e.g., as mates), then selection might favor a female mating psychology that finds status attractive. In Buss's (1989) landmark cross-cultural study on mate preferences, females across cultures valued status-relevant traits in a romantic partner (e.g., earning capacity, ambition) more than men. In lab studies, females express greater sexual interest in dominant men, but men do not express greater sexual interest in dominant women (Sadalla, Kenrick, & Vershure, 1987). When asked to "build a mate" using a limited budget, women prioritize status and resources in constructing their mate more than men (Li, Bailey, Kenrick, & Linsenmeier, 2002). Men are not blind to this preference; they are more likely to advertise their status and resources on personal romantic advertisements relative to women (Pawlowski & Dunbar, 1999).

Women's mate preferences for status could reflect both preferences for the direct (i.e., protection and resources) and indirect (i.e., heritable quality) benefits that high-status men might possess. The former is certainly true, with women prioritizing social status and resources more in long-term mates relative to short-term sexual partners (Li & Kenrick, 2006). The latter also appears to be true. For example, women's preferences for the type of dominant facial structures described previously are highest at peak fecundability (Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak & Perrett, 2000), as are preferences for men's intrasexually competitive behaviors

(Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004). Further, preferences for such traits are often observed only when female participants judge attractiveness as a short-term sexual partner (see Thornhill and Gangestad, 2008, for a theoretical overview; see Gildersleeve, Haselton, & Fales, 2014, for a recent meta-analysis). The data suggest a clear picture—women prefer status, resources, and morphological and social dominance displays in men, both for the direct and indirect benefits that these traits afford.

A final note on sex differences is that men and women might follow different tactics to acquire status. In one study, men and women rated the social desirability of many different dominance acts (Buss, 1981). The main conclusion is that men are more accepting of egoistic dominant acts such as "Managing to get one's way" or "Complaining about having to do a favor for someone." Women were more accepting of more prosocial, prestigious acts such as "Being active in many community and campus activities" or "Taking charge of things at the committee meeting."

THE EVOLUTIONARY PSYCHOLOGY OF LEADERSHIP

The final section focuses on one particular hierarchical position in groups: leadership. Leaders enjoy considerable prestige in most human societies, and the associated benefits should make leadership positions particularly attractive (van Vugt, 2006). The dynamics of leadership are complicated, though, and not all individuals seek out leadership positions, nor are all leaders afforded similar status. Evolutionary biologists have had an enduring interest in leadership, and there is a growing literature on the subject dedicated to unraveling some of these complications (e.g., King, Johnson, & van Vugt, 2009). Although leadership has been and continues to be a hugely popular theme in the social sciences, this literature has traditionally not addressed fundamental questions about leadership, such as why individuals allow leaders to emerge, why individuals would incur the costs of taking up leadership roles, and so on (Gillet, Cartwright, & van Vugt, 2011). Following Price and van Vugt (2014), we view the topic as a reciprocal exchange between leaders and followers where status and prestige benefits accrue to individual leaders as they successfully coordinate group activities.

Service for Prestige

In human societies, leaders are often highly respected, liked, and admired, with Nelson Mandela and Mohandas Gandhi serving as peak examples. This stands in stark contrast with the highest-status individual in nonhuman primate groups such as gorillas and chimpanzees, where dominant males (alphas) appear to be feared and, at the risk of anthropomorphizing internal states, loathed by lower-ranking individuals (King et al., 2009; van Vugt, 2006). Also, leaders in human groups cannot monopolize resources to the same degree as the alpha in nonhuman primates. This raises a critical question: If human leaders do not dominate access to resources as nonhuman primate alphas do, but they still invest disproportionate resources into their groups, then why would they seek out and accept such positions? The service-for-prestige theory (Price & van Vugt, 2014) contributes to solving this puzzle.

Human leadership is characterized by voluntary, reciprocal arrangements between leaders and followers (cf. Trivers, 1971). In this reciprocal dynamic, leaders trade their expertise, skills, education, personal risks, and time in exchange for prestige offered by followers. This dynamic works best for followers when power differentials between leaders and followers are small— thus when leaders have limited opportunities to use their position to exploit followers. Situations in which power differentials between leaders and followers are large tend to produce status hierarchies based on dominance rather than prestige (van Vugt, Hogan, & Kaiser, 2008). Furthermore, giving prestige benefits to leaders poses a collective action problem among followers as it is cheaper to profit from leaders' group contributions while not deferring to them. To the extent that groups are better at solving this free-rider problem, this will facilitate good leadership.

Several observations support the service-for-prestige idea. First, individuals who achieve leadership positions in foraging societies often do so via public displays of expertise (e.g., hunting, political influence). Among Amazonian Shuar, individuals who are perceived as providing the most valuable service to their social groups are preferred as group leaders and receive more esteem from others in the group (Price, 2003). Lab experiments similarly show that participants who demonstrate a willingness—and ability—to provide benefits to the group receive more status (Anderson & Kilduff, 2009; Hardy & van Vugt, 2006; Willer, 2009). Finally, the status benefits associated with taking on leadership roles are often converted into reproductive success (von Rueden, 2014).

Second, traits valued in leaders in Western societies include intelligence, vision, persistence, communication skills, persuasion, fairness, and ethical decision making (Judge, Colbert, & Ilies, 2004). These are also among the leader traits most valued by followers within traditional societies (Tooby, Cosmides, & Price, 2006; von Rueden, 2014). This suggests that there is cross-cultural consistency in what followers expect from leaders (Den Hartog, House, Hanges, Ruiz-Quintanilla, & Dorfman, 1999). Communication and oratory skills facilitate social coordination, higher intelligence would conceivably relate to better decision making, and fairness would guard against exploitation of followers (van Vugt et al., 2008).

A third observation in line with service for prestige is based upon considerations of the costs that leaders can impose upon followers (Padilla, Hogan, & Kaiser, 2007). As leaders accumulate power over time, their positions in status hierarchies can transition from prestige based to dominance based as they can start to monopolize resources. In mutually beneficial reciprocal relationships between partners of relatively equal power, individuals are partially motivated to treat their partners well, because poor treatment can lead the partner to exit the relationship and devote resources elsewhere (van Vugt, Jepson, Hart, & de Cremer, 2004). As individuals become more dependent on leaders for organizing collective action and the distribution of resources, they become less able to leave the relationship; hence, leaders' incentives to treat their followers fairly decreases. With increases in group size and population density, and, perhaps most importantly, decreases in population mobility, leaders can accumulate power more easily, and leader–follower relationships can transition toward being dominant and exploitative. This is especially the case when leveling mechanisms that might rein in power abuses such as criticism, salary caps, and replacement of leaders are absent (Boehm, 1999; van Vugt & Ahuja, 2011). The consequences of such shifts in power are underscored by the psychological literature, which suggests that increases in power decrease empathy (Galinsky, Magee, Inesi, & Gruenfeld, 2006) and increase abuse (Kipnis, 1972). Furthermore, anecdotal reports suggest that among the higher-echelon leaders in politics and business, there is a preponderance of males with dark triad personalities—a combination of Machiavellianism, narcissism, and psychopathy (Babiak & Hare, 2006; A. Ludwig, 2002).

CONCLUSIONS

By analyzing status from an evolutionary perspective, this chapter attempts to make various contributions to the literature. First, it distinguishes status from a number of related constructs that are often used interchangeably in the literature, including power, dominance, prestige, and leadership. Second, it differentiates conceptually status hierarchies from decision-making hierarchies. Third, it contributes to a foundation for better understanding status via an adaptationist lens by considering the origins, functions, development, and psychological mechanisms underlying status striving in humans, partially by viewing status competitions via a simple game theory model. In doing so, it highlights distinctions between evolved psychological systems for signaling status, assessing status, managing status change, and converting status into reproductive opportunities. Fourth, it highlights the role that hormones, physical attributes, and emotions can play in aiding individuals to negotiate status hierarchies more effectively.

Although we have endeavored to cover a wide range of topics on status, this chapter has also been limited in scope, partially based on outstanding questions that have yet to be solved. Notably, we have not examined the causes of the variability in status hierarchies between human societies, and between humans and nonhumans. Yet it is clear that some societies (and species) are more hierarchical than others. Theorists have asserted that hierarchies are attenuated when (a) resources are more difficult to monopolize, (b) sharing resources is essential for survival, (c) individuals can easily leave groups, and (d) individuals can form coalitions to overthrow a dominant. Further work should investigate the importance of these leveling mechanisms in the formation of status hierarchies (Cashdan, 1983; Plavcan, van Schaik, & Kappeler, 1995). Additionally, more work can be done on the game. Our treatment of the Chicken game implied two different phenotypes. Yet, there is naturally great variability in human personality (Buss, 2009; Nettle, 2006), which might partially reflect frequency-dependent selection on dispositions analogous to the two status strategies. Future research could test the degree to which heritable personality variation relates to behavior in status competitions (cf. Verweij et al., 2012). Our treatment of female status striving has been limited (see Campbell, Chapter 27, this volume, for an in-depth treatment of female status). The literature describing female intrasexual competition is building (e.g., Benenson, 2013; Campbell, 1999, 2013; Grant & France, 2001; Hess & Hagen, 2006; Pusey, Williams, & Goodall, 1997), but more work is required to elucidate the effects of intrasexual competition on losers and winners in female–female contests, and, ultimately, the fitness benefits that women procure by moving up female-specific status hierarchies. Other lines of research might further investigate status-striving tendencies throughout the lifespan of humans, and the different tactics to gain status by older and younger individuals (Wilson & Daly, 1985). Answering questions such as these can shed light onto the psychology of human status, and can help us understand questions regarding the evolutionary foundations of status hierarchy.

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CHAPTER 33

Reputation

PAT BARCLAY

INTRODUCTION

Evolutionary scientists are increasingly coming to the conclusion that an organism's reputation can affect its social and reproductive success. Humans are not the only organisms to have reputations: Behavioral ecologists now recognize that nonhuman animals use a combination of observation and personal experience to determine who to challenge, avoid, or mate with (e.g., McGregor & Peake, 2000). Humans rely even more on reputation because language allows us to transmit information to those who do not directly observe events (Smith, 2010). Because of its ubiquity, reputational factors constitute a major selective force in human evolution.

What consequences has this had for the evolution of human behavior? I will argue that reputation is at least partly responsible for the high levels of nonkin cooperation found in humans, and has also affected the evolution of violence. An organism benefits when others believe that it is willing and capable of conferring benefits and imposing costs on others. Such an organism will be chosen for cooperative interactions and be avoided in competition, both of which historically impacted, and perhaps currently impact, social and reproductive success. This creates competition to be—and be seen to be—a better partner and tougher competitor than others. I will review some of the evidence of how reputations have affected the evolution of human cooperation and conflict. To better understand the impact of reputations on evolution, we need to first establish what reputation is, why it matters, and what sort of information organisms will track about others.

WHAT IS REPUTATION?

An organism's reputation in a particular domain is the belief—held by others—that it possesses a particular trait. Reputation is specific to a trait: Others believe that you do, or do not, possess that trait. Such traits can be physical (e.g., athletic, strong fighter), dispositional (e.g., honest, faithful, hard-working, willing to escalate fights), social (e.g., has powerful allies), or a combination of these. These reputations for various traits are distinct and potentially separable: For example, one's reputation as a basketball player is different from one's reputation as a brawler, cooperator, hard worker, liar, alcoholic, or lover. The same organism could be high on one of these traits and low on others. There can be overlap between traits—one's reputation in one trait may generalize to conceptually related domains, especially when possession of one trait predicts possession of another. For example, if honesty and cooperative intent are both caused by the same underlying psychology, then one's reputation for honesty will affect others' beliefs of one's willingness to cooperate with others. The degree of generalization should depend on how well one trait predicts another. An overall "good reputation" implies that most others view a person positively on a number of relevant traits.

One's reputation is not absolute or objective: It exists solely in the minds of others. Each individual must form its own impression of everyone else on various traits, using a combination of personal experience, observation, physical or behavioral cues, and information transmitted from others (gossip). These impressions may be accurate or inaccurate, and impressions may vary from person to person due to misperceptions, biases, or different interaction histories. For example, my ally may be perceived as honest by my coalition members, yet other coalitions may perceive him as dishonest—the other coalitions may be biased, may have misinterpreted his actions, or perhaps my ally actually *is* less honest when dealing with rival coalitions.

Thus, in its simplest definition, "reputation" is a simple function of others' beliefs, that is, the average belief held by relevant audiences. More complex definitions may rely on a perception of what others think, that is, a belief about how other people view someone. This more complex definition limits the study of reputation by restricting it to species with a Theory of Mind, situations with multiple observers who all have the opportunity to assess others' beliefs, and cases where audience members generally agree. Because of these limits, the simplest definition of reputation is preferable because it is more general.

WHY DOES REPUTATION EXIST?

It is obviously advantageous to remember what others have done to you: This allows you to assess their likelihood of doing it again. You can then approach those who are likely to confer benefits upon you in the future and avoid those who will impose costs. However, direct interaction carries potential costs such as losing a fight or being cheated. It pays to predict what others will do before directly interacting with them, for example, by observing them interact with third parties (Dabelsteen, 2005).

Many studies show that nonhuman animals "eavesdrop" on the interactions or communications of others in order to gain useful information (McGregor & Peake, 2000). For example, male and female Siamese fighting fish (*Betta splendens*) assess other males' fighting ability by watching them fight, and then approach or avoid them as appropriate (Doutrelant & McGregor, 2000; McGregor & Peake, 2000; Oliveira, McGregor, & Latruffe, 1998). Female great tits (*Parus major*) listen to the outcomes of male–male interactions and preferentially approach winners to assess them for extra-pair copulations (Otter et al., 1999; Otter et al., 2001). Sexually experienced female Japanese quail (*Coturnix japonica*) avoid males they have seen being too aggressive (Ophir, Persaud, & Galef, 2005). Reef fish observe the interactions between cleaner fish and other clients to determine whether to associate with that cleaner

(Bshary, 2002; Bshary & Grutter, 2006). These are but a few of the examples showing that nonhumans in taxonomically diverse species can observe others' interactions—in competitive or cooperative situations—to glean important information about the costs and benefits of associating or competing with those others. These examples also show that observing an encounter changes the subsequent behavior of the observer, which affects the fitness of the individual being observed.

Humans extend the reliance on observation by incorporating the observations of others. Because of language, we can hear about others' past behaviors (via gossip), and then use that information to assess their ability and willingness to confer benefits or impose costs on us. Such socially transmitted reputations are often what people mean by "reputation," but this is simply an extension of the more general case of predicting others' behavior based on their interactions with third parties. Hearing about past behaviors gives listeners access to events they did not directly observe. Most conversations are indeed about social topics (Dunbar, 2006), and of those topics, most discussion involved exchanging information on the speakers' or others' behavior and experiences (Dunbar, Duncan, & Marriott, 1997). The use of language allows reputation to be even more effective at shaping behavior than direct observation alone (Dunbar, 2006; Smith, 2010); the ability to spread information will effectively increase the size of the "audience," and thus the fitness consequences of behavior (Nowak & Sigmund, 2005).

There are time, energetic, and cognitive costs associated with attending to others' interactions (Peake, 2005); learning by observation requires cognitive abilities beyond the ability to learn from personal reinforcement and punishment. Information may be transmitted inaccurately, like in the children's game of "Broken Telephone," or even deliberately manipulated by others for their own gain. An organism may behave differently depending on its partner—X's interactions with Y are an imperfect cue of how X will interact with Z (Krasnow, Cosmides, Pedersen, & Tooby, 2012). Nevertheless, as long as the information carries some statistically predictive ability, it can be beneficial to observe third-party interactions or use socially transmitted information about others' past actions, abilities, and general behavioral tendencies.

INFLUENCING ONE'S REPUTATION AND THE REPUTATIONS OF OTHERS

Given that others are influenced by what they see or what they hear from others, it pays for an organism to influence how it is viewed by others—to "manage" its reputation. This does not require the ability to attribute mental states to others (Theory of Mind); it simply requires the ability to recognize the presence of an audience, and an evolved or learned decision rule to behave differently when observed.

Individuals in many species alter their behaviors when they are watched by a relevant observer. For example, male Siamese fighting fish vary their aggressive displays depending on whether an audience is present and whether the audience is male or female, male vervet monkeys are more affiliative towards infants when the infant's mother is watching, and male budgerigars spend more time courting extra-pair partners when their primary mate is not watching (all reviewed by Matos & Schlupp, 2005). Cleaner fish give better cleaning service (e.g., fewer bites) to their clients when they are observed by another potential client (Bshary & Grutter, 2006), especially when the observer is a highly desirable client (Bshary, 2002). These cleaner fish may even be deceptive, in that they lure in desirable clients by behaving nicely when observed, only to exploit those desirable clients (Bshary, 2002). Victory displays occur after winning a fight in species ranging from crickets to frogs, from songbirds to canids, and may function to broadcast one's success to audiences (Bower, 2005). Primates who lose a fight often redirect their aggression towards lower-ranking group members, which may function to display that they are still formidable despite losing to a high-ranking individual (Kazim & Aureli, 2005). As for humans, the effects of observation are so ubiquitous that whole areas of psychology are dedicated to understanding the effects of observation (e.g., social facilitation, impression management), and researchers have to be very careful about how observation may affect the results of their studies (e.g., demand effects, socially desirable responding).

Although impression management does not require Theory of Mind, a Theory of Mind adds considerable strategic complexity by allowing an organism to tailor its impression management according to what an observer knows. Highly social organisms should have psychological mechanisms for monitoring not only the likelihood of being observed, but also the characteristics of the potential audience, the value of a reputation to that audience, how any given act will change how that audience will see oneself, and how one might even avoid an audience to prevent them from observing one's undesirable behaviors (Barclay, 2013).

Reputations often involve an implicit comparison with others: One is seen as strong*er*, tough*er*, nice*r*, or *more* cooperative than others. As such, organisms should also have psychological mechanisms for monitoring their reputation relative to others and acting accordingly (Barclay, 2013). For example, are one's competitors seen as more generous, and if so, should one compete by acting more generously or by attacking the reputation of the competitors?

Just as it is advantageous to manipulate one's own reputation, it is also advantageous to manipulate audience perceptions of one's allies and competitors (Hess & Hagen, 2006). Gossip is arguably all about influencing the reputations of other people, making one's allies seem better than they are and one's competitors seem worse. We should predict that people will be most likely to spread information about domains that are most important in making allies look good and competitors look bad (e.g., Buss & Dedden, 1990). Given the potential for its manipulation, people assess the veracity of gossip using cues such as the number of sources they hear it from and the vested interests of the person from whom they hear the gossip (Hess & Hagen, 2006; Sommerfeld, Krambeck, & Milinski, 2008).

TYPES OF REPUTATION

The costs and benefits of social interactions depend on who one is interacting with and the type of interaction, such as a cooperative versus competitive situation. Some individuals are highly capable of conferring benefits upon others (e.g., good hunters) or are more likely to do so (e.g., honest cooperators), whereas other individuals are less willing and able to confer benefits. Some individuals will continue to confer such benefits (e.g., faithful partners), whereas others will not. Some individuals are more capable of imposing costs on others (e.g., good fighters) or are more likely to do so (e.g., chronically angry people), whereas others are less willing and able to impose costs. This is obviously important information to track.

Any organism gains from seeking out situations where it receives benefits from others. Good cooperators are often worth approaching; bad cooperators are usually not. Faithful partners will provide benefits for longer than unfaithful or fraudulent partners. Because others differ in their ability and willingness to confer benefits in both the short and long term, we should expect organisms to track who is most able, willing, and available to do so.

Much evidence shows that humans do judge others based on these three qualities: *abilities*, *tendencies*, and *availability* (reviewed by Barclay, 2013). The value of a cooperative partner is some function of these three traits. The best cooperative partners are very able to help, willing to help, and available to do so. The worst partners are none of those three. Intermediate partners have intermediate levels of these traits or are high on one but low on others (e.g., able to help but less willing to do so). We should then expect organisms to track this information, and to approach and preferentially help partners who have a reputation for being able to help, willing to help, and available as a cooperative partner. This does not require conscious tracking of these traits or any awareness that they affect one's partner preferences, just as people do not consciously track the MHC genotypes of their romantic partners (e.g., Alvergne & Lummaa, 2009). Instead, our proximate psychological mechanisms (e.g., emotions) do this tracking for us.

Organisms should also avoid situations where others will impose costs that outweigh the benefits. For example, conflict over resources can be worthwhile if one will win the competition, but is usually not worthwhile if one will lose. Courting the spouse of a powerful individual carries high risks, whereas there are fewer costs associated with courting the spouse of a weaker individual or someone who is absent and unable to retaliate. Because others differ in their ability and willingness to impose costs, we should expect organisms to track who is most able, willing, and available to impose costs, and avoid conflict with those who score high on those traits (Daly & Wilson, 1988; Sell, Tooby, & Cosmides, 2009).

This chapter focuses on a reputation for cooperation (conferring benefits), and to a certain extent, a reputation for aggression (imposing costs). There are specific examples of these that are beyond the scope of the chapter; for example, people carry reputations for commitment and fidelity to their mates or allies. Ultimately, these are specific instantiations of the more general principles of benefit conferral and cost imposition; in this case, a mate's reputation for infidelity indicates there are fewer long-term benefits of associating with him or her. Many of the same principles underlie partner choice for mating and partner choice for other social relationships (Barclay, 2013). As such, many principles that apply to reputations in one domain will also apply to reputations in other domains.

REPUTATION FOR COOPERATION

Humans rely heavily on each other's cooperation for survival and social success, so it is unsurprising that we track others' reputation for cooperation. This can come in at least three forms: indirect reciprocity, signals of the ability to confer benefits, and signals of willingness to confer benefits. We discuss each of these in turn.

INDIRECT RECIPROCITY

Axelrod's (1984) seminal computer simulations of the evolution of cooperation in the Prisoner's Dilemma game, and the success of conditional cooperators like the Tit for Tat strategy, is an example of *direct reciprocity*: Individuals help those who have helped them in the past, or likely will in the future. A conditional cooperator helps those who help, thus reaping the long-term rewards of mutual cooperation, but refuses to be suckered for long by noncooperators. Years of mathematical models and computer simulations show that most successful strategies involve some conditional willingness to reciprocate help, and much evidence shows that people are more likely to help those who have previously helped them.

Humans go beyond direct reciprocity by also helping others who have not personally helped them, or who will not have an opportunity to reciprocate. Helpful acts may be reciprocated not just by the recipient, but by others who observe it or hear about it; this is known as *indirect reciprocity* (Alexander, 1987; reviewed by Nowak & Sigmund, 2005). Indirect reciprocity works when those who help gain a good reputation and are thus more likely to be helped by observers. Those who refuse to help get a bad reputation and are more likely to be refused help.

Wedekind and Milinski (2000) gave participants the chance to donate to others and have these donations (or lack thereof) be made public to others. Participants were more likely to give to people who had given to others in the past, even though the design ensured that no one would have the opportunity to reciprocate a donation directly. Subsequent experiments have also shown that people give more to generous people (Milinski, Semmann, Bakker, & Krambeck, 2001; Seinen & Schram, 2006; Semmann, Krambeck, & Milinski, 2004; Wedekind & Braithwaite, 2002). People base their giving on a combination of personal experience and social information about others (Roberts, 2008; Sommerfeld, Krambeck, Semmann, & Milinski, 2007); the more positive things we hear about someone, the more likely we are to give to that person (Sommerfeld et al., 2008). Field research suggests that people gossip about the cooperation of others and that this has "real economic consequences" (Fessler, 2002; Kniffin & Wilson, 2005). For example, hunters who share meat are more likely to receive meat from group members (Gurven, Allen-Arave, Hill, & Hurtado, 2000), though this could also be because group members have a vested interest in the well-being of food providers (Barclay & van Vugt, 2015).

Given that people pay attention to others' cooperativeness, it pays to be more cooperative when others are watching. Much research shows that the presence of observers increases "good behavior" in many domains, including donations in monetary games within laboratories (e.g., Barclay, 2004; Hardy & van Vugt, 2006; Hoffman, McCabe, Schachat, & Smith, 1994; Milinski, Semmann, & Krambeck, 2002; Rege & Telle, 2004), willingness to volunteer (Bereczkei, Birkas, & Kerekes, 2007), contributions towards educating others about climate change (Milinski, Semmann, Krambeck, & Marotzke, 2006), voter turnout (Gerber, Green, & Larimer, 2008), and simulated tax donations (Coricelli, Joffily, Montmarquette, & Villeval, 2010). People are also more likely to cooperate if others might gossip about them (Feinberg, Willer, & Schultz, 2014; Piazza & Bering, 2008). This effect of observation can be harnessed to promote cooperation in many situations, including contributions to public goods (Milinski, Semmann, & Krambeck, 2002; Panchanathan & Boyd, 2004), responsible consumerism (Barclay, 2012; Griskevicius, Cantú, & van Vugt, 2012), and the fight against climate change (Milinski et al., 2006). Increased giving under observation is sometimes strategic (Barclay & Willer, 2007; Semmann et al., 2004), but it is also possible that cooperative emotions like empathy and guilt are experienced more strongly in the presence of observation. This latter possibility requires future investigation.

There are different types of indirect reciprocity that differ in what constitutes a "good" (or "bad") act that is worthy (or unworthy) of reciprocation (reviewed by Nowak & Sigmund, 2005). In some models, helping anyone is seen as good and increases one's reputation ("image scoring"). In other models ("standing strategies"), helping a defector does not increase one's reputation, and it may even be seen as "bad" to help someone who is "unworthy" of help. "Image scoring" is less likely to be evolutionarily stable than variants of "standing strategies," because in the former it would not pay to discriminate against defectors (Ohtsuki & Iwasa, 2004, 2006, 2007). However, current experimental evidence suggests that people use image scoring rather than standing strategies (Milinski et al., 2001). This may be because it is difficult to tell whether a defection against a defector is truly "justified" (see also Barclay, 2006), and whether such defection represents moralistic discrimination or a cheap excuse to cheat someone—a topic for future work.

SIGNALS OF ABILITY TO CONFER BENEFITS

Some acts are difficult to perform, and can be done best by those with special abilities. For example, it takes strength and agility to leap from a moving boat to catch a 150-kilogram green sea turtle; uncoordinated individuals would be less likely to catch turtles. Billionaires can give away sums of money that would bankrupt normal people. Good swimmers can dive into raging rivers to save drowning babies, whereas bad swimmers might drown. Because these acts are easier or less costly for some people to perform, they carry information about the performer: The ability to share turtle meat at feasts is a credible signal of the hunter's strength and agility (Smith & Bliege Bird, 2000), Bill Gates's billion-dollar donations are a credible signal of his vast wealth, and diving into a river to save a baby is a credible signal of swimming ability. Such acts thus convey information about an individual's agility, strength, wealth, and other such qualities, all of which are desirable in social partners because they indicate an ability to confer benefits on others.

These are all examples of costly signaling theory (Grafen, 1990; Zahavi, 1977), where the cost of a signal is used to maintain signal honesty. It would be beneficial for anyone to appear strong, agile, and wealthy, but the fitness costs of some acts are not worth it for someone who does not actually possess the necessary qualities (Gintis, Smith, & Bowles, 2001; Searcy & Nowicki, 2005). For example, even if I managed to borrow 1 billion dollars to give to charity, the cost of bankruptcy would far outweigh any reputational benefits to me. Such a donation would be worth it for Bill Gates, because for him the cost is trivial. Similar arguments hold for the other examples: The anticipated hunting success (and subsequent reputation) is worth the time and risk for a good hunter but not a bad hunter, and a reputation as a baby-saving hero is worth the drowning risk only for someone who is unlikely to drown. Thus, the cost (or potential cost; Getty, 2006) deters those who do not possess the necessary qualities, so they can be used as honest signals of one's qualities. Audiences benefit from attending to those signals and gaining useful information. Again, this does not imply that people consciously assess the costs and benefits or consciously track them in others; our emotions (e.g., fear, bravado, empathy) do this for us.

Costly signaling theory has been used to explain many types of extravagant helping, including lavish sharing at feasts (Boone, 1998), large-scale philanthropy (Harbaugh, 1998), big-game hunting (Hawkes & Bliege Bird, 2002; Smith & Bliege Bird, 2000), and blood donations (Lyle, Smith, & Sullivan, 2009). These all require wealth, political connections, physical abilities, or health, which are all related to the actor's ability to confer benefits on others. There may be direct reproductive advantages for such behavior: For example, good hunters have more children than poor hunters (Smith, 2004), including more children with other men's wives (Hill & Kaplan, 1988). Of course, the benefits of such signaling need not be in terms of mate attraction—those who possess such abilities may be chosen more often as allies or avoided more often as competitors (Smith & Bliege Bird, 2000).

The above examples all involve conspicuous generosity as a signal of resources or abilities, but obviously, many signals do not involve generosity. Conspicuous consumption and conspicuous leisure have been seen as signals of wealth for over 100 years (Veblen, 1899/1994). Physical abilities could be signaled via athletic displays and sporting wins; intellectual abilities could be signaled via wit, vocabulary, or problem solving; and so on (Barclay, 2013). In fact, signaling via nongenerous means is arguably more common than signaling via generosity. Signaling via generosity may also carry information about one's character, which is beneficial, but there may be a risk of "diluting the signal" by signaling more than one trait in a single act. Future research should investigate when people will signal their traits via generosity, and whether this is as effective as using nongenerous means like conspicuous consumption.

SIGNALS OF WILLINGNESS TO CONFER BENEFITS

If someone has helped you in the past, it suggests that they are more likely to help in the future as well (André, 2010). This generalizes beyond established pairs: People who are cooperative within one group tend to be cooperative within other groups also (Kurzban & Houser, 2005). This is the basis of stable personality traits like agreeableness: Niceness generalizes across situations. Someone who creates a reputation for helping others is essentially broadcasting a willingness to confer benefits on others. Similarly, someone with a reputation for commitment has succeeded in broadcasting his or her willingness to provide benefits to partners (McNamara & Houston, 2002).

What maintains the honesty of such signals? The previous section described how signals of abilities are kept honest by the high potential cost of extravagant generosity (Gintis et al., 2001). By contrast, many signals of willingness to help do not appear very costly and could seemingly be done by anyone. It does not require wealth or athletic ability to spend time with someone, groom a person, or volunteer in a soup kitchen. Such acts cost the same time for anyone. In these cases, honesty is maintained not by differential costs, but by differential benefits: It would not be worth it to cooperate at time A if one intended to cheat at time B and lose out on future cooperative interactions (André, 2010; Bolle, 2001; Ohtsubo & Watanabe, 2009; Smith & Bliege Bird, 2005). Signals will be honest as long as the cost of public helping is (a) greater than the immediate benefits of "suckering" someone and also (b) less than the long-term benefits of mutual cooperation. The former condition makes cheaters not bother trying to appear cooperative, whereas the latter condition makes it pay off for long-term cooperators to broadcast their willingness to help. Thus, honesty is maintained by differential long-term benefits accrued to cheaters and cooperators, not differential costs (Barclay & Reeve, 2012; Grafen, 1990).

Not surprisingly, people treat public helping as though it carries information about the helper's future trustworthiness. People entrust more money to those who have given money to a charity or public good (Albert, Güth, Kirchler, & Maciejovsky, 2007; Barclay, 2004, 2006; Keser, 2003), preferentially associate with those who have given to others (Barclay & Willer, 2007; Feinberg et al., 2014), and prefer generous people to neutral controls for romantic relationships (Barclay, 2010). This adds up to substantial benefits for those with a good reputation. In business, online reputation systems are prevalent in places like eBay, Amazon, and TripAdvisor; these are designed so that sellers can acquire a good reputation, and this can directly benefit honest companies (Frank, 2004). Cooperative reputations are so valuable that they are worth maintaining in order to sell a reputable business (Pfeiffer, Tran, Krumme, & Rand, 2012), or possibly to pass along to offspring.

PUBLIC HELPING: INDIRECT RECIPROCITY OR COSTLY SIGNAL OF COOPERATIVE INTENT?

There are many overlapping predictions if we view helping behavior as indirect reciprocity versus as a costly signal of cooperative intent. For example, both theories predict that organisms will be more cooperative while observed, be concerned about their reputation, attempt to enhance their reputation, and so on. In fact, these two theories may not even be separate: Reciprocation itself could be seen as a signal of future willingness to help (André, 2010). Indirect reciprocity may simply be the outcome of organisms attempting to assess the probability that another organism will cooperate in the future, combined with their tendency to signal their own willingness to cooperate. A similar argument has been made about moral judgment: When people judge the morality of acts, perhaps what they are really assessing is the probability that the actor is a good person and future cooperator (Pizarro, Tannenbaum, & Uhlmann, 2012; Tannenbaum, Uhlmann, & Diermeier, 2011).

Some evolutionary psychologists (e.g., McCullough, Kurzban, & Tabak, 2013; Sell et al., 2009) argue that we observe others' actions in order to assess their "welfare trade-off ratio" (WTR) towards us—that is, how much they value our welfare relative to their own. Some acts imply a high WTR (i.e., actor values our welfare), some imply low WTR (i.e., actor does not value us), and some even imply a negative WTR (i.e., actor values our demise). What currently appears to be indirect reciprocity could simply be people attempting to assess the welfare trade-off ratio of others and then initiate or maintain positive relationships with those who appear likely to cooperate in the future. Future theoreticians and empiricists should test whether indirect reciprocity is simply the outcome of this same process, with different acts having different predictive ability of one's future cooperation.

COMPETITIVE HELPING

Individuals differ in their ability and willingness to confer benefits on social partners like allies, friends, and mates. Whenever organisms can choose whom to interact with, this creates a market-like competition over the "best" partners (Noë & Hammerstein, 1994, 1995). The best way to attract a good partner is to be a good partner, so each organism gains from appearing more able or more willing to confer benefits on its partners. Much social competition is about demonstrating abilities (e.g., sports), but one can also compete using generosity: There is a market-based incentive to compete to be more generous than others in order to attract more social partners and / or higher-quality partners. This process of "competitive altruism" or "competitive helping" consists of not just appearing nice, but appearing *nicer* than one's competitors (Barclay, 2004, 2011, 2013; Barclay & Willer, 2007; Roberts, 1998; van Vugt, Roberts, & Hardy, 2007).

Competing over social partners is similar to competing over mates, and many of the same principles apply to both (Barclay, 2013). In fact, sexual selection is just a specific instantiation of social selection, which is when one's fitness depends on the actions and choices of others (West-Eberhard, 1979, 1983). In this particular case, individuals compete over nonromantic relationships just as they do over romantic relationships. This competition over social partners can lead to a "runaway" process towards higher levels of generosity (McNamara, Barta, Frohmage, & Houston, 2008; Nesse, 2007), up to the point where the marginal benefits of attracting additional partners is outweighed by the marginal costs spent to attract them (Barclay, 2011, 2013).

Experimental evidence shows that people actively escalate their generosity when it can affect others' choice of partners. For example, people give more money in laboratory experiments when observed by others (e.g., Hardy & van Vugt, 2006; Rege & Telle, 2004), but they give the most when those observers can choose whom to interact with in the future (Barclay, 2004; Barclay & Willer, 2007; Sylwester & Roberts, 2010). These latter findings show that people are not only trying to appear nice, but are actively trying to appear *nicer* than competitors. People will also compete to give more to environmental charities when it will affect observers' choice of partners, and this effect is above and beyond the effect of simply being observed (Barclay & Barker, in preparation).

Additionally, other research shows that generous people are accorded higher status, both in laboratory tasks (Hardy & van Vugt, 2006; Willer, 2009) and in anthropological studies (Price, 2003). Extravagant helping may be a way to compete over mates and social partners: Anthropological examples such as big-game hunting, large-scale philanthropy, and hosting large feasts have all been interpreted as competition to be more generous than others (Barclay, 2013; Boone, 1998; Harbaugh, 1998; Hawkes & Bliege Bird, 2002; Smith & Bliege Bird, 2000).

REPUTATION FOR AGGRESSION

Humans excel at nonkin cooperation but also use aggression. Fatal and nonfatal conflict is endemic in nonstate societies, with many men dying violently at the hands of other men (Chagnon, 1997; Daly & Wilson, 1988; Pinker, 2011; Puts, 2010). Given the prevalence and costs of violence, it obviously pays to know whom to avoid challenging. We should thus expect that organisms will track others' reputations for aggression.

ABILITY AND WILLINGNESS TO INFLICT COSTS

How does an organism know who is worth challenging and who is best avoided? If an individual is highly willing and able to inflict costs on others, then it is dangerous to challenge him or her. Organisms can assess this from personal experience, valid cues like physical size or behavioral displays (Sell et al., 2009), observations about others' willingness to engage in conflict or risk-taking in general (Fessler, Tiokhin, Holbrook, Gervais, & Snyder, 2014; Johnstone & Bshary, 2004), observations of the outcomes of others' fights (McGregor & Peake, 2000), or indirectly hearing about any of the above, that is, transmitted reputation.

In their seminal book on human aggression, *Homicide*, Martin Daly and Margo Wilson (1988) summarize the importance of a formidable reputation in many environments, that is, a reputation for being willing and able to inflict costs on others in response to affronts. A complete summary of their evidence is beyond the scope of this chapter, but it is worth requoting their oft-quoted words:

> Men are known by their fellows as "the sort who can be pushed around" or "the sort who won't take any shit," as people whose word means action and people who are full of hot air, as guys whose girlfriends you can chat up with impunity or guys you don't want to mess with. (Daly & Wilson, 1988, p. 128)

Exactly what information is assessed and passed on about others' ability to inflict costs? Physical abilities, intellectual abilities, and political connections can all be used to help or hurt someone. In the previous section, "Ability to Confer Benefits," I discussed a number of traits that could be used to infer others' ability to confer benefits on partners. Many or most of those traits would also apply to one's ability to inflict costs—the same reputation is useful for both attracting allies and deterring competitors. For example, sporting ability can signal one's ability to physically confer benefits or physically impose costs. Future work should determine the relative importance of these two abilities—benefit conferral and cost imposition—for people's reputations, in order to determine when and why audiences attend to certain signals.

Some displays may be designed to enhance or repair one's reputation for formidability. Many animals perform victory displays after winning a fight, which can broadcast their success—and corresponding formidability—to others who may not have observed the victory (Bower, 2005); this display function has also been suggested for the postures of human athletes after a triumph (Matsumoto & Hwang, 2012). Many primates show redirected aggression, where the loser of a fight aggresses against someone else even lower in the hierarchy, which could potentially function to deter challenges from others by signaling the loser's residual formidability (Kazim & Aureli, 2005). Even the willingness to fight itself could signal one's formidability, because fighting is less costly for more formidable individuals, such that they will engage in it more readily (Benard, 2013; Johnstone & Bshary, 2004).

People's aggression is certainly affected by opportunities for reputation (reviewed by Benard, 2013; Daly & Wilson, 1988; Felson, 1978; Frank, 1988). For example, men are more likely to violently retaliate against transgressions if there is an audience than when there is no audience (reviewed by Felson, 1978). This should be unsurprising to anyone who has observed a physical fight in school, in a bar, or elsewhere. Laboratory experiments confirm that opportunities for reputation cause people to challenge others more often over resources in an attempt to convey high competitive ability (Benard, 2013). Furthermore, much research shows that people are more likely to back down from aggressive confrontations if they can do so without "losing face," that is, without gaining a reputation for cowardice (reviewed by Daly & Wilson, 1988; Felson, 1978). In laboratory experiments, status motives make men more likely to engage in face-to-face confrontations, and make women more likely to engage in indirect aggression (Griskevicius et al., 2009). Reputation is also involved in bargaining, with people attempting to establish a reputation as a "tough bargainer" in order to receive better bargains in the future, even if it means engaging in irrational behavior in the present (DeClerck, Kiyonari, & Boone, 2009; Frank, 1988; Nowak, Page, & Sigmund, 2000; Yamagishi et al., 2009).

A reputation for toughness may seem at odds with a reputation for cooperation: If people value cooperation, wouldn't they avoid highly aggressive individuals? These two qualities—conferring benefits on others versus imposing costs—have different values in different environments. In environments characterized by social exchange and with central authorities to limit interpersonal conflict, the former will be more important for social success. In environments with intense competition over limited resources, the latter will be more important. When people form alliances to aggressively compete with other alliances, then both are important. Ultimately, the best partners are those who are highly able to confer benefits and impose costs, and are highly willing to selectively confer benefits upon oneself and impose costs on one's rivals.

HARNESSING THE POWER OF REPUTATION

Given that people are so concerned about reputations, we can use this knowledge to promote prosocial behaviors and decrease antisocial behaviors (Barclay, 2012). For example, people who are made to think about status and good reputation tend to make more benevolent decisions (Griskevicius et al., 2007) and purchase more environmentally friendly products (Griskevicius, Tybur, & van den Bergh, 2010). People do more to preserve the environment when observed than when anonymous (Milinski et al., 2006), and will even compete to give more to environmental causes (Barclay & Barker, in preparation). After being told about others' high cooperation, people are more likely to give to fundraisers (Shang & Croson, 2006), cut energy use (Allcott, 2011), and reuse hotel towels (Goldstein, Griskevicius, & Cialdini, 2007). Under some circumstances, it could even be useful to limit reputational opportunities, for example, to reduce aggressive retaliations and escalations of conflict.

Even false cues of reputation can be effective at changing behavior. Observation is one component of reputation, and photographs of eyes (a false cue of observation) have been shown to trigger higher monetary donations in laboratory games (Burnham & Hare, 2007; Haley & Fessler, 2005; Mifune, Hashimoto, & Yamagishi, 2010), more payment for coffee on an "honor system" (Bateson, Nettle, & Roberts, 2006), more cleaning of litter (Ernest-Jones, Nettle, & Bateson, 2011; Francey & Bergmuller, 2012), higher charitable donations in supermarkets (Ekström, 2011), and lower bike thefts (Nettle, Nott, & Bateson, 2012). However, the effects of such false cues may be transient: People quickly habituate to images of eyes (Sparks & Barclay, 2013) and eventually come to ignore verbal punishment that is not followed by tangible consequences (Sparks & Barclay, in preparation). Would-be social engineers would be unwise to rely forever on false cues of reputation, unless those cues are at least occasionally followed by real opportunities for reputational costs and benefits.

Despite the benefits of harnessing reputation, there are several risks associated with doing so. Barclay (2012) identified the following limitations and unknowns, in increasing order of importance: (1) reputational benefits must outweigh the costs of helping; (2) reputational cues must be stronger than other situational factors; (3) people may habituate to noninformative cues of reputation; (4) not everyone values reputation; (5) reputation only pays off in the long term; (6) extrinsic incentives may "crowd out" intrinsic motivations; (7) reputation can promote negative behaviors like aggression; (8) reputations can be manipulated; and (9) publicly identifying reputational incentives may reduce the benefits to cooperators and thus undermine cooperation. It is important to understand and overcome these limitations before relying on untested means of harnessing reputation.

FUTURE DIRECTIONS: TOWARD A MORE COMPREHENSIVE SCIENCE OF REPUTATION

Evolutionary researchers have learned much about the power of reputation and how it has affected the evolution of cooperation and conflict. Despite these advances, there are currently many unknowns about the evolution and dynamics of reputation. The following are some future directions that warrant investigation.

Broader roles of reputation: To what extent does reputation underlie other phenomena? For example, in his classic book *Passions Within Reason*, Robert Frank (1988) ultimately relies on reputation as the reason why emotions are hard-to-fake signals of future intent. Ohtsubo and Watanabe (2009) argue that the costs of apologies make them effective as signals of cooperative intent. Other researchers rely on reputation when they argue that religious rituals serve as a costly signal of cooperative intent towards fellow believers (Sosis, 2004). Similarly, could xenophobia be a signal to ingroup members that one is committed to cooperate with (and only with) other ingroup members, with the honesty of the signal maintained by the opportunity costs of foregone partnerships with outgroup members? Are moral judgments a way of advertising one's beliefs—and thus future behavior—to audience members? What other phenomena might ultimately rely on reputation?

Proximate mechanisms: What proximate psychological mechanisms have been selected for as a result of past reputational consequences? To what extent has this resulted in a genuine concern for others (e.g., see Barclay, 2013) versus simply a conscious concern for reputation? Are reputational effects caused by an increase in the causal emotions themselves; for example, does genuine empathy (cooperation) or anger (aggression) increase in response to the presence of an audience?

Interactions between different reputations: How do different types of reputation interact, such as a reputation for conferring benefits versus imposing costs, or a reputation for ability versus willingness to confer benefits? How and why does a reputation for one trait affect one's reputation for other traits? If one act signals multiple traits, is there a risk of "diluting" the signal across too many domains? What is the optimal balance between an able partner versus a willing partner, or a partner who both confers benefits and imposes costs, and how does this affect what information people track and transmit about others?

Getting into specifics: What traits are signaled by what acts? How useful are different acts at conveying information about the actor, and how much do audiences rely on them? Is this information passively conveyed as a by-product of the actor's normal actions ("cues"), or is the information actively transmitted and exaggerated by an actor that has evolved to perform that action for its information value ("signals")?

Information value of different actions: What affects the honesty of the signals that affect one's reputation? For example, exactly why does cooperation at time A predict cooperation at time B—that is, why do stable individual differences exist? If the honesty of signals is maintained by costs, then what types of costs are involved (e.g., performance costs vs. opportunity costs, Barclay & Reeve, 2012). There is much theoretical work on costly signals of stable traits like genetic quality, but much less done on signals of intent or future behavior.

Novel environments, plasticity, and the importance of reputation: How does reputation in today's world differ from reputation in ancestral environments? What effect does this have? For example, given that most of us no longer live in small, tight-knit societies where everyone knows everyone's business, does this diminish the importance of reputation? To what extent can people adjust to the changing role of reputation, or are our evolved reputation-based emotions no longer as adaptive as they once might have been (Barclay & van Vugt, 2015)? Will the Internet compensate for this? Which false cues of reputation will people readily habituate to (e.g., photos of eyes; Sparks & Barclay, 2013), and which will continue to have an effect?

Novel environments, plasticity, and evolved cues of underlying traits: Are some cues less informative in modern environments than in ancestral environments, and how do people react to those? For example, politicians' emotional rhetoric is arguably a less reliable signal of their cooperative intent than would be the case in a small, reputation-based band, yet people still seem to treat it as a valid cue. To what extent will people continue to rely on ancestral cues versus show adaptive plasticity in which cues they rely on?

Dealing with new actions, cues, and signals: How does a given act initially come to signal a given trait, such that people then track those acts in others' reputations (Panchanathan & Boyd, 2004)? For example, how could an act like protecting the environment come to signal good character or to be valued within a system of indirect reciprocity (Barclay, 2012)? Does this require a preexisting correlation between character traits and a given act (e.g., nice people just happen to support the environment), which audiences pick up on, and which is then later exaggerated by the actors as an active signal?

Audience skepticism: Given that people tend to behave differently when observed, how does this affect the information that can be inferred from someone's public actions? To what extent do audiences change their impressions of someone's actions depending on the number and nature of other audience members; for example, how skeptical should one be of public generosity relative to private generosity? What happens when people become aware of the reputational consequences of various actions? For example, will people trust cooperators less if they know that cooperators can benefit from their actions (Barclay, 2012)? If so, this leads to a recursive problem, because it would affect the level of cooperation that would be displayed, which then affects skepticism, and so on, in a feedback cycle. How can we resolve this?

These are just a few of the questions that remain when attempting to understand reputation. The science of reputation is just getting started, so we should look forward to more theoretical and empirical investigations of these questions. Eventually we should hope to see predictions that are much more nuanced than "people will be nicer when observed," and be able to quantify exactly how much nicer, when, in what situations, to whom, and exactly how audiences will respond.

CONCLUSIONS

Reputations are an important part of the lives of many social organisms. Humans' ability to transmit information verbally has increased the importance of reputation because it gives individuals access to information they did not directly observe. Each individual's reputation affects how others act towards it, such that reputations have real fitness consequences. An organism benefits from being seen as more effective at conferring benefits on allies and imposing costs on competitors. This selects for higher levels of cooperation, but also higher levels of aggression—and manipulation of the appearance of both—as organisms compete to have a better reputation than others. This can occur in any organism, but is particularly relevant in humans because language makes reputations much more important for us than for other species. As a result of such past selective pressures, humans most likely have psychological adaptations specifically for tracking the reputations of others, monitoring their own reputations, adjusting their behavior according to the reputational consequences, and manipulating information to make themselves look better and rivals look worse. By understanding the role of reputation in our daily lives and its role in the evolution of human behavior, we can be more effective at harnessing its power to promote positive change.

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CHAPTER 34

The Evolution and Ontogeny of Ritual

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RITUALS ARE UNIVERSAL features of human behavior (Boyer & Liénard, 2006; Whitehouse, 2000, 2004). The ethnographic record is rife with evidence for exotic and seemingly unusual ritual behavior (Humphrey & Laidlaw, 1994; Whitehouse, 1995). Consider the ritual cycle of pig slaughter of the Tsembaga of New Guinea, as described by Rappaport (1967, 1984). The Tsembaga ritual cycle centers around periodic warfare between groups who compete over resources and retaliate over transgressions. The timing of warfare is closely related to the size and spread of pig herds. Alliances with other neighboring groups, usually through extended kin networks, are formed to aid in battle. There are a number of rituals performed prior to the beginning of the warfare to inform the ancestors of the intention to fight. If an amicable agreement cannot be reached through negotiations and tensions escalate, "fighting stones" are hung, indicating that debts will be repaid to ancestors and allies who will be compensated for their assistance in the fight. Hanging the stones also indicates that a number of taboos must be followed throughout the period of warfare. For example, taboos against eating particular kinds of animals and plants take effect and group members are no longer permitted to engage with members of the enemy group (even looking at the enemy is prohibited).

Pig slaughter is a key feature of the ritual cycle. Pigs are highly valuable and are never slaughtered outside of ritual contexts. At the beginning of the ritual cycle, two pigs are killed as offerings to the ancestors and are cooked overnight. On the morning of the battle, the warriors consume one of the pigs, and taboos against engaging in social and sexual intercourse with women take effect. Men cover their bodies with the ash from the fire to encourage the spirits to "come into their heads where they burn, informants say, like fires, imbuing [the warriors] with strength, anger, and the desire for revenge" (Rappaport, 1984, p. 134). The black ash also masks their faces, resulting in anonymity on the battlefield. Fighting may continue for weeks or months, but it is often interrupted by various ritual performances and mounting casualties.

Fighting typically ends through a truce between the warring groups. If a truce is reached, both groups return to their region and plant a *rumbim* (a local bush) and slaughter more pigs to offer to the ancestors for their assistance in the fight. After removing the ash from their bodies, all of the men place their hand upon the *rumbim* before it is planted in the ground. This action solidifies each individual's connection to the group and the communal land. The truce period denotes a time of repayments of debts to ancestors and allies who helped during the war, and many of the taboos remain in effect. The truce period typically remains in effect (and the *rumbim* remains in the ground) until there are enough pigs to sacrifice for the pig festival (*kaiko*). When there are sufficient pigs for the festival, the *rumbim* is uprooted and taboos are lifted. During the approximately yearlong pig festival, the Tsembaga host and give gifts to ally groups. During these visits, the men dance together in mass dances that last all night. The number of men from ally groups who come to dance indicates the amount of support the Tsembaga can anticipate in future fighting efforts. At the conclusion of the pig festival, the majority of the group's pigs are slaughtered and some of the meat is offered to ally groups through a fence that is ceremonially torn down at the conclusion of the *kaiko*. If a truce is not reached, and one of the groups is conquered and their land appropriated, the survivors take up residence with neighboring ally groups (in which case, particular rituals are enacted to secure their membership in the new group).

What function, if any, do rituals like these serve in human social groups? "The problem of ritual is the familiar 'rationality problem' in a new guise—old wine in a new bottle" (Sax, 2010, p. 4). Ritual is often interpreted in both popular scientific discourse and in ritual studies as action that is ineffective, irrational, or purely conventional. Rituals often represent sacred beliefs, express inner states of feeling and emotion, symbolize theological ideas or social relations, and invoke psychophysical states (Csordas, 2002; Ruffle & Sosis, 2003; Sax, Quack, & Weinhold, 2010; Shore, 1996). Yet ritual serves important social functions in human culture.

Rituals are socially stipulated group conventions that are opaque from the perspective of physical causality (Legare & Souza, 2012). Rituals are the result of "a positive act of acquiescence in a socially stipulated order," and thus are not the product of individual innovation. "The peculiar fascination of ritual lies in the fact that here, as in few other human activities, the actors both are, and are not, the author of their acts" (Humphrey & Laidlaw, 1994, p. 5). Even when rituals are explained in the context of a certain belief (e.g., engaging in a ritual action will result in a desired outcome), there is often not an expectation of a direct causal connection between the ritual actions and outcomes (Schoejdt et al., 2013). Because humans are expert intention-readers, seeing someone engage in a detailed course of (ritual) actions gives the impression that features of the action sequence (i.e., repetition, number of steps, time specificity) have the potential to produce the intended outcome, even if the underlying mechanism responsible for the outcome is imperceptible, supernatural, or simply unknowable (Legare & Souza, 2012, 2014).

The recurrent features of ritual have been difficult to define due to the complexity and diversity of ritual forms (Rappaport, 1999). Thus, the diversity of ritual across the globe has made it difficult to establish robust generalizations about the causes and effects of features of rituals on social cognition and behavior. The historical separation between the disciplines of psychology and anthropology has also resulted in ritual becoming the exclusive domain of anthropology (Bruner, 1996). Because ritual has been primarily studied from an anthropological lens, until recently, rituals have also been studied with almost exclusively qualitative methods. While this has provided substantial insight into the diversity of ritual forms, using only qualitative methods has limited the establishment of strong causal inferences about the impact of ritual on human cognition and behavior (Rossano, 2012).

New experimental research on the social function of ritual provides fresh insight into the relationship between ritual and the evolution and ontogeny of social group cognition. Over the course of human history, the ratio of kin to nonkin has increased. With this increase in nonkin within social groups, rituals have allowed groups to remain cohesive, while reducing the need for physical and social intimacy and proximity. We argue that although the capacity to engage in ritual is psychologically prepared, rituals are a culturally inherited, behavioral trademark of our species. The structures and functions of rituals have been selected for and transmitted through a process of cultural evolution.

The first objective of this chapter is to describe the social functions of ritual within human groups. We propose that ritual aids in solving the adaptive problems associated with group living by: identifying group members, ensuring their commitment to the group, facilitating cooperation with coalitions, and maintaining group cohesion. Findings from a variety of social scientific disciples provide evidence that rituals facilitate coordinated and cooperative group action, one of the greatest challenges of group living. We also provide a psychological account of how the structure of ritual facilitates high-fidelity cultural transmission over time. Next, we examine evidence that the threat of social exclusion and loss of status motivates engagement in ritual throughout development. In the final section, we provide a psychological account of the ontogeny of ritual cognition. Prior work examining ritual and group processes has focused on adult samples (Sosis, 2000, 2003, 2005; Sosis & Alcorta, 2003; Sosis & Bressler, 2003) and mathematical modeling (Henrich, 2009). We review recent research examining the mechanisms by which children learn the rituals of their group and the cues children use to interpret the behavior of group members (Herrmann, Legare, Harris, & Whitehouse, 2013; Watson-Jones, Legare, Whitehouse, & Clegg, 2014). Combining theory and findings from these lines of inquiry promises to open up new avenues for research on ritual and the evolution and ontogeny of social group cognition.

THE FUNCTIONS OF RITUAL IN SOCIAL GROUP BEHAVIOR

Living in cohesive groups has helped solve the adaptive problems faced by humans (Buss, 1990; Buss & Kenrick, 1998). Living in groups decreased predation risk (Shultz, Noe, McGraw, & Dunbar, 2004; van Schaik, 1983), allowed for coordinated caretaking of offspring (Hawkes, 2014; Kaplan, Hill, Lancaster, & Hurtado, 2001), and facilitated technological innovation (Reader & Laland, 2002). Our larger-than-average primate brains (Byrne & Whiten, 1988; Dunbar, 1998) and species-specific cultural complexity (Boyd, Richerson, & Henrich, 2011) are adaptations to the demands of group living (Cosmides & Tooby, 1992; Kurzban & Neuberg, 2005). Individual fitness benefited from psychological mechanisms that facilitated coordinated problem solving and increased social cohesion (Dunbar & Shultz, 2007), for example, the capacity to understand the intentions of others, to track social relationships, and to form coalitional alliances all aid in cooperation with ingroup members (Brewer, 2007; Dunbar & Shultz, 2010; Kurzban, Tooby, & Cosmides, 2001; Tomasello, Carpenter, Call, Behne, & Moll, 2005). The evolution of cooperation also selected for tactical deception within social exchanges, in which an individual strategically changes the perception of another for his or her own benefit (McNally, Brown, & Jackson, 2012; McNally & Jackson, 2013). Large-scale sociality was facilitated by the same behavioral predispositions that allowed for the evolution of small-scale sociality (Jordan et al., 2013).

Cooperation with kin, as well as nonkin, is a core feature of human social group living (Mathew, Boyd, van Veelen, 2013; Rekers, Haun, & Tomasello, 2011; Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2014). There are reasons to think that cooperation among kin versus nonkin relationships may operate differently, however. Individuals have adaptations to cooperate with those who share their genes, based on the principles of inclusive fitness, and thus the closer the genetic relatedness, the more cooperation (helping behavior) individuals engage in, all else equal (Hamilton, 1964). Psychological adaptations for tracking exchange relationships, such as reciprocal altruism and mutualism, may account for the evolution of cooperation with nonkin group members (Axelrod & Hamilton, 1981; Trivers, 1971). Individuals track exchange relationships over extended periods of time, thus allowing for selective cooperation with ingroup members.

Living in large groups introduces additional adaptive problems, problems different from those involved in reciprocal dyadic exchange, such as coordination of group members for collective action, minimizing free-ridings, increasing group commitment to joint goals, and preventing the defection of group members to rival groups. Thus, the ability to engage in cooperation is a necessary but not sufficient prerequisite for participation in goal-directed coalitional alliances (Tooby, Cosmides, & Price, 2006). The adaptive problems presented by living in large groups of nonkin in turn required the evolution of psychological mechanisms to solve them (Chudek & Henrich, 2010; Chudek, Zhao, & Henrich, 2013). We propose that rituals solve adaptive problems associated with group living by (a) identifying group members, (b) demonstrating commitment to the group, (c) facilitating cooperation with social coalitions, and (d) increasing social group cohesion.

To illustrate how ritual functions within a social system, we reference the ritual cycle of pig slaughter of the Tsembaga of New Guinea, as described by Rappaport (1967, 1984). In the following section, we use examples of the Tsembaga ritual warfare cycle to demonstrate the social functions of ritual. We will also describe how the same behavior can serve multiple functions within the ritual context.

IDENTIFY GROUP MEMBERS

Through providing practical and psychologically powerful markers of group membership, rituals allow identification of ingroup members. This provides important information about who is more likely to cooperate and less likely to free ride (Cosmides & Tooby, 2013; McElreath, Boyd, & Richerson, 2003). Humans can keep track of approximately 150 of their group members (Dunbar, 1992), although other estimates are somewhat higher (McCarty, Killworth, Bernard, Johnsen, & Shelley, 2000), and the preference to interact with ingroup members may be evolutionarily stable (McElreath et al., 2003). Rituals provide a demonstration of shared beliefs and behaviors. Recognizing that another person shares the same behavior and values as one's self indicates that he or she is likely to be a trustworthy reciprocator. Thus, markers of group membership facilitate cooperative interactions because they provide a marker of one's "behavioral type" (McElreath et al., 2003, p. 127). Rituals often involve special communication systems or "languages," and thus may act in much the same way that accent acts for identifying group members in both children (Kinzler, Dupoux, & Spelke, 2007) and adults (Pietraszewski & Schwartz, 2014a, 2014b). Identifying group members is also crucial for determining whom to imitate and for tracking status hierarchies (Henrich, 2009).

An example of how rituals are used as identity markers comes from the Maring-speaking people to which the Tsembaga belong. As Rappaport (1984) notes, "The rituals surrounding the *rumbim* provide an additional criterion for distinguishing the Tsembaga from adjacent groups" (p. 19). For the Tsembaga, a distinguishing feature of their rituals from neighboring groups is the timing of their planting rituals. "It is on the basis of their coordination of some of these rituals and their joint and exclusive participation in others that we may distinguish the Tsembaga as a single congregation distinct from all others" (p. 19). These rituals identify the members of the group that can be trusted in future interactions. Markers of group membership can also be exploited by those who seek to gain the benefits of group membership without contributing to group-specific goals. Thus rituals that demonstrate commitment to the group act as powerful mechanisms that ward off exploitation against potential free riders.

Demonstrate Commitment to the Group

Actions that might be considered costly, in terms of the ability to perform them and the time it takes to perform them, operate both as reliable signals that convey the signaler's commitment to the group or its beliefs, and as credibility-enhancing displays, which foster the cultural transmission of these commitments to others, including children. Consistent with costly signaling theory (Irons, 2001; Zahavi, 1975), rituals serve as hard-to-fake or honest signals of group commitment. For example, the greater the amount of costly rituals within a group, the longer that group will last (Sosis & Bressler, 2003). Similarly, Monsma (2007) demonstrated that ritual participation and resource donation are positively correlated.

Related to costly signaling accounts of ritual, Henrich (2009) has proposed that costly rituals act as credibility-enhancing displays (CREDs). CREDs provide evidence of an individual's commitment to in-group values. CREDs are important because verbally expressed beliefs and commitments are open to deception. Thus, humans may have evolved cognitive mechanisms that privilege behavioral commitment over verbal commitment. Rituals, as CREDs, provide salient evidence of behavioral commitment to groups. When rituals are costly to perform, in terms of time, energy expenditure, pain, and sacrifice, they act as signals of commitment to group values (Lanman, 2012; Whitehouse, 1996; Xygalatas et al., 2013).

For the Tsembaga, the importance of demonstrating commitment to the group is evident in the ritual taboos that are enforced at the onset and through the duration of warfare. For example, warriors engage in taboos that entail a high personal cost; they are prohibited from drinking any liquids during a battle, are required to consume salted pork, and are not allowed to engage in social or sexual intercourse with women. Similarly, community members also observe a variety of food restrictions (e.g., marsupials may not be trapped and eels may not be eaten). The competing group formally becomes the enemy through observing ritual taboos, such as prohibitions against entering their territory, speaking to a member of the enemy group, eating food grown on their land, or even looking at them. These taboos require group members to demonstrate their commitment to their local group by incurring personal cost by not engaging in typical activities during a period of intergroup conflict.

Continued protection and cooperation between allied groups is also encouraged through the costly ritualized slaughter of pigs during the *kaiko.* The slaughter of the group's pigs sends a signal to ancestors and allies that the group is willing to incur a cost (in terms of pork) for their assistance in the fight.

FACILITATE COOPERATION WITH COALITIONS

Rituals contribute to cooperative behavior with ingroup members (Sosis, 2000, 2005; Sosis & Alcorta, 2003; Sosis & Bressler, 2003) by signaling group commitment. Cooperation must be conditional and involve mutualism for group action to provide a benefit to the individual (Cosmides & Tooby, 2013). Evidence for this comes from research conducted with men living in an Israeli kibbutz where it was found that religious males who engaged in public religious rituals were more likely to cooperate in an economic game than secular males (Ruffle & Sosis, 2003). Adherents of a Brazilian religious tradition called Candomble who reported greater religious commitment were more likely to behave generously in an economic game and were also more likely to be the recipients of cooperation from other group members (Soler, 2012).

Free-riding (reaping the benefits of attaining a group goal without contributing to the outcome) and defection are two potential problems associated with collective action (Cosmides & Tooby, 2013). Because the ecological and social environment is in many ways opaque and uncertain, to determine the best behavior for any given situation, humans also use social learning biases, such as conformity to the most common behavior witnessed within a group. Conformist transmission stabilizes cooperation and punishment in social groups (Chudek & Henrich, 2011; Henrich & Boyd, 2001). Much of the Tsembaga ritual cycle, such as strengthening ties with allied groups through meat sharing, is oriented toward promoting cooperation and strengthening coalitions. Through their ritual participation, allies demonstrate that they share norms of reciprocation with the Tsembaga, and thus can be recruited in future cooperative endeavors. The Tsembaga also have means of detecting potential defectors within the ritual cycle. Before the first day of fighting, the men sacrifice two pigs to the spirits and engage in a divination ritual involving the "smoke woman" who will name the members of the enemy group who may be easily killed in the fight the next day. The members of the enemy group that are named often coincides with the shaman's "fight packages" (bags containing "exuviae"—traces of human skin and hair—of an enemy male or his father). Rappaport (1984) reports that it is often the case that the man whose exuviae is given has provoked some antagonism from his ingroup members. This usually occurs because the man is suspected of being a sorcerer and because the man "has departed sufficiently from certain approved modes of behavior to arouse covert, but not general, animosity" (p. 131). The fighting packages may provide a means for groups to punish members who do not adhere to the norms of the group, are greedy, and are likely to free ride and also functions to deter others in the group that might be tempted to free ride. Finally, by collectively seeking out and punishing free riders, group cohesion may be increased. Group cohesion is an essential aspect of collaborative problem solving that results in the achievement of group goals.

INCREASE GROUP COHESION

Beyond demonstrating commitment to the group and allowing for the identification of ingroup members, rituals function as mechanisms of social group cohesion, which in turn fosters the longevity of social groups. Classic ethnographies and sociological theory posit that rituals promote interpersonal bonding (Durkheim, 1915; Turner, 1969) and shared beliefs (Geertz, 1973). How ritual is connected to belief is another interesting avenue of research that is increasingly being explored using quantitative methods, a full discussion of which lies outside the scope of this chapter. Recent evidence suggests that rituals may provide a mechanism by which the self becomes "fused" with other group members through shared experiences (Atkinson & Whitehouse, 2011; Swann, Gomez, Seyle, Morales, & Huici, 2009; Swann, Jetten, Gomez, Whitehouse, & Bastian, 2012). Individuals who are highly fused with their group(s) can experience a feeling of "oneness" with the group that promotes acting for the group the same as one would act for one's self (Swann et al., 2012). Rituals also increase group cohesion because they involve shared experiences that require personal sacrifice (Atkinson & Whitehouse, 2011; Whitehouse, 1995, 2000, 2004; Whitehouse & Lanman, 2014). Simply engaging in synchronous movement (even synchronous singing) increases cooperation, self-reported feelings of connection to group members, and increased trust of group members when playing economic games (Wiltermuth & Heath, 2009).

Collective activities, with both group members and closely allied groups, feature prominently in Tsembaga ritual. Commitment to group goals is demonstrated through the shared sacrifice of observing the many taboos enacted during wartime. The massed dancing performed at the *kaiko* is a synchronous activity that could also amplify group cohesion. The combination of continued ethnographic and experimental research promises to elucidate the mechanisms through which ritual activity increases group cohesion. Possibly as a result of the group commitment rituals display, these kinds of activities are passed from generation to generation with high fidelity.

CULTURAL TRANSMISSION OF RITUAL

For cultural groups to maintain cohesion over time, there must be mechanisms for high-fidelity transmission of group beliefs, values, and practices (Liénard & Boyer, 2006). We propose that rituals facilitate high-fidelity imitation and resist individual innovation because they are socially stipulated and not interpretable from the perspective of physical causality (Legare & Souza, 2012, 2014). This makes them ideally suited to high-fidelity cultural transmission (Legare & Herrmann, 2013).

The causal opacity associated with many of the ritual elements of the Tsembaga ritual cycle contribute to high-fidelity reproduction of the cycle intergenerationally. For example, even though many of the rituals within the Tsembaga cycle were "elaborate and exotic" (Rappaport, 1984, p. 176), ritual participants could often not offer any clear explanation for the significance of the ritual procedures. Anthropologists examining ritual often remark on ritual participants' inability to articulate why the ritual they are performing is done in the specified manner, only that they must be done in the way they were done before (Bloch, 2005; Boyer, 2001; Sperber, 1975; Whitehouse, 2012). The causal opacity of ritual also invites rumination of meaning based on symbolism, supernatural beings, and metaphor (Whitehouse, 2004, 2013).

How might rituals have evolved? One possibility is that collective ritual is not the outcome of an adaptive capacity but instead is the by-product of evolved cognitive architecture and therefore an indirect consequence of its evolution by natural selection (Boyer, 2001). According to Liénard and Boyer (2006, p. 825), "a collective ritual typically activates the hazard-precaution system. Given this system and its input format, a pattern of interaction that activates them may well become attention demanding and intuitively compelling. In this view, rituals can be considered highly successful cultural 'gadgets' whose recurrence in cultural evolution is a function of (1) how easily they are comprehended by witnesses and (2) how deeply they trigger activation of motivation systems and cognitive processes that are present in humans for other evolutionary reasons." Psychological mechanisms adapted for group living, such as selective social learning biases, which evolved through natural selection, may have been coopted by a process of cultural evolution. The behaviors that emerged from group living were then selected for by an ongoing process of cumulative cultural evolution (Liénard & Boyer, 2006).

Rituals are cultural adaptations to the problems of group living that are built upon reliably developing features of our social group cognition. This raises compelling questions about the process by which the elements of rituals were aggregated and honed so as to address these adaptive problems. Are rituals culturally evolved to have this adaptive fit (like blow guns and kayaks) or are they genetically evolved cognitive mechanisms like cheater-detection mechanisms or pregnancy sickness?

We argue that the organizational complexity of rituals is the result of selective cultural evolution and not from selective genetic evolution. For example, the rituals of various human groups are unlikely to be equally effective at promoting solidarity, cohesion, and cooperation. Instead, rituals likely vary within and between groups in how successfully they solve the adaptive problems of social groups. This variation in efficacy and cultural success provides the raw materials upon which different groups of individuals can pick and chose, presumably favoring those that are more effective at achieving social goals.

Evolved cultural learning biases, such as conformity bias, operating over generations, could adapt the form of ritual to local environmental challenges. For example, divination rituals may allow hunters to effectively randomize their hunting strategies (Moore, 1957) and overcome the gambler's fallacy (Henrich et al., 2001). This could be achieved by merely copying more successful hunters within the group. However, intergroup competition *also* shapes rituals, producing collective rituals that foster solidarity and success in intergroup competition (Henrich, 2009). This process, carried out over many generations, is known as *cultural group selection* (Richerson & Boyd, 2005). The cultural evolution of ritual may operate similarly to how language has evolved. Humans have evolved the cognitive machinery *for* language, but the lexicons of all languages continue to evolve through processes of cultural selection. Indeed, recent detailed quantitative work shows that languages vary substantially in their complexity and communicative efficiency (Deutscher, 2005).

For rituals to provide utility for social group functioning, individuals must be motivated to engage in collective behaviors that promote their inclusion and status within the group. In the next section, we examine the threat of social exclusion as a motivational mechanism underlying ritual cognition.

MOTIVATIONAL MECHANISMS: SOCIAL EXCLUSION AND GROUP AFFILIATION

Collective group rituals often concern addressing, averting, and mitigating danger. Addressing perceived threat is also a common theme in many individual ritualized behaviors (Boyer & Liénard, 2006). As demonstrated by the Tsembaga ritual cycle, ritual is often associated with violence, misfortune, and dangerous activities. Magical rituals are thought to provide a means of coping with the stress of dangerous circumstances and activities. They are also thought to provide a sense of control over the uncontrollable (Malinowski, 1925/1948). Indeed, recent evidence indicates that engaging in group-specific rituals helps ease the stress of dangerous circumstances. For example, Sosis (2007) found that psalm recitation was successful in helping Israeli women cope with the stress of war. Interestingly, the most powerful component associated with the palliative coping benefits of ritual was the sense of power and community associated with psalm recitation in this population (Sosis & Handwerker, 2011). On the other side of the coin, Legare and Souza (2014) have recently provided evidence that the perception of a ritual's efficacy (its ability to bring about the desired outcome) is increased when primed with randomness (lack of control).

Many collective rituals involve prescriptive and rigid behavioral patterns geared toward averting perceived threat. Perceived threats are thought to activate mental security systems, such as the "hazard precaution system" (Boyer & Liénard, 2006), designed to signal an alarm to direct resources toward coping with the threat (Szechtman & Woody, 2004). The activation of mental security systems results in security-related behavior, of which ritual may be a part. In collective rituals, fear of potential danger of not following the ritual rules (i.e., moral threat, social exclusion, or negative outcomes) may activate the hazard-precaution system (Liénard & Boyer, 2006).

In general, implied threats to fitness (e.g., avoid snakes, spiders, large carnivores, dangerous humans, strangers, social exclusion, contamination) have been found to result in stronger adherence to in-group normative ideologies (Navarrete & Fessler, 2005; Navarrete, Kurzban, Fessler, & Kirkpatrick, 2004). Environmental and social cues that were recurrently associated with threats to fitness are likely to result in coalitional thinking and the implicit goal to foster alliances. This is because conspecific aid can be useful in addressing most threats to individual fitness. Perceived threats prime coalitional thinking and due to psychological systems geared toward enabling coordination with social groups, people endorse a stricter adherence to ingroup ideologies (Navarrete & Fessler, 2005). We propose that increased endorsement of ingroup ideology is used as a means of strengthening group bonds and increasing affiliation with group members.

Due to the importance of group membership, selection has favored individuals who engage in affiliative behaviors as a means of promoting inclusion within a group (Chartrand & Bargh, 1999; Lakin & Chartrand, 2003; Lakin, Chartrand, & Arkin, 2008; Pickett, Gardner, & Knowles, 2004). Thus, the threat of social exclusion, or ostracism, may be especially likely to result in increased affiliative efforts (Williams, 2007; Williams & Nida, 2011). Individuals who had mechanisms to anticipate and address the threat of ostracism had an advantage over those who did not possess such mechanisms. Consistent with error-management theory (Haselton & Buss, 2000), an ostracism-detection system of this kind may be geared toward overdetection, because misperceiving the threat of ostracism when it is not present is much less costly than not perceiving it when it is (Kerr & Levine, 2008; McKay & Efferson, 2010; Spoor & Williams, 2007). Simply maintaining group membership is important, yet possibly more important is achieving status within a group, as high-status individuals typically garner more resources and reproductive opportunities (Betzig, 1986; Buss, 2012). Rituals provide evidence of affiliation with social groups; they display investment in social group values and endorsement of social norms and, in some cases, may increase status within a group.

Individuals are thus motivated to participate in and accurately reproduce group specific rituals. This motivation need not be conscious and deliberate. Indeed, much research indicates that individuals engage in affiliative behaviors without conscious awareness of doing so (see Chartrand & Lakin, 2013, for a review). People unintentionally mimic the actions of others; they engage in behavioral matching or automatic mimicry. Automatic mimicry increases positive affect between interaction partners; participants who had been mimicked by a confederate, as compared to those in a control condition, reported liking their partner more and perceived the interaction to have gone more smoothly (Chartrand & Bargh, 1999). Further, when given the conscious or nonconscious goal to affiliate, participants displayed increased automatic mimicry (Lakin & Chartrand, 2003). Individuals also increase automatic mimicry following social exclusion from ingroup members (Lakin et al., 2008).

Automatic mimicry may thus have a social function, most obviously for coordination and communication purposes. For example, it facilitates the coordination of action by allowing vital social affiliation cues to be transmitted between group members (Lakin, Jefferis, Cheng, & Chartrand, 2003), and may serve as social glue. The propensity to engage in behavioral matching promotes affiliation, and vice versa, and results in a virtuous circle of automatic mimicry and prosocial attitudes that contributes to cooperation among group members (Heyes, 2013).

Despite convergent evidence across social scientific disciplines for the function of ritual in social group cognition and behavior and for the motivational mechanisms underlying ritual participation with adults, the process by which rituals are learned and come to influence group attitudes has not been studied from a developmental perspective until very recently. In the following section, we examine new experimental research on the ontogeny of ritual cognition.

THE ONTOGENY OF RITUAL COGNITION

The development of ritualistic behavior has important implications for understanding the ontogeny of cultural learning in childhood (Herrmann et al., 2013; Watson-Jones et al., 2014) as well as for informing our understanding of the evolution of social cognition in humans (Brewer, 2007; Caporael, 1997; Kurzban & Neuberg, 2005; Richerson & Boyd, 2005). To understand the ontogeny of ritual cognition, we must first examine the development of cognitive systems that support social categorization and social group cognition. Social group cognition develops early in human ontogeny and is developmentally privileged (Killen & Rutland, 2011). Young children view social categories as having a stable, unchanging psychological essence (Gelman, 2009; Gelman, Heyman, & Legare, 2007; Hirschfeld, 1996; Rhodes, 2012; Rhodes & Gelman, 2009). Our propensity for social categorization is so strong, in fact, that simply placing individuals into arbitrary groups creates ingroup biases among adults (Billig & Tajfel, 1973; Diehl, 1990; Tajfel, 1970; Tajfel, Billig, Bundy, & Flament, 1971; Tajfel & Turner, 1979, 1985) and children (Abrams & Rutland, 2008; Dunham, Baron, & Banaji, 2008). For example, when children experience novel social groups (i.e., based on T-shirt color) they have expectations for ingroup reciprocity, positive behavioral attributions for the ingroup, and preferences for in- over outgroup members (Dunham, Baron, & Carey, 2011). There is also evidence that children preferentially interact with ingroup members (Kinzler et al., 2007).

To coordinate behavior for cooperative efforts, children must learn and adhere to the norms and conventions of their social groups through a process of imitation (Kalish, 2005) and social learning (Heyes & Frith, 2014). Even young children tacitly accept status assignments, rules, and prescriptions and expect others to do the same (Diesendruck & Markson, 2011). They also readily engage in normative protest when rules are violated (Rakoczy, Warneken, & Tomasello, 2008). By the age of 4, children attribute conventional knowledge selectively to ingroup members (Diesendruck, 2005). Young children placed within groups expect group members to behave in conventional ways (customs, traditions, and etiquette) and can differentiate conventional from moral rules (Killen & Rutland, 2011; Smetana, 2006; Turiel, 1998).

Even infants expect members of social groups to act similarly (Powell & Spelke, 2013) and are more likely to imitate members of an ingroup than an outgroup (Buttelmann, Zmyj, Daum, & Carpenter, 2013). New research on high-fidelity imitation in early childhood indicates that imitation has evolved social functions, such as encoding normative behavior (Kenward, Karlsson, & Persson, 2011; Keupp, Behne, & Rakoczy, 2013), affiliation (Over & Carpenter, 2012), and detecting ostracism (Lakin et al., 2008; Over & Carpenter, 2009; Watson-Jones et al., 2014).

Evolved selective social learning mechanisms are attuned to detect social conventionality and promote high-fidelity imitation, a mechanism of cultural transmission (Legare, Wen, Herrmann, & Whitehouse, 2015). A growing body of research has demonstrated that as highly specialized cultural learners, children are well equipped to engage in high-fidelity imitation, a potential indicator of group affiliation through conformity (Herrmann et al., 2013). For example, there is now substantial evidence that young children readily overimitate or overcopy the behavior of others (Nielsen & Tomaselli, 2010; Over & Carpenter, 2009, 2012). Overimitation is a uniquely human predisposition; even when it is obvious that some actions are causally irrelevant to retrieve a reward from a puzzle box, children still faithfully copy all of the actions of a demonstrator, as compared to chimpanzees, who omit obviously irrelevant actions to retrieve the reward (Horner & Whiten, 2005).

Overimitation may thus be an adaptive human strategy facilitating more rapid social learning of instrumental skills than would be possible if copying required a full representation of the causal structure of an event. As a social learning strategy, overimitation may be so adaptive that it is employed at the expense of efficiency (Flynn & Whiten, 2008; McGuigan, Whiten, Flynn, & Horner, 2007; McGuigan & Whiten, 2009; Whiten, Custance, Gomez, Teixidor, & Bard, 1996; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). The tendency to overimitate is consistent with the "copy-when-uncertain" social learning strategy (Toelch, Bruce, Newson, Richerson, & Reader, 2014). This proposal is akin to that of error management theory (Haselton & Buss, 2000) in which, in this case, the costs of not imitating with high fidelity in an uncertain situation outweigh the benefits of the reduced effort entailed in imitating with low fidelity. Children infer from the purposeful and intentional nature of an action that they are supposed to copy it (Horner & Whiten, 2005). The underlying logic of these arguments is consistent with dual inheritance theory. For example, according to the costly information hypothesis, unless the world is at least somewhat uncertain (or opaque), natural selection would not favor imitation (Richerson & Boyd, 2005).

Overimitation has also been interpreted as overattribution of causal efficacy to redundant elements or automatic causal encoding (Lyons, Young, & Keil, 2007; Lyons, Damrosch, Lin, Macris, & Keil, 2011). This interpretation has been challenged by accounts of imitation that emphasize the social and normative function of imitation (Kenward et al., 2011; Nielsen, 2012; Over & Carpenter, 2012). In fact, despite substantial psychological evidence for the early developing and sophisticated capacity to reason causally (Baillargeon, Li, Gertner, & Wu, 2011; Carey, 2009; Gopnik & Schulz, 2007; Keil & Wilson, 2000; Legare, 2012, 2014; Legare, Gelman, & Wellman, 2010), much of what people need to learn and interpret is not based on understanding physical causality and instead is based on social conventionality.

Young children are thus highly sensitive to social and contextual cues to high-fidelity imitation (Herrmann et al., 2013; Watson-Jones et al., 2014). For example, children are sensitive to cues to consensus and synchrony, potential markers of conventionality (Chudek, Heller, Birch, & Henrich, 2012; Claidière & Whiten, 2012; Corriveau, Fusaro, & Harris, 2009; Corriveau & Harris, 2010; Pasquini, Corriveau, Koenig, & Harris, 2007). Children have also been shown to conform to a group consensus in purely social situations, where no new instrumental knowledge can be gained (Schmidt, Rakoczy, & Tomasello, 2011). For example, they disguise their correct opinions in order to conform to a group consensus (Haun & Tomasello, 2011). Based on these early developing capacities, research by Henrich and colleagues have argued for an early developing "norm psychology" that supports reasoning about the conventionality of behavior (Chudek et al., 2013; Chudek & Henrich, 2010), an essential prerequisite for ritual cognition.

Additionally, children, as cultural learners, are also sensitive to credibility-enhancing displays (Henrich, 2009). For example, a child witnessing, and adhering to, the ritual taboos of the Tsembaga may implicitly use information about social categorization within their ingroup to determine that this is a social convention adhered to in times of turmoil when alliances and group affiliations are salient and important.

We propose that children and adults imitate ritual actions with high fidelity as a means of ingroup affiliation and that threats to group membership or social exclusion amplify motivation to engage in collective rituals. There is evidence that young children are highly sensitive to the threat of ostracism (Over & Carpenter, 2009; Watson-Jones et al., 2014) and that following an experience of social exclusion from their ingroup, children imitated an ingroup ritual with higher fidelity than children excluded by outgroup members or than children included by in- or outgroup members. These studies demonstrate that young children may use "affiliative imitation" as a behavioral strategy to reaffiliate with social group members when faced with the threat of social exclusion.

In sum, early developing social cognitive capacities provide the foundation for the development of ritual cognition. Young children are adept at using social and contextual cues to determine which actions are conventional and attempt to imitate these actions with high fidelity (Herrmann et al., 2013; Watson-Jones et al., 2014). Children are also highly motivated to imitate ritual as a means of affiliation with group members.

CONCLUSION

Despite the fact that ritual has been understudied from a psychological and an evolutionary perspective, convergent developments in cognitive science (Legare & Souza, 2012, 2014; McCauley & Lawson, 2002; Rossano, 2012), social psychology (Norton & Gino, 2014; Vohs, Wang, Gino, & Norton, 2013), and cognitive and evolutionary anthropology (Atran & Henrich, 2010; Boyer & Liénard, 2006; Bulbulia, 2004; Henrich, 2009; Humphrey & Laidlaw, 1994; Ruffle & Sosis, 2007; Shore, 1996; Whitehouse, 2011) have opened up new directions for research on ritual. New experimental research on the function of ritual in human social behavior provides fresh insight into the role of ritual in cultural transmission and the development of social group cognition.

Rituals serve four core functions within social groups that help address the problems of coordinated and cooperative group action associated with the ultrasociality of our species: They (1) provide reliable markers of group membership, (2) demonstrate commitment to the group, (3) facilitate cooperation with social coalitions, and (4) increase social group cohesion. The social stipulation and causal opacity of rituals make them ideally suited to high-fidelity cultural transmission over time. We have also provided evidence that the threat of social exclusion and group affiliation motivates engaging in ritual.

Finally, we have provided a cognitive developmental account of the psychological foundations of ritual behavior. Examining the ontogeny of ritual cognition increases our understanding of the emergence of social group cognition in general and provides unique insight into high-fidelity cultural transmission over time. We propose that the capacity to engage in ritual is a distinctly human predisposition, a psychologically prepared, culturally inherited, species-specific behavior.

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CHAPTER 35

The Origins of Religion

ARA NORENZAYAN

TWO PUZZLES OF HUMAN PSYCHOLOGY AND CULTURAL EVOLUTION

THE WORLD'S OLDEST known religious temple, Göbekli Tepe, is about 11,500 years old, perched on a dry hilltop in southeastern Turkey. It consists of massive, humanlike stone pillars carved with images of animals such as gazelles and scorpions, arranged into a set of rings (Schmidt, 2010). While archeologists are unearthing clues and debating their meaning, there are many unanswered questions: Who built this monumental religious site, how did they do it, and why?

There has been little evidence of domestication of plants or animals. It is plausible that it could have been built and occupied by preagricultural foragers (or hunters and gatherers). Was Göbekli Tepe an early cosmopolitan center, where people periodically came together, worshipped, and performed rituals? While Göbekli Tepe raises more questions than yields answers, it points to two of the deepest puzzles of human psychology and civilization. How did human societies scale up from comparatively small, mobile groups of foragers to increasingly large societies, even though anonymity is the enemy of cooperation? And how did the great polytheistic and monotheistic world religions culturally spread to colonize most minds in the world, even though in the long run, almost all religious movements fail?

THE PUZZLE OF LARGE-SCALE COOPERATION

The first puzzle belongs to psychology and is of large-scale cooperation. For most of its evolutionary history, human beings lived in relatively small bands of foragers. Yet, today, the vast majority of human beings live in vast, cooperative groups of mostly unrelated strangers. Total strangers regularly depend on each other for livelihood, economic exchange, shelter, and mutual defense (Seabright, 2004). This puzzle deepens further when we realize two additional facts: This expansion of cooperation happened primarily since the Holocene era, around 12,000 years ago[1] (when agricultural settlements emerged), and its intensity and scope is found only in humans, despite phylogenetic continuities (Chudek & Henrich, 2011).

In evolutionary biology, a great deal of cooperation can be explained by one of two forms of altruism: one based on kinship or helping among genetic relatives (Hamilton, 1964) and one based on reciprocal altruism among regularly interacting strangers (Axelrod, 1984). But cooperation within expanding groups of strangers is not easily explained by either. As group size increases, both forms of altruism break down. With ever-greater chances of encountering strangers, opportunities for cooperation among kin rapidly decline. Without extra safeguards, such as institutions for punishing freeloaders, and cultural norms that encourage cooperation with strangers, reciprocal altruism also stops paying off. So how did human minds, possessing temperaments and instincts calibrated for life in small, foraging bands, expand group size to unprecedented levels? How did the human cooperative sphere "scale up" so dramatically and so rapidly?[2]

THE PUZZLE OF WORLD RELIGIONS

The second puzzle emerges from cultural evolution and refers to the peculiar cultural distribution of religious beliefs and practices that we see in the world today. Religions have always been multiplying, growing, mutating, and dying at a brisk pace. But religious ideas and practices, although created in abundance, have markedly different sticking power. In fact, while new religious entities are created in the legion, most of them die out, save a potent few that survive and flourish. The outcome of this process is that the vast majority of humanity today adheres to a disproportionately few of these surviving movements that have achieved "world religion" status. If you are a Christian, Muslim, Jew, Hindu, Buddhist practitioner, or nonbelieving descendant of any of these or related traditions, you are the heir to an extraordinarily successful religious movement that once was an obscure cultural experiment.

Almost all religious movements that have ever existed eventually succumbed to myriad internal and external threats that undermine social cohesion, demographic stability, and cultural influence. The triple success of world religions—their demographic growth, geographic expansion, and historical persistence—is therefore a remarkable fact that begs for explanation. In one groundbreaking study that illustrates this point, Sosis (2000) analyzed the stability over a 110-year span of 200 utopian communes, both religious and secular, in 19th-century America. The average life span of the religious communes was a mere 25 years. In 80 years, 9 out of 10 had disbanded. Secular communes fared even worse: They lasted for an average of 6.4 years; 9 out of 10 disappeared in less than 20 years. If most religious communes fail even within as little as a century, how is it that a few religious movements endured and went global, uniting diverse peoples across geography, language, and ethnicity? Here we have a fascinating case study of how cultural evolution—itself a product of interacting

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[1] I use 12,000 years as a convenient starting point when the first human groups in the Middle East began to scale up (see also Diamond, 2005). However, human populations expanded at different times in different regions, and there were fluctuations in the size and social complexity of human groups even in the Pleistocene era.

[2] Some evolutionary arguments do not see this as a puzzle, maintaining that large-scale cooperation is, from an evolutionary point of view, a "big mistake" (Burnham & Johnson, 2005; Dawkins, 2006). The limitations of this argument have been discussed in detail elsewhere (e.g., Richerson & Boyd, 2005).

human brains shaped by evolution—can harness different aspects of evolved psychology to build global communities of strangers.

OUTLINE OF A SOLUTION

In this chapter, I explore the explanatory reach of a potential solution—that the two puzzles are importantly linked. (For a fuller, book-length account, see Norenzayan, 2013; see also Norenzayan et al., in press, and associated commentaries.) In this evolutionary scenario, religious beliefs and behaviors arose as evolutionary by-products of cognitive architecture that arose independently of religion and preceded it. Once that happened, the stage was set for rapid cultural evolution—nongenetic, socially transmitted cumulative changes in beliefs and behaviors (Chudek, Muthukrishna, & Henrich, Chapter 30, this volume; Richerson & Christiansen, 2013) that acted on an interrelated suite of religious ideas and behaviors that coevolved with large-scale cooperation. This argument integrates and extends previous and contemporary "social solidarity" accounts of religious elements (Durkheim, 1915; Haidt, 2012; Sosis & Alcorta, 2003; Wilson, 2002) and places them in a Darwinian framework that is grounded in both genetic and cultural evolution.

To be clear, this idea does not claim that large-scale cooperation cannot happen without religion, and obviously it does not claim that religion is necessary for morality of any scale. World religions, with their belief-ritual complexes, have broadened the moral sphere, but other processes and institutions can have the same effect. Religions are neither necessary for moral behavior, nor are they unique in having this effect (Norenzayan, 2014). Precursors of moral sentiments, such as empathy, shame, and anger, have ancient evolutionary origins (de Waal, 2008) and disapproval of antisocial behavior emerges even in preverbal babies (Hamlin, Wynn, & Bloom, 2007) before they are exposed to or affected by religious practices.

The idea is that any beliefs, behaviors, norms, or institutions that enhanced social cohesion and cooperation while allowing cultural groups to scale up at the expense of their rivals were selected in cultural evolution. Therefore, there are many pathways to large-scale cooperation; some of these pathways draw from religious beliefs and practices, while others draw on institutions, norms, and practices that are unrelated to the supernatural or the sacred. To understand how requires the integration of two important theoretical developments in evolutionary science, described next: (1) insights from the cognitive science of religion and (2) cultural evolution supported by evolved cultural learning strategies. In what follows, I describe this integration, review the evidence from various fields that speaks to the hypotheses derived from this cultural evolutionary-cognitive by-product framework, briefly examine similarities and differences with alternative evolutionary theories, and finally conclude with outstanding questions for future research.

THE CULTURAL EVOLUTION/COGNITIVE BY-PRODUCT FRAMEWORK

Religious beliefs and behaviors are rooted in ordinary cognitive capacities. These capacities generate various supernatural intuitions, which then become targets of cultural evolution. Here I provide a summary of these two insights, and describe the resulting synthesis.

Cognitive Biases That Support Religious Beliefs and Behaviors

One key cognitive capacity implicated in religion is mentalizing (theory of mind), which enables people to detect and infer the existence and content of other minds (Epley & Waytz, 2010; Frith & Frith, 2003). This capacity also facilitates two key intuitions that ground religious belief: that minds can operate separately from bodies, or mind-body dualism (Bloom, 2007; Willard & Norenzayan, 2013), and that all people, things, and events exist for a purpose, or teleology (Banerjee & Bloom, 2013; Kelemen, 2004). By recruiting mentalizing abilities, believers treat gods as disembodied beings who possess humanlike goals, beliefs, and desires (Barrett, 2004; Bering, 2011; Epley, Waytz, & Cacioppo, 2007; Guthrie, 1993). Consistent with the by-product argument that religious thinking recruits ordinary capacities for mentalizing, thinking about or praying to God activates brain regions associated with theory of mind (Schjoedt, Stødkilde-Jørgensen, Geertz, & Roepstorff, 2009), and reduced mentalizing tendencies or abilities, as found in the autistic spectrum, predicts reduced belief in God (Norenzayan, Gervais, & Trzesniewski, 2012).

These and other cognitive biases make religious ideas compelling and plausible to human minds, and generate constrained but diverse sets of intuitions, beliefs, and behaviors that are recurrent all over the world (Atran & Norenzayan, 2004). Once intuitions about supernatural beings and ritual-behavior complexes are in place, they coexist with other ordinary intuitions and beliefs (Legare, Evans, Rosengren, & Harris, 2012). The stage is set for cultural evolution to act on variants of these beliefs and behaviors, such that some proliferate more successfully than others.

Successful Religious Movements Are the Products of Cultural Evolutionary Processes

The question as to why a few religious movements spread at the expense of their cultural rivals can be answered in a cultural evolutionary framework. Here I briefly outline why cultural evolution is key to understanding the cultural dominance of world religions. For a more thorough discussion on cultural evolution and evolved capacities for cultural learning, interested readers can consult Chudek and colleagues (Chapter 30, this volume; see also Richerson & Christiansen, 2013).

As a cultural species, humans extract vital information from others, and therefore their brains are equipped with evolved cultural learning biases that enable a second inheritance system: a cultural evolutionary process that runs in parallel to, and can interact with, genetic evolution (Richerson & Boyd, 2005). These cultural learning biases include content biases that give a transmission advantage to some aspects of mental representations over others, for example, the fact that some ideas are inherently more memorable or attention-arresting than others (Sperber, 1996). In addition, other evolved cultural learning mechanisms bias learners to attend to cues such as whether the opinion or idea is held by the majority (conformist bias), and by people with perceived skill or success (prestige bias). But the fitness benefits of learning from others are offset by learners' vulnerability to being duped or misinformed (the so-called evil teacher problem). In most likelihood, then, human minds are equipped with epistemic vigilance (Sperber et al., 2010) or a suite of preferences that guard against such manipulation. One key solution is an evolved bias in cultural learners to attend to cues that a cultural model is genuinely committed to his or her advertised belief. Cultural learners are therefore more likely to be influenced by cultural models when the latter engage in credibility-enhancing displays, or CREDs (Henrich, 2009). This is, in essence, the idea that actions speak louder than words, and when they do, they bias the cultural transmission process.

Content biases in religious representations have received the most attention so far (e.g., Boyer, 2001), but all three types of cultural learning biases play an important role in the transmission of religious beliefs and practices. For example, CREDs are important in proselytizing religious groups where faith in gods spreads by cultural influence, and where believers are vigilant against religious hypocrisy. There are two additional reasons why cultural evolution plays an important part in explaining the dominance of world religions. Relative to genetic evolution, cultural evolutionary pressures can exert powerful effects in relatively short periods of time (Richerson & Boyd, 2005). Moreover, cultural and historical variability and culturally transmitted group differences (Henrich, Heine, & Norenzayan, 2010) are the central focus of cultural evolution. It can therefore contribute to an account of the massive changes in some human groups that have occurred in the relatively short time scale of 10,000 to 12,000 years.

AN EMERGING SYNTHESIS

Bringing insights from the cognitive science of religion and cultural evolution together, the picture that emerges is a process of coevolution between societal size and complexity on one hand, and a suite of religious elements that enhance social solidarity on the other. Here I focus on devotional practices to increasingly potent Big Gods—powerful, interventionist, and morally concerned supernatural monitors of the expanding group. But clearly, this is only one of several interrelated religious elements that play a role in the expansion of the social scale. The idea is that these Big Gods and supporting practices were early cultural variants of "natural religion" that promoted prosocial behavior—features like cooperation, trust, and self-sacrifice. These features outcompeted rival cultural variants of morally indifferent deities with limited omniscience and powers to intervene in human affairs. As a result, Big Gods and other beliefs in supernatural punishment, supported by extravagant loyalty displays and an amalgam of intensely prosocial rituals and practices, culturally spread with these expanding, cooperative groups, also explaining the prevalence of what we now call world religions (Norenzayan, 2013). These religions thus forged anonymous strangers into imagined moral communities (Graham & Haidt, 2010; Haidt, 2012) tied together with sacred bonds that are overseen by supernatural surveillance.

COMMITMENTS TO BIG GODS CO-EMERGE WITH BIG GROUPS ACROSS CULTURES AND HISTORY

The reasoning outlined above depends on the empirical claim that across cultures and history, Big Gods and other beliefs and behaviors coemerged with big groups by mutually energizing each other. As societies scale up, gods become more powerful and morally involved. If so, then we ought to observe a positive correlation between the prevalence of Big Gods and group size. In this section, I explore anthropological and historical evidence that speaks to this hypothesis.

SMALL AND BIG GODS ACROSS CULTURES: ANTHROPOLOGICAL EVIDENCE

In foraging and other small-scale societies, people must tackle an extensive variety of cooperative challenges, and therefore they are guided by a sophisticated set of local moral norms that apply to a wide range of domains, including food sharing, caring for offspring, kinship relations, marriage, leveling of risk, and mutual defense (Powell, Shennan, & Thomas, 2009). Yet, the ethnographic evidence suggests that the gods play a small part, if any, in the rich and varied cooperative lives of these societies.

In fact, the gods and spirits of the smallest foraging groups, such as the Hadza of Eastern Africa (Marlowe, 2010) and the San of the Kalahari (Marshall, 1962), have little omniscience and moral concern. In other small-scale societies, the picture is similar; the gods and morality are largely disconnected (e.g., Purzycki, 2011). While some gods are pleased by rituals and sacrifices offered to them, they care little about how people treat each other.

These ethnographic observations begin to make sense if we consider the social dynamics of life in small-scale societies. Although people in these societies do intermingle with strangers under limited conditions, face-to-face interaction is the norm, and in these transparent societies, it is hard to escape the social spotlight. Granted, there is considerable diversity in the cultural traits of modern-day and ancestral foragers that limit broad generalizations (Kelly, 1995). Nevertheless, if foraging groups tell us anything, it is that the connection between religion and morality has in fact emerged culturally over human history, probably rather recently.

Quantitative analysis of the anthropological record is consistent with this idea. In moving from the smallest-scale human societies to the largest and most complex, interventionist supernatural watchers go from relatively rare to increasingly common, and morality and religion move from largely disconnected to increasingly intertwined (Johnson, 2005; Roes & Raymond, 2003; Sanderson & Roberts, 2008). While there are important issues in these cross-cultural patterns that are open to debate (e.g., see Atkinson, Latham, & Watts, in press; Norenzayan, 2014), these results hold controlling for several variables that covary with group size and religion, such as economic inequality, population densities, and exposure to missionary activity. Interventionist Big Gods are also more prevalent in places with water scarcity (Snarey, 1996), as well as in agricultural societies and those that are engaged in animal husbandry (Peoples & Marlowe, 2012). One interpretation of these patterns is that these gods and related practices are more likely to spread in all these conditions, where group survival is highly dependent on the group's ability to curb free-riding. Other studies have found a complementary cultural shift in ritual forms: As societies get larger and more complex, rituals become routinized affairs at the service of transmitting and reinforcing shared doctrines (Atkinson & Whitehouse, 2011). Notions of supernatural punishment, damnation and salvation, heaven and hell, and karma are common features of modern religions but are relatively infrequent in small-scale cultures.

GODS GET BIGGER AS GROUPS EXPAND: A VERY BRIEF OVERVIEW OF THE HISTORICAL RECORD

These anthropological findings converge with archaeological and historical evidence suggesting that both Big Gods and routinized rituals coevolved with large, complex human societies, along with increasing reliance on agricultural modes of production (e.g., Marcus & Flannery, 2004; Whitehouse & Hodder, 2010). Although interpreting the written historical record is no simple matter and is open to many active debates, once it begins, links between large-scale cooperation, ritual elaboration, Big Gods, and morality become more apparent. It has been argued that ideas of morally concerned gods did not emerge until the so-called Axial Age (800–300 BCA) (e.g., Baumard & Boyer, 2014). However, there is evidence from many cultures long before this period, such as Babylon and Egypt (Assmann, 2001; Bellah, 2011), that as societies grew larger and more complex, they also developed divinely inspired guidelines for public morality. A case in point is Hammurabi's code (1772 BCE) in Babylon that was inspired by fear of Marduk, patron god of Babylon, and the powers of Shamash, god of justice (Bellah, 2011). A great deal of the historical work related to this topic focuses on the Abrahamic faiths. For instance, Wright (2009) provides a summary of textual evidence that reveals the gradual evolution of the Abrahamic god from a rather limited, whimsical, tribal war god—a subordinate in the Canaanite pantheon—to the unitary, supreme, moralizing deity of two of the world's largest religious communities.

The highly organized Greek city-states and imperial Rome are sometimes portrayed as possessing only amoral and fickle deities (e.g., Baumard & Boyer, 2014). However, new scholarship has increasingly challenged this view. The gods of the Greek city-states were believed by the populace to be humanlike, but this should not be confused with indifference to human morality. Not only did they demand costly sacrifices and elicit elaborate rituals, they also played an active role in enforcing oaths and supporting public morality (Mikalson, 2010, pp. 150–168). This pattern is seen in Greek city-states and even more starkly in the case of the deities of imperial Rome (Rives, 2007, pp. 105–131). For instance, cults dedicated to Mercury and Hercules in the second and first centuries BCE in Delos—an important maritime trade center—leaned on supernatural surveillance and divine punishment in order to overcome cooperation dilemmas in long-distance trade relations (Rauh, 1993).

China also has sometimes been portrayed as lacking moralizing gods, or even religion at all (e.g., Ames & Rosemont, 2009). New work suggests otherwise (Clark & Winslett, 2011; Slingerland, 2013). While there are arguments that Chinese civilization developed secular alternatives to religious morality much earlier than did Middle Eastern and European civilizations (e.g., Sarkissian, in press), in the earliest Chinese societies for which written records exist, the worshiped pantheon includes both literal ancestors of the royal line as well as a variety of nature gods and cultural heroes, all under the dominion of a supreme deity, the "Lord on High" (*shangdi*). The ability of the royal family to rule was a direct result of their possessing the "Mandate" of Heaven, the possession of which was—at least by 1000 BCE or so—seen as linked to moral behavior and proper observance of costly sacrificial and other ritual duties. The written record reveals, over time, an increasingly clear connection in early China between morality and religious commitments. Failure to adhere to these norms—either in outward behavior or one's inner life—was to invite supernatural punishment (Eno, 2009).

These ethnographic, archeological, and historical patterns offer suggestive evidence that prosocial religions with Big Gods coemerged with large, complex societies. It is important to note that this process is not an all-or-nothing phenomenon. Rather, both the ethnographic and historical record reveal that it is a gradual process with many intermediate cases. For example, in chiefdom societies, such as in Fiji, groups are larger and more hierarchical than in foraging societies, and the gods appear to have more powers and moral concern than the gods of foragers, but less so than in much larger state societies (McNamara, Norenzayan, & Henrich, in press). Moreover, these associations cannot be taken to suggest causation, of course—at least some of these anthropological and historical data would also be consistent with the alternative hypothesis that bigger and more prosocial societies simply imagined bigger and more prosocial gods in their own image. The theoretical framework I explore here is not inconsistent with that possibility either, as the causal pathways can go in either direction (hence the assertion that the two coemerged), and their importance may vary in different places and historical periods (Atkinson et al., in press; Watts et al., 2015). However, this framework does depend on the claim that one important causal arrow goes from conceptions of increasingly moralizing and interventionist gods and related practices to cooperation. Next, I examine this causal hypothesis and explore the psychological mechanisms behind this process.

RELIGIOUS SOLUTIONS TO THE PROBLEM OF LARGE-SCALE COOPERATION

A key problem for large-scale cooperation is the threat of anonymity; when groups expand in size, anonymity erodes the bonds of cooperation. Consistent with this, studies show that even illusory anonymity, such as the act of wearing dark glasses or sitting in a dimly lit room, encourages selfishness and cheating (Zhong, Bohns, & Gino, 2010). Social surveillance, such as being in front of cameras or audiences, has the opposite effect. Even subtle exposure to drawings resembling human eyes encourages good behavior towards strangers (Bateson, Nettle, & Roberts, 2006; Haley & Fessler, 2005).[3] As the saying goes, "Watched people are nice people." It makes sense, therefore, that the world over, many cultures that have successfully tackled the problem of large-scale cooperation have stumbled upon the idea of "eyes in the sky"—watchful deities who see far and particularly care about human morality (Norenzayan, 2013). People play nice when they think a morally concerned, punishing god is watching them—even when nobody is.

Pressure From Above

Here I highlight several lines of converging experimental evidence that give support to this hypothesis (for further details, see Norenzayan, Henrich, & Slingerland, 2013). In cooperation research, economic games have been used as a prism through which prosocial behavior can be measured. The dictator game, for example, involves two anonymous players engaged in a one-off interaction. Player 1 is allotted a sum of real money and must decide how to divide this sum between herself and Player 2. Player 2 then receives the allocation from Player 1, and the game ends. Henrich, Ensminger, et al. (2010) found that across 15 diverse societies of foragers, pastoralists, and horticulturalists from all over the world, and controlling for a wide range of demographic variables and other factors that predict cooperative tendencies, adherence to

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[3] This doesn't imply that there can be no prosocial behavior without social monitoring. Some residue of prosocial behavior arguably remains even in complete anonymity (see for example, Gintis, Bowles, Boyd, & Fehr, 2003). This important point does not, however, change the observation that prosocial behavior markedly increases under social surveillance.

the Abrahamic "Big God" predicted larger offers compared to adherence to local deities who are not as omniscient and morally concerned.

The study by Henrich and colleagues is an important piece of the puzzle, because it demonstrates that participation in religions with Big Gods (relative to religions having local gods with limited scope) encourages actual prosocial behavior towards strangers. However, it does not conclusively demonstrate causality. Recent religious priming experiments address this issue. In one study conducted in Canada, we planted reminders of God under the pretext of playing a word game and without arousing suspicion. Other participants played the same word game without religious content. Finally, a third group played the word game with words reflecting secular sources of monitoring. Then all participants played the dictator game (Shariff & Norenzayan, 2007). Self-reported belief in God was not associated with generosity. However, reminders of God had a reliable effect on generosity. In the unexposed group, the typical response was selfish: Most players pocketed the entire amount. In the God group, the typical response shifted to fairness. Importantly, the secular prime had a similar effect as the religious prime, suggesting that secular mechanisms can also encourage nice behavior towards strangers.

A recent meta-analysis of religious priming, pooling the results of 25 experiments, shows that religious priming effects on prosocial behavior are reliable and remain robust even after correcting for publication bias in psychology (Shariff, Willard, Andersen, & Norenzayan, 2015). These religious priming effects found in the laboratory also can be seen in the real world. One example of this is the "Sunday Effect." One study looked at responsiveness to an online charity drive over a period of several weeks. Christians and nonbelievers were equally likely to give to charity except on Sundays, when Christians were 3 times more likely to give (Malhotra, 2008).

Bringing these experimental findings together, several important conclusions can be reached about the mechanisms behind religious priming. First, belief in supernatural punishment is more strongly associated with reductions in moral transgressions, whereas belief in supernatural benevolence, if anything, has the opposite effect (Shariff & Norenzayan, 2011; Shariff & Rhemtulla, 2012). Second, there is evidence that believers offload punishing duties to God, and therefore belief in a punishing God leads to less punishing behavior towards free-riders (Laurin, Shariff, Henrich, & Kay, 2012). Third, reaction time analyses suggest that believers intuit that God has knowledge about norm-violating behaviors more than they believe God does about normative behaviors (Purzycki et al., 2012). Fourth, religious primes on average do not have reliable effects on nonbelievers (Shariff et al., 2015). Finally, the same religious primes that increase generosity towards strangers also increases believers' perceptions of being under social surveillance (Gervais & Norenzayan, 2012a).

These and other findings suggest that salient beliefs in punitive supernatural monitors increase prosociality towards strangers. These findings contradict the idea that already prosocial individuals spontaneously imagine conceptions of prosocial deities, or that religious priming brings to mind thoughts of benevolence, which in turn encourage benevolent behaviors such as generosity (Norenzayan et al., 2013). Neither is the evidence consistent with the idea that religious priming effects are the result of low-level associations or cultural knowledge that are generalized to everyone regardless of religious socialization.

ADDITIONAL MECHANISMS THAT GALVANIZE RELIGIOUS COOPERATION: EXTREME RITUALS, SYNCHRONY, SELF-CONTROL, AND FICTIVE KINSHIP, AMONG OTHERS

In the logic of cultural evolution, multiple solutions to large-scale cooperation are cobbled together in historical time. Therefore, it is likely that there are myriad other mechanisms found in world religions (and their secular successors and competitors) that converge with supernatural monitoring and have cooperative effects. These mechanisms are not unique to religions, of course—the idea is that culturally successful religions draw on these mechanisms to promote social solidarity. These include participation in extreme rituals (Xygalatas et al., 2013); synchronous movement and music, that is, collectively moving together in time (McNeill, 1995; Wiltermuth & Heath, 2009); practices that cultivate self-control, which may in turn help people suppress selfishness (McCullough & Willoughby, 2009); fictive kinship (Nesse, 1999); and cultural practices that promote high fertility rates (Blume, 2009; Kaufmann, 2010). There are likely many more that are open to investigation. Given the limited space, here I highlight extreme rituals.

World religions, by virtue of encouraging prosociality in the group, commonly create opportunities for participation in extreme rituals that build social solidarity. Xygalatas et al. (2013) investigated the prosocial effects of participation in, and witnessing of, the Kavadi, an extreme devotional ritual among Hindus in Mauritius for Murugan, the Tamil war god. This ritual is practiced in the context of the Thaipusam festival, and can range from the mild, such as shaving one's head and carrying a light load, to the extreme, such as days of fasting, piercing the flesh with skewers, and walking on metal nails. The greater the pain experienced, the more participants gave. Moreover, the act of witnessing this intense, pain-inducing set of rituals increased anonymous donations to the temple as much as participating did. This suggests that extreme ritual worship like the Kavadi is not only a commitment device for the participants, it is also a credible display that is culturally contagious (that is, a CRED).

RELIGIOUS COOPERATION IS SHAPED BY, AND CONTRIBUTES TO, INTERGROUP CONFLICT AND DISTRUST

For all its virtues in binding strangers together, religious cooperation is likely born of competition and conflict between groups. It follows that religious cooperation in turn fuels the very conflicts—real or imagined—that are seen to threaten it. This dynamic helps us understand and resolve the seeming paradox that religions with Big Gods are both the handmaiden of cooperation within the group, and of conflict between groups (Atran & Ginges, 2012).

INTERGROUP COMPETITION INTENSIFIES RELIGIOUS COOPERATION

Intergroup conflict, and particularly warfare, is a key driver of societal complexity (Turchin, Currie, Turner, & Gavrilets, 2013). As competition between groups intensify, and when other factors such as war technology and population size are similar, groups that happen to have members who subordinate self-interest for group interests—that is, groups that possess social solidarity—will tend to win out. When the whole group wins out, the individuals in the group win out as well, which explains how self-sacrificial strategies that led to the group's success spread in human populations (Atran & Henrich, 2010). Moreover, these are the conditions that foster the evolution of "parochial altruism," or a suite of tendencies (whether genetic or cultural, or both, is open to debate) that combine preferential self-sacrifice for the group with hostility towards rival groups when the latter are seen to threaten one's group. There are lively debates about how important parochial altruism has been in human evolution (e.g., Bowles, 2008). But to the extent that it has been, religious cooperation might be a paradigm example of it.

For example, in one recent global study spanning 97 sites, it was found that threatened minority groups that have high levels of religious participation were more likely to direct aggression towards majority groups than threatened minority groups with low levels of religious participation, suggesting that the perception of being under threat turns the solidarity-building potential of religion toxic and adds fuel to intergroup conflict (Neuberg et al., 2014; see also Ginges, Hansen, & Norenzayan, 2009). Not surprisingly, then, as religious cooperation went global, so did the potential for religious conflict. Religious communities "cooperate in order to compete," and this imperative can be seen in quantitative analysis of the ethnographic and the cross-cultural record. What causes what remains open to debate, but we do know that the prevalence of intergroup conflict and warfare, resource-rich environments, large group size, and religions with Big Gods are interrelated (e.g., Gelfand, Raver, Nishii, Leslie, & Lun, 2011; Roes & Raymond, 2003).

IN ATHEISTS WE DISTRUST

Supernatural surveillance by Big Gods helped religions expand while sustaining social solidarity within the group. Concern with supernatural surveillance also explains one of the most persistent but hidden prejudices tied to religion: intolerance of atheists.[4] Surveys consistently find that in the United States (Edgell, Gerteis, & Hartmann, 2006), as well as in other societies with religious majorities composing most of the world (see Gervais & Norenzayan, 2013), atheists have one of the lowest social approval ratings of any social group. Even enlightenment ideals of religious tolerance did not spare atheists. "Those are not at all to be tolerated who deny the Being of a God," philosopher John Locke wrote in *Letter Concerning Toleration*. "Promises, Covenants, and Oaths, which are the Bonds of Humane Society, can have no hold upon an Atheist."

Intolerance of atheists is a puzzle. In societies with religious majorities, atheists are not a visible, powerful, or even a coherent social group. There is no such thing as atheist music, cuisine, or attire. Why wouldn't believers simply ignore atheists? An evolutionary approach to prejudice, combined with the psychology of supernatural monitoring, helps demystify this prejudice. From an evolutionary psychology perspective, it makes little sense to treat prejudice as a one-dimensional construct ("like" vs. "dislike" of different groups). To understand prejudice towards a specific group, it helps to know what specific threat a group is perceived to pose, which in turn would help identify the particular psychological response to the particular imagined or real threat, such as the threat of violence triggering fear, and the threat of contamination triggering disgust (Kurzban & Leary, 2001; Schaller & Neuberg, 2008). Research shows

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[4] There is the related but distinct perceived threat to religious groups coming from within: "religious hypocrites," or individuals who profess religious faith but in fact do not really believe. For evolutionary explanations, see Henrich, 2009; Norenzayan, 2013, Chapter 6; Schloss, 2008.

that intolerance towards atheists is rooted in another perceived threat—that of free-riding, triggering moral distrust (Gervais, Shariff, & Norenzayan, 2011).

This analysis further predicts when distrust of atheists among believers waxes and wanes. If concerns about monitoring are fueling this distrust, and if exposure to secular sources of monitoring can replace religious sources, then secular monitoring should dilute believers' distrust of atheists. Both cross-cultural (Norenzayan & Gervais, in press) and experimental findings (Gervais & Norenzayan, 2012b) support this prediction. The simple act of reminding believers in Canada and the United States (countries that have strong rule of law) of police effectiveness softens distrust of atheists, but has no effect on prejudice towards other groups (Gervais & Norenzayan, 2012b). This also partly explains why, in places such as northern Europe, where people can depend on the rule of law and have access to wide social safety nets that buffer against life's adversities, believers no longer see religion as necessary for moral conduct (Zuckerman, 2008).

From Big Gods to No Gods

These same conditions have also initiated a key social transition in some parts of the world, from religious to secular means of large-scale cooperation (Norris & Inglehart, 2004). The recent spread of secular institutions and traditions since the industrial revolution—courts, policing authorities, and contract-enforcing cultural mechanisms—has created conditions for large-scale cooperation without God. These institutions and mechanisms also offer an alternative source of psychological control that relieves fears of randomness and chaos (Kay, Gaucher, Napier, Callan, & Laurin 2008). Studies of cooperative behavior find that believers put their best foot forward when they think God is monitoring their actions (Shariff et al., 2015). However, these same studies show that awareness of human institutions that monitor anonymous interactions and ensure the rule of law also encourage cooperation and trust (Shariff & Norenzayan, 2007), in addition to rupturing religion's link with perceived moral conduct (Gervais & Norenzayan, 2012b).

If nonbelievers in the world were grouped together, their numbers would be in the hundreds of millions, rivaling the size of major world religions (Zuckerman, 2007). This process of secularization can be understood by combining the same insights that help us explain the prosocial religions with Big Gods. Since religious belief is a joint product of cognitive biases, core motivations, and cultural learning strategies, these psychological pathways, if altered, jointly or in isolation, lead to disbelief (Norenzayan & Gervais, 2013). These multiple interacting pathways occasionally converge and reinforce each other, and when they do, secular societies, such as the ones found in northern Europe, achieve a cultural equilibrium. These societies with atheist majorities, some of the most cooperative, peaceful, and prosperous in the world, have climbed religion's ladder, and then kicked it away.

CONCLUSIONS AND IMPLICATIONS

This framework offers one approach at a theoretical synthesis in the evolutionary study of religion. It also offers a possible answer as to why the term religion is a slippery concept, eluding definition. Finally, I conclude with open questions and future directions.

TOWARD A THEORETICAL SYNTHESIS IN THE EVOLUTIONARY STUDIES OF RELIGION

The theoretical framework presented here incorporates key elements of the two most influential evolutionary approaches to religion to date—the *by-product* and *adaptationist* approaches. Both approaches have made distinct and important contributions to the evolutionary study of religion, and continue to generate empirical research. Yet, these contributions have often remained theoretically disconnected, with opportunities for synthesis open for exploration (for discussions that address this issue, see Bulbulia et al., 2013; Purzycki, Haque, & Sosis, 2014; Schloss & Murray, 2011; Sosis, 2009).

The present framework aims to be one such synthesis (there could be others). It builds directly on the insights gleaned from the cognitive by-product perspective. It then grounds these insights within a framework that considers both genetic and cultural inheritance, and explains both the recurrent features of religions as well as their cultural and historical variability. In doing so, it also tackles additional phenomena that deserve more attention than received.

One such phenomenon is *faith or commitment* to particular gods that are a key aspect of life in cooperative religious communities. This is the "Zeus Problem" (Gervais & Henrich, 2010), which asks how the same supernatural agent draws passionate commitment in one historical period but is treated as fictional in another, even when the content of the idea remains similar. Put another way, believers do not commit to any and all cognitively plausible supernatural agents. They commit to a subset of them that are backed up by credible displays, endorsed by prestigious leaders, and supported by most people in the local community. If these cultural learning cues are altered, significant shifts occur in the particular deities people are committed to.

Another key phenomenon that cognitive by-product approaches confront is the growing body of empirical evidence showing that some elements of religion spread by having cooperative effects. Baumard and Boyer (2013) attempt to explain world religions as cultural reflections of evolved moral intuitions, such as proportionality and fairness, and argue against the idea that some religions spread by having prosocial effects. However, this "by-product only" account is incompatible with the experimental evidence reviewed here that shows such prosocial effects, and the cross-cultural and historical evidence that suggests powerful cultural selection for such religious groups at the expense of rival ones. However, as the framework developed here illustrates, the important insights gleaned from the cognitive by-product perspective can be retained, while also explaining why some, but not most, cultural variants that arise as cognitive by-products can have downstream cooperative effects (see Baumard & Boyer, 2014, and Norenzayan, 2014, for a debate on these issues).

The current framework also speaks to a set of important phenomena that are addressed by two distinct adaptationist theories of religion: costly signaling approaches and the supernatural punishment hypothesis. Costly signaling approaches argue that extravagant religious displays are the product of a naturally selected genetic adaptation for life in cooperative groups that allows individuals to reliably signal their degree of cooperation or their group commitment to solve the free-rider problem (Bulbulia, 2004, 2008; Sosis & Alcorta, 2003). The current framework recognizes and integrates insights from this approach in two ways. First, it accounts for both the cultural contagion generated by these extravagant displays and what they communicate to others about the actor's commitment. In this sense, CREDs and signals are compatible strategies and can be mutually reinforcing. Second, by embedding signaling approaches within a cultural evolutionary framework (Henrich, 2009), we can explain why people might acquire religious beliefs with varying degrees of commitment.

Another adaptationist account that has generated interest and has made important contributions to the evolutionary study of religion is the supernatural punishment hypothesis (SPH; e.g., Bering, 2011; Johnson, 2009). The SPH is an error-management account (Johnson, Blumstein, Fowler, & Haselton, 2013) that argues that fear of supernatural punishment is a naturally selected genetic adaptation targeting moral self-constraint. By fearing supernatural punishment, people refrain from social defection and avoid the genetic fitness costs of being ostracized.

There are many similarities between the SPH and the cultural evolutionary-cognitive by-product framework, and the two draw from some of the same body of evidence. The two approaches make a range of empirical predictions that are similar, and converge on the hypothesis that supernatural threats (the stick) are stronger and more impactful than the supernatural rewards (the carrot). However, there are also important theoretical differences that make somewhat different empirical claims, inviting new opportunities to further test and refine hypotheses about the evolution of religion. Whereas in the cultural evolutionary account, supernatural punishment beliefs were culturally selected by having effects on individuals and cultural groups, the SPH argues that fear of punishing gods is an evolved mindguard that curbs social defection (Johnson, 2009; Johnson & Bering, 2006; Schloss & Murray, 2011). I presented evidence that, consistent with the cultural evolutionary scenario outlined here, in small-scale societies, and especially among foragers, the gods have limited omniscience and moral concern, and they become more moralizing and interventionist (not less) as societies become more anonymous (where the costs of defection are arguably smaller than in small-scale societies). These hypothesized observations are currently being investigated in greater detail. (For further discussion and debate, see Norenzayan, 2013; Norenzayan, 2014; Schloss & Murray, 2011; and associated commentaries, particularly Johnson, 2014.)

THE CULTURAL EVOLUTIONARY-COGNITIVE BY-PRODUCT FRAMEWORK CAN EXPLAIN THE SLIPPERINESS OF THE CONSTRUCT "RELIGION"

The reader might have noticed that in this chapter, I avoided the issue of defining the construct "religion." This was a deliberate move, and now that the theoretical framework has been fleshed out, we are in a position to pay this issue its due. Scholars who study religion do not agree on a definition, or even if the term constitutes a coherent category of beliefs or behaviors (Clarke & Byrne, 1993; Stausberg, 2010). In the evolutionary study of religion, there is less concern about definitions. Scientists pick out certain aspects of the construct and operationalize it, but whether the construct lends itself to clear semantic boundaries is actively debated (Bulbulia et al., 2013). In the cultural evolutionary-cognitive by-product framework outlined here, this is to be expected; the religious bundle is a predictable but statistical pattern, rather than a concept with necessary or sufficient features. There is therefore no expectation of a single overarching definition of religion or clear semantic boundaries across cultural and historical contexts. The suite of traits that gets labeled "religion," while containing recurrent elements, culturally mutates, taking different shapes in different groups and at different historical times (Bulbulia et al., 2013; Norenzayan, 2013; for a similar but distinct account, see Taves, 2009).

OPEN QUESTIONS AND FUTURE DIRECTIONS

Despite significant advances in the evolutionary study of religion, there are many unknowns and open questions. Where and how did the spread of world religions coincide with the unleashing of large-scale cooperation? How did these belief-ritual complexes take shape and diffuse across continents? There is little systematic exploration of how believers around the world (and throughout history) mentally represent their deities (see, for example, Purzycki, 2013), and how these mental representations are implicated in human psychology. Are supernatural beliefs in Buddhism and Hinduism, notions such as karma and fate (Obeyesekere, 2002), acting as deterrent mechanisms similar to some core beliefs found in the Abrahamic faiths, notions such as hell and divine wrath? Which forms of rituals are felt to be efficacious, and why (Legare & Souza, 2012)? There are also many open psychological questions regarding religious disbelief. How do children come to adopt belief in supernatural agents, and how is it that they come to maintain faith in some but not others? Are there implicit theistic intuitions, such as dualism, reincarnation, and fate, even among self-declared atheists (e.g., Bering, 2011)? On a theoretical level, the evolutionary study of religion is in the midst of a vibrant period with fecundity of hypotheses and perspectives that are breaking disciplinary boundaries, generating new findings, and consolidating seemingly disparate facts and theoretical perspectives in an increasingly unifying framework. While research is ongoing and there are many debates, we are beginning to see the forest for the trees, as evolutionary science tackles religion—one of the most far-reaching and enduring aspects of human minds and cultures.

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CHAPTER 36

The False Allure of Group Selection

STEVEN PINKER

Human beings live in groups, are affected by the fortunes of their groups, and sometimes make sacrifices that benefit their groups. Does this mean that the human brain has been shaped by natural selection to promote the welfare of the group in competition with other groups, even when it damages the welfare of the person and his or her kin? If so, does the theory of natural selection have to be revamped to designate "groups" as units of selection, analogous to the role played in the theory by genes?

Several scientists whom I greatly respect have said so in prominent places. And they have gone on to use the theory of group selection to make eye-opening claims about the human condition.[1] They have claimed that human morality, particularly our willingness to engage in acts of altruism, can be explained as an adaptation to group-against-group competition. As E. O. Wilson explains, "selfish individuals beat altruistic individuals, while groups of altruists beat groups of selfish individuals" (Wilson, 2012, p. 243). They have proposed that group selection can explain the mystery of religion, because a shared belief in supernatural beings can foster group cohesion. They suggest that evolution has equipped humans to solve tragedies of the commons (also known as collective action dilemmas and public goods games), in which actions that benefit the individual may harm the community; familiar examples include overfishing, highway congestion, tax evasion, and carbon emissions. And they have drawn normative moral and political conclusions from these scientific beliefs, such as that we should recognize the wisdom behind conservative values like religiosity, patriotism, and puritanism, and that we should valorize a communitarian loyalty and sacrifice for the good of the group over an every-man-for-himself individualism.

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[1] Examples include Bowles and Gintis (2011); Haidt (2012); Henrich (2004); Richerson, Boyd, and Henrich (2003); Traulsen and Nowak (2006); D. S. Wilson and Wilson (2008); and E. O. Wilson (2012).

I am often asked whether I agree with the new group selectionists, and the questioners are always surprised when I say I do not. After all, group selection sounds like a reasonable extension of evolutionary theory and a plausible explanation of the social nature of humans. Also, the group selectionists tend to declare victory, and write as if their theory has already superseded a narrow, reductionist dogma that selection acts only at the level of genes. In this essay, I explain why I think that this reasonableness is an illusion. The more carefully you think about group selection, the less sense it makes, and the more poorly it fits the facts of human psychology and history.

Why does this matter? I'll try to show that it has everything to do with our best scientific understanding of the evolution of life and the evolution of human nature. And though I won't take up the various moral and political colorings of the debate here (I have discussed them elsewhere), it ultimately matters for understanding how best to deal with the collective action problems facing our species.

The first big problem with group selection is that the term itself sows so much confusion. People invoke it to refer to many distinct phenomena, so casual users may literally not know what they are talking about. I have seen "group selection" used as a loose synonym for the evolution of organisms that live in groups, and for any competition among groups, such as human warfare. Sometimes the term is needlessly used to refer to an individual trait that happens to be shared by the members of a group; as the evolutionary biologist George Williams noted, "a fleet herd of deer" is really just a herd of fleet deer. And sometimes the term is used as a way of redescribing the conventional gene-level theory of natural selection in different words: Subsets of genetically related or reciprocally cooperating individuals are dubbed "groups," and changes in the frequencies of their genes over time is dubbed "group selection."[2] To use the term in these senses is positively confusing, and writers would be better off referring to whichever phenomenon they have in mind.

In this chapter I concentrate on the sense of "group selection" as a version of natural selection that acts on groups in the same way that it acts on individual organisms, namely, to maximize their inclusive fitness (alternatively, that acts on groups in the same way it acts on genes, namely, to increase the number of copies that appear in the next generation; I treat these formulations as equivalent). Modern advocates of group selection don't deny that selection acts on individual organisms; they only wish to add that it acts on higher-level aggregates, particularly groups of organisms, as well. For this reason, the theory is often called "multilevel selection" rather than "group selection." This all sounds admirably ecumenical and nonreductionist, but my arguments also apply to multilevel selection. I don't think it makes sense to conceive of groups of organisms (in particular, human societies) as sitting at the top of a fractal hierarchy with genes at the bottom, with natural selection applying to each level in parallel ways.

First, I examine the idea that group selection is a viable explanation of the traits of human groups such as tribes, religions, cultures, and nations. Then I turn to group selection as an explanation of the traits of individual humans, that is, the intuitions and emotions that make it possible for people to learn their culture and coexist in societies. (No one denies that such faculties exist.) Finally, I examine the empirical phenomena that have been claimed to show that group selection is necessary to explain human altruism.

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[2] See West, Griffin, and Gardner (2007, 2008) for extensive discussion.

GROUP SELECTION AS AN EXPLANATION OF THE TRAITS OF GROUPS

Natural selection is a special explanatory concept in the sciences, worthy, in my view, of Daniel Dennett's designation as "the single best idea that anyone ever had." That's because it explains one of the greatest mysteries in science, the illusion of design in the natural world. The core of natural selection is that when replicators arise and make copies of themselves, (a) their numbers will tend, under ideal conditions, to increase exponentially; (b) they will necessarily compete for finite resources; (c) some will undergo random copying errors ("random" in the sense that they do not anticipate their effects in the current environment); and (d) whichever copying errors happen to increase the rate of replication will accumulate in a lineage and predominate in the population. After many generations of replication, the replicators will show the appearance of design for effective replication, while in reality they have just accumulated the copying errors that had successful replication as their effect.

What's satisfying about the theory is that it is so mechanistic. The copying errors (mutations) are random (more accurately, blind to their effects). The outcome of interest is the number of copies in a finite population. The surprising outcome is a product of the cumulative effects of many generations of replication. If the copying errors were not random (that is, if Lamarck had been correct that changes in an organism arise in response to a felt need, or if creationists were right that a superior intelligence directed mutations to be beneficial to the organism), then natural selection would be otiose—the design could come from the mutation stage. If the outcome of interest were not the number of copies in a finite population, but some human-centered criterion of success (power, preeminence, influence, beauty), then natural selection would not be mechanistic: The dynamics of change in the population could not be mathematically computed from its prior state. And if it took place in a single generation, then natural selection would be banal, since it would add nothing to ordinary physical cause and effect. When a river erodes the soft rock layers on its bed and leaves behind the harder layers, or when the more volatile compounds in petroleum evaporate faster than the less volatile ones, one hardly needs to invoke the theory of natural selection. One can just say that some things are stronger, or longer-lasting, or more stable than others. Only when selection operates over *multiple generations* of replication, yielding a cumulative result that was not obvious from cause and effect applying to a single event, does the concept of natural selection add anything.

The theory of natural selection applies most readily to genes because they have the right stuff to drive selection, namely making high-fidelity copies of themselves. Granted, it's often convenient to speak about selection at the level of individuals, because it's the fate of individuals (and their kin) in the world of cause and effect that determines the fate of their genes. Nonetheless, it's the genes themselves that are replicated over generations and are thus the targets of selection and the ultimate beneficiaries of adaptations. Sexually reproducing organisms don't literally replicate themselves, because their offspring are not clones but rather composites of themselves and their mates. Nor can any organism, sexual or asexual, pass onto its offspring the traits it has acquired in its lifetime. Individual bodies are simply not passed down through the generations the way that genes are. As Stephen Jay Gould put it, "You can't take it with you, in this sense above all."

Now, no one "owns" the concept of natural selection, nor can anyone police the use of the term. But its explanatory power, it seems to me, is so distinctive and important that it should not be diluted by metaphorical, poetic, fuzzy, or allusive extensions that only serve to obscure how profound the genuine version of the mechanism really is.

To be sure, some extensions of natural selection to replicators other than genes are rigorous and illuminating, because they preserve the essential features of replicator dynamics. Examples include bits of code in genetic algorithms, the analogs of genes in artificial-life simulations, and, if the physicist Lee Smolin is correct, the laws and constants of entire universes.

But other extensions are so poetical that they shed no light on the phenomenon and only obscure the real power of natural selection. There's no end to the possibilities for pointlessly redescribing ordinary cause-and-effect sequences using the verbiage of natural selection. Cities have more old buildings made of stone than of wood because of the process of edifice selection. Cars today are equipped with steel-belted radials because they outcompeted polyester-belted tires in a process of tire selection. Touch-tone phones have prevailed over dial phones because of their competitive advantages in telephone selection. And so on. Sure, some things last longer or do better in competition than others because they have traits that help them last longer or compete more effectively. But unless the traits arose from multiple iterations of copying of random errors in a finite pool of replicators, the theory of natural selection adds nothing to ordinary cause and effect.

What about groups? Natural selection could legitimately apply to groups if they met certain conditions: The groups made copies of themselves by budding or fissioning; the descendant groups faithfully reproduced traits of the parent group (which cannot be reduced to the traits of their individual members), except for mutations that were blind to their costs and benefits to the group; and groups competed with one another for representation in a meta-population of groups. But everyone agrees that *this is not what happens in so-called group selection*. In every case I've seen, the three components that make natural selection so indispensable are absent.

1. The criterion of success is not the number of copies in a finite population (in this case, the meta-population of groups), but some analogue of success like size, influence, wealth, power, longevity, territory, or preeminence. An example would be the "success" of monotheistic religions. No one claims that monotheistic religions are more fission-prone than polytheistic ones, and that as a consequence there are numerically more monotheistic belief systems among the thousands found on earth. Rather, the "success" consists of monotheistic religions having more people, territory, wealth, might, and influence. These are impressive to a human observer, but they are not what selection, literally interpreted, brings about.
2. The mutations are not random. Conquerors, leaders, elites, visionaries, social entrepreneurs, and other innovators use their highly nonrandom brains to figure out tactics and institutions and norms and beliefs that are intelligently designed in response to a felt need (for example, to get their group to predominate over their rivals).
3. The "success" applies to the entity itself, not to an entity at the end of a chain of descendants. It was the Roman Empire that took over most of the ancient world, not a group that splintered off from a group that splintered off from a group that splintered off from the Roman Empire, each baby Roman Empire very much like the parent Roman Empire except for a few random alterations, and the branch of progeny empires eventually outnumbering the others.

On top of these differences, most of the groupwide traits that group selectionists try to explain are cultural rather than genetic. The trait does not arise from some gene whose effects propagate upward to affect the group as a whole, such as a genetic tendency of individuals to disperse that leads the group to have a widespread geographic distribution, or an ability of individuals to withstand stressful environments that leads the species to survive mass extinction events. Instead, they are traits that are propagated culturally, such as religious beliefs, social norms, and forms of political organization. Modern group selectionists are often explicit that it is cultural traits they are talking about, or even that they are agnostic about whether the traits they are referring to are genetic or cultural.

What all this means is that so-called group selection, as it is invoked by many of its advocates, is not a precise implementation of the theory of natural selection, as it is, say, in genetic algorithms or artificial-life simulations. Instead it is a loose metaphor, more like the struggle among kinds of tires or telephones. For this reason the term "group selection" adds little to what we have always called "history." Sure, some cultures have what it takes to become more populous or powerful or widespread, including expansionist ideologies, proselytizing offensives, effective military strategies, lethal weaponry, stable government, social capital, the rule of law, and norms of tribal loyalty. But what does "natural selection" add to the historian's commonplace that some groups have traits that cause them to grow more populous, or wealthier, or more powerful, or to conquer more territory than others?

GROUP SELECTION AS AN EXPLANATION OF THE TRAITS OF INDIVIDUALS

Let's now turn to the traits of individuals. Is group selection necessary to explain the evolution of psychological traits adapted to group living, such as tribalism, bravery, self-sacrifice, xenophobia, religion, empathy, and moralistic emotions? This section looks at theory, the next one at psychological and historical data.

The reproductive success of humans undoubtedly depends in part on the fate of their groups. If a group is annihilated, all the people in it, together with their genes, are annihilated. If a group acquires territory or food or mates, the windfall will benefit some or all of its members. But recall the fleet herd of deer and the herd of fleet deer. If a person has innate traits that encourage him to contribute to the group's welfare and as a result contribute to *his own* welfare, group selection is unnecessary; individual selection in the context of group living is adequate. Individual human traits evolved in an environment that includes other humans, just as they evolved in environments that include day-night cycles, predators, pathogens, and fruiting trees.

Some mathematical models of group selection are really just individual selection in the context of groups.[3] The modeler arbitrarily stipulates that the dividend in fitness that accrues to the individual from the fate of the group does not count as "individual fitness." But the tradeoff between "benefiting the self thanks to benefiting the group" and "benefiting the self at the expense of the rest of the group" is just one of many tradeoffs that go into gene-level selection. Others include reproductive versus somatic effort, mating versus parenting, and present versus future offspring. There's no need

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[3] Again, see West, Griffin, and Gardner (2007, 2008) for examples.

to complicate the theory of natural selection with a new "level of selection" in every case.

It's only when humans display traits that are *disadvantageous* to themselves while benefiting their group that group selection might have something to add. And this brings us to the familiar problem that led most evolutionary biologists to reject the idea of group selection in the 1960s.[4] Except in the theoretically possible but empirically unlikely circumstance in which groups bud off new groups faster than their members have babies, any genetic tendency to risk life and limb that results in a net decrease in individual inclusive fitness will be relentlessly selected against. A new mutation with this effect would not come to predominate in the population, and even if it did, it would be driven out by any immigrant or mutant that favored itself at the expense of the group.

Let's take the concrete example of collective aggression. Often the benefits to the self and to the group may coincide. A warrior may scare off a party of attackers and save the lives of his fellow villagers together with the lives of himself and his family. In other cases, the benefits may diverge: The warrior may stay at the rear or sneak off to the side and let everyone else fight. In still others, the outcome may be uncertain, but because selection works on probabilities, he may play the odds, say, taking a 1-in-10 chance of getting killed in a raid that promises a 1-in-2 chance of abducting a few extra wives. We should expect selection to favor traits that maximize the individual's expected reproductive output, given these tradeoffs.

What we *don't* expect to see is the evolution of an innate tendency among individuals to predictably sacrifice their expected interests for the interests of the group—to cheerfully volunteer to serve as a galley slave, a human shield, or cannon fodder. Take the extreme case of a gene that impelled a person to launch a suicide attack that allowed his group to prevail over an enemy. That is hardly a gene that could be selected! (I'll put aside for now the potential benefits to the suicide warrior's kin.) What could evolve, instead, is a tendency to manipulate *others* to become suicide attackers, and more generally, to promulgate norms of morality and self-sacrifice that one intends to apply in full force to everyone in the group but oneself. If one is the unlucky victim of such manipulation or coercion by others, there's no need to call it altruism and search for an evolutionary explanation, any more than we need to explain the "altruism" of a prey animal who benefits a predator by blundering into its sights.

Thus we have a nice set of competing empirical predictions for any examples of group-benefiting self-sacrifice we do observe in humans. If humans were selected to benefit their groups at the expense of themselves, then self-sacrificial acts should be deliberate, spontaneous, and uncompensated, just like other adaptations such as libido, a sweet tooth, or parental love. But if humans were selected to benefit themselves and their kin in the context of group living (perhaps, but not necessarily, by also benefiting their groups), then any guaranteed self-sacrifice should be a product of manipulation by others, such as enslavement, conscription, external incentives, or psychological manipulation.

To be sure, if we go back to group selection as an explanation of *group* traits, particularly cultural ones, then it's easy to see how a group that successfully coerced or manipulated a renewable supply of its own members to launch suicide attacks might expand relative to other groups. But that would have nothing to do with its members'

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[4] Williams (1966) is the classic reference; see also Dawkins (1976/1989).

inherited psychology, in this case, their willingness to sacrifice themselves without manipulation. The same is true for less extreme sacrifices.

DO HUMANS IN FACT HAVE ADAPTATIONS THAT BENEFIT THE GROUP AT THE EXPENSE OF THE SELF?

The recent surge of interest in group selection has been motivated by two empirical phenomena. One is eusociality in insect taxa such as bees, ants, and termites, whose worker or soldier castes forgo their own reproduction and may sacrifice their lives to benefit their fellows, as when a bee dies when stinging an invader. E. O. Wilson notes that a self-sacrificing insect benefits the colony, and concludes that eusociality must be explained by selection among colonies. But most other biologists point out that the sacrificer benefits the queen (her sister or mother), who founds a new colony when she reproduces, so the simplest explanation of eusociality is that the genes promoting self-sacrifice were selected because they benefited copies of themselves inside the queen.[5] The same is true for other collectives of genetic relatives in which only a select few reproduce, such as the individuals making up a colonial organism and the cells making up a body.

The other phenomenon is the existence of altruism and self-sacrifice among humans, such as martyrdom in warfare, costly punishment of free-riders, and generosity toward strangers. Group selectionists often analogize self-sacrifice among humans to eusociality in insects, and explain both by group selection. In *The Social Conquest of Earth*, a book whose title alludes to the evolutionary success of humans and social insects, Wilson writes (2012, p. 56): "An unavoidable and perpetual war exists between honor, virtue, and duty, the products of group selection, on one side, and selfishness, cowardice, and hypocrisy, the products of individual selection, on the other side." In *The Righteous Mind* (2012, p. xxii), Jonathan Haidt agrees, explaining the evolution of moral intuitions such as deference to authority, loyalty to community, and conformity to social norms by proposing that "Humans are 90 percent chimp and 10 percent bee."

Many questionable claims are packed into the clustering of inherent virtue, human moral intuitions, group-benefiting self-sacrifice, and the theory of group selection. One is the normative moral theory in which virtue is equated with sacrifices that benefit one's own group in competition with other groups. If that's what virtue consisted of, then fascism would be the ultimate virtuous ideology, and a commitment to human rights the ultimate form of selfishness. Of course, that is not what Wilson meant; he apparently wanted to contrast individual selfishness with something more altruistic, and wrote as if the only alternative to benefiting oneself is contributing to the competitive advantage of one's group. But the dichotomy ignores another possibility: that an individual can be virtuous by benefiting *other individuals* (in principle, all humans, or even all sentient creatures), whether or not he enhances the competitive prowess of the group to which he belongs.

Another problem with the bundling of human altruism, insect eusociality, and group selection is that insect eusociality itself is not, according to most biologists other than Wilson, explicable by group selection. But let's provisionally grant one part of the

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[5] See Abbot et al. (2011); Boomsma et al. (2011); Herre and Wcislo (2011); Nowak, Tarnita, and Wilson (2010); and Strassmann, Page, Robinson, and Seeley (2011).

association for the sake of the empirical tests. The gene-centered explanation of eusociality depends on the relatedness of sterile workers and soldiers to a small number of queens who are capable of passing along their genes, and of course that reproductive system is absent from human groups. Nonetheless, according to this argument, humans are like bees in contributing to the welfare of their community. Since the gene-centered theory of insect eusociality cannot apply to humans, perhaps it is unnecessary to explain bees either. In that case, the most parsimonious theory would explain both human altruism and insect eusociality with group selection.

So for the time being, we can ask, Is human psychology really similar to the psychology of bees? When a bee suicidally stings an invader, presumably she does so as a primary motive, as natural as feeding on nectar or seeking a comfortable temperature. But do humans instinctively volunteer to blow themselves up or advance into machine-gun fire, as they would if they had been selected with group-beneficial adaptations? My reading of the study of cooperation by psychologists and anthropologists, and of the study of group competition by historians and political scientists, suggest that in fact human are nothing like bees.

The huge literature on the evolution of cooperation in humans has done quite well by applying the two gene-level explanations for altruism from evolutionary biology, nepotism and reciprocity, each with a few twists entailed by the complexity of human cognition.

Nepotistic altruism in humans consists of feelings of warmth, solidarity, and tolerance toward those who are likely to be one's kin. It evolved because any genes that encouraged such feelings toward genetic relatives would be benefiting copies of themselves inside those relatives. (This does not, contrary to a common understanding, mean that people love their relatives because of an unconscious desire to perpetuate their genes.) A vast amount of human altruism can be explained in this way. Compared to the way people treat nonrelatives, they are far more likely to feed their relatives, nurture them, do them favors, live near them, take risks to protect them, avoid hurting them, back away from fights with them, donate organs to them, and leave them inheritances.[6]

The cognitive twist is that the recognition of kin among humans depends on environmental cues that other humans can manipulate.[7] Thus people are also altruistic toward their adoptive relatives, and toward a variety of fictive kin such as brothers in arms, fraternities and sororities, occupational and religious brotherhoods, crime families, fatherlands, and mother countries. These faux-families may be created by metaphors, simulacra of family experiences, myths of common descent or common flesh, and other illusions of kinship. None of this wasteful ritualizing and mythologizing would be necessary if "the group" were an elementary cognitive intuition that triggered instinctive loyalty. Instead, that loyalty is instinctively triggered by those with whom we are likely to share genes, and extended to others through various manipulations.

The other classic form of altruism is reciprocity: initiating and maintaining relationships in which two agents trade favors, each benefiting the other as long as each protects himself from being exploited. Once again, a vast amount of human cooperation is elegantly explained by this theory.[8] People are "nice," both in the everyday sense and the technical sense from game theory, in that they willingly confer a large

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[6] See Gaulin and McBurney (2003) and Lieberman, Tooby, and Cosmides (2007).

[7] See Daly, Salmon, and Wilson (1997); Fiske (1991); and Lieberman et al. (2007).

[8] See Cosmides and Tooby (1992) and McCullough (2008) for reviews.

benefit to a stranger at a small cost to themselves, because that has some probability of initiating a mutually beneficial long-term relationship. (It's a common misunderstanding that reciprocal altruists never help anyone unless they are soliciting or returning a favor; the theory in fact predicts that they will sympathize with the needy.) People recognize other individuals and remember how they have treated and been treated by them. They feel gratitude to those who have helped them, anger to those who have exploited them, and contrition to those whom they have exploited if they depend on them for future cooperation.

One cognitive twist on this formula is that humans are language-using creatures who need not discriminate reciprocators from exploiters only by direct personal experience, but can also ask around and find out their reputation for reciprocating with or exploiting others. This in turn creates incentives to establish and exaggerate one's reputation (a feature of human psychology that has been extensively documented by social psychologists), and to attempt to see through such exaggerations in others.[9] And one way to credibly establish one's reputation as an altruist in the probing eyes of skeptics to *be* an altruist, that is, to commit oneself to altruism (and, indirectly, its potential returns in the long run, at the expense of personal sacrifices in the short run).[10] A third twist is that reciprocity, like nepotism, is driven not by infallible knowledge but by probabilistic cues. This means that people may extend favors to other people with whom they will never in fact interact with again, as long as the situation is representative of ones in which they *may* interact with them again.[11] Because of these twists, it's a fallacy to think that the theory of reciprocal altruism implies that generosity is a sham, and that people are nice to one another only when each one cynically calculates what's in it for him.

Group selection, in contrast, fails to predict that human altruism should be driven by moralistic emotions and reputation management, since these may benefit individuals who inflate their reputations relative to their actual contributions and thus subtract from the welfare of the group. Nor is there any reason to believe that ants, bees, or termites have moralistic emotions such as sympathy, anger, and gratitude, or a motive to monitor the reputations of other bees or manage their own reputations. Group welfare would seem to work according to the rule "From each according to his ability, to each according to his need." Ironically, Wilson himself, before he came out as a group selectionist, rejected the idea that human altruism could be explained by going to the ants, and delivered this verdict on the Marxist maxim: "Wonderful theory; wrong species" (Getlin, 1994). Haidt, too, until recently was content to explain the moral emotions with standard theories of nepotistic and reciprocal altruism.[12]

The only empirical phenomenon that has been directly adduced as support for group selection is a set of experimental games in which people seem to sacrifice their interests for those of a group.[13] In a laboratory version of a Public Goods game, participants are allocated a sum of money and invited to contribute as much as they want to a communal pot, which is then multiplied by the experimenter and divided evenly among them. The optimum strategy for the group is for everyone to contribute the maximum; the optimum strategy for the individual is to be a free-rider and stint on

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[9] See Kurzban (2011) and Trivers (2011).

[10] See Frank (1988).

[11] Delton, Krasnow, Tooby, and Cosmides (2011).

[12] Haidt (2002).

[13] Fehr and Gächter (2002).

his public contribution, thereby enjoying both the group dividend and his private stash. In a typical experiment with repeated rounds of play, free riding takes over and the public contribution dwindles to zero.

A natural conclusion is that this shows that humans are *not* a group-selected adaptation that capitalizes on opportunities to make sacrifices for the common good. But oddly enough, this research has been interpreted as evidence *for* group selection, because of the outcome of one variant of the procedure. When people are given an opportunity to punish free-riders by levying a fine on them, then free riding decreases and everyone's profit increases—no surprise there. The surprise is that people will sometimes punish free-riders even if they have to pay for the privilege, and are assured by the experimenters that everyone is anonymous and no one will meet up with their partners again. Since the punishment is costly, and cannot even be rewarded by a reputation for civic-mindedness, it has been described as "altruistic," and has been touted as evidence for group-selected self-sacrifice.

It seems hard to believe that a small effect in one condition of a somewhat contrived psychology experiment would be sufficient reason to revise the modern theory of evolution, and indeed there is no reason to believe it. Subsequent experiments have shown that most of the behavior in these and similar games can be explained by an expectation of reciprocity or a concern with reputation.[14] People punish those that are most likely to exploit them, choose to interact with partners who are least likely to free ride, and cooperate and punish more, and free ride less, when their reputations are on the line. Any residue of pure altruism can be explained by the assumption that people's cooperative intuitions have been shaped in a world in which neither anonymity nor one-shot encounters can be guaranteed. Consider, too, that in real societies the punishment of free-riders need not be costly to the punisher. An individual or small group can cheaply injure a social parasite or sabotage his possessions, and they can be rewarded for their troubles in gratitude, esteem, or resources. After all, police, judges, and jailers don't work for nothing.

Finally, let's turn to the role of altruism in the history of group-against-group conflict. Many group selectionists assume that human armed conflict has been a crucible for the evolution of self-sacrifice, like those in insect soldier castes. They write as if suicide missions, kamikaze attacks, charges into the jaws of death, and other kinds of voluntary martyrdom have long been the norm in human conflict. My reading of the history of organized violence is that this is very far from the case.

In tribal warfare among nonstate societies, men do not regularly take on high-lethal risks for the good of the group. Their pitched battles are noisy spectacles with few casualties, while the real combat is done in sneaky raids and ambushes in which the attackers assume the minimum risks to themselves.[15] When attacks do involve lethal risks, men are apt to desert, stay in the rear, and find excuses to avoid fighting, unless they are mercilessly shamed or physically punished for such cowardice (see, for example, the recent meticulous study of Turkana warfare by Sarah Mathew and Robert Boyd).[16]

What about early states? States and empires are the epitome of large-scale coordinated behavior and are often touted as examples of naturally selected groups. Yet the first complex states depended not on spontaneous cooperation but on brutal

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[14] Delton, Krasnow, Tooby, and Cosmides (2011); Krasnow, Cosmides, Pedersen, and Tooby (2012); Price (2012).

[15] Gat (2006).

[16] Mathew and Boyd (2011).

coercion. They regularly engaged in slavery, human sacrifice, sadistic punishments for victimless crimes, despotic leadership in which kings and emperors could kill with impunity, and the accumulation of large harems, with the mathematical necessity that large number of men were deprived of wives and families.[17]

Nor has competition among modern states been an impetus for altruistic cooperation. Until the Military Revolution of the 16th century, European states tended to fill their armies with marauding thugs, pardoned criminals, and paid mercenaries, while Islamic states often had military slave castes.[18] The historically recent phenomenon of standing national armies was made possible by the ability of increasingly bureaucratized governments to impose conscription, indoctrination, and brutal discipline on their powerless young men. Even in historical instances in which men enthusiastically volunteered for military service (as they did in World War I), they were usually victims of positive illusions that led them to expect a quick victory and a low risk of dying in combat.[19] Once the illusion of quick victory was shattered, the soldiers were ordered into battle by callous commanders and goaded on by "file closers" (soldiers ordered to shoot any comrade who failed to advance) and by the threat of execution for desertion, carried out by the thousands. In no way did they act like soldier ants, willingly marching off to doom for the benefit of the group.

To be sure, the annals of war contain tales of true heroism—the proverbial soldier falling on the live grenade to save his brothers in arms. But note the metaphor. Studies of the mindset of soldierly duty shows that the psychology is one of fictive kinship and reciprocal obligation within a small coalition of individual men, far more than loyalty to the superordinate group they are nominally fighting for. The writer William Manchester, reminiscing about his service as a Marine in World War II, wrote of his platoonmates, "Those men on the line were my family, my home. . . . They had never let me down, and I couldn't do it to them. . . . Men, I now knew, do not fight for flag or country, for the Marine Corps or glory of any other abstraction. They fight for one another" (Thayer, 2004, p. 183).

What about the ultimate in individual sacrifice, suicide attacks? Military history would have unfolded very differently if this were a readily available tactic, and studies of contemporary suicide terrorists have shown that special circumstances have to be engineered to entice men into it. Scott Atran, Larry Sugiyama, Valerie Hudson, Jessica Stern, and Bradley Thayer have documented that suicide terrorists are generally recruited from the ranks of men with poor reproductive prospects, and they are attracted and egged on by some combination of peer pressure, kinship illusions, material and reputational incentives to blood relatives, and indoctrination into the theory of eternal rewards in an afterlife (the proverbial 72 virgins).[20] These manipulations are necessary to overcome a strong inclination *not* to commit suicide for the benefit of the group.

The historical importance of compensation, coercion, and indoctrination in group-against-group competition should not come as a surprise, because the very idea that group combat selects for individual altruism deserves a closer look. Wilson's dictum that groups of altruistic individuals beat groups of selfish individuals is true only if one classifies slaves, serfs, conscripts, and mercenaries as "altruistic." It's more

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[17] Betzig (1986); Otterbein (2004).

[18] Gat (2006); Levy, Walker, and Edwards (2001).

[19] Johnson (2004).

[20] Atran (2003); Blackwell and Sugiyama (2008); Thayer and Hudson (2010).

accurate to say that groups of individuals that are *organized* beat groups of selfish individuals. And effective organization for group conflict is more likely to consist of more powerful individuals incentivizing and manipulating the rest of their groups than of spontaneous individual self-sacrifice.

And once again, it won't work to switch levels and say that group selection is really acting on the norms and institutions of successful states. The problem is that this adds nothing to the conventional historian's account in which societies with large tax bases, strong governments, seductive ideologies, and effective military forces expanded at the expense of their neighbors. That's just ordinary causation, enabled by the fruits of human ingenuity, experience, and communication. The truly Darwinian mechanisms of high-fidelity replication, blind mutation, differential contribution of descendants to a population, and iteration over multiple generations have no convincing analogue.

A SUMMARY OF THE TROUBLE WITH GROUP SELECTION

The idea of group selection has a superficial appeal because humans are indisputably adapted to group living and because some groups are indisputably larger, longer-lived, and more influential than others. This makes it easy to conclude that properties of human groups, or properties of the human mind, have been shaped by a process that is akin to natural selection acting on genes. Despite this allure, I have argued that the concept of group selection has no useful role to play in psychology or social science. It refers to too many things, most of which are not alternatives to the theory of gene-level selection but loose allusions to the importance of groups in human evolution. And when the concept is made more precise, it is torn by a dilemma. If it is meant to explain the cultural traits of successful groups, it adds nothing to conventional history and makes no precise use of the actual mechanism of natural selection. But if it is meant to explain the psychology of individuals, particularly an inclination for unconditional self-sacrifice to benefit a group of nonrelatives, it is dubious both in theory (since it is hard to see how it could evolve given the built-in advantage of protecting the self and one's kin) and in practice (since there is no evidence that humans have such a trait).

None of this prevents us from seeking to understand the evolution of social and moral intuitions, nor the dynamics of populations and networks that turn individual psychology into large-scale societal and historical phenomena. It's just that the notion of "group selection" is far more likely to confuse than to enlighten—especially as we try to understand the ideas and institutions that human cognition has devised to make up for the shortcomings of our evolved adaptations to group living. I offer a simple solution: Stop using the term "group selection" as a loose synonym for the evolution of group living, group competition, group norms, group practices, social networks, culture, selflessness, kindness, empathy, altruism, morality, clannishness, tribalism, or coalitional aggression.

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PART VII

INTERFACES WITH TRADITIONAL PSYCHOLOGY DISCIPLINES

DAVID M. BUSS

THE FIELD OF psychology historically has been organized around subdisciplines, such as cognitive, social, developmental, personality, and clinical. Evolutionary psychology, in many ways, dissolves these subdisciplinary boundaries. The topics of this *Handbook* are largely organized around adaptive problems and evolved psychological solutions. As a consequence, each of the traditional subdisciplines in the field of psychology has relevance to many psychological adaptations. Consider, for example, the evolved fear of snakes. This adaptation has an underlying cognitive (information-processing) architecture, emerges at a predictable point in development, is susceptible to social input through observing the fear reactions of others, shows stable individual differences, and can become dysfunctional or pathological. Examined through the lens of evolutionary psychology, the subdisciplinary boundaries of mainstream psychology appear somewhat arbitrary, and do not cleave nature at its natural joints.

Nonetheless, since most psychologists are trained within the coalitional guilds and conceptual frameworks of these traditional subdisciplines, it is useful to see how evolutionary psychologists can approach the main questions and problems of these subdisciplines. What can evolutionary psychology offer to these disciplines as they are traditionally conceived? What new insights can be brought to bear on them? The chapters in this section address these questions.

Peter Todd, Ralph Hertwig, and Urlich Hoffrage (Chapter 37) provide a fascinating evolutionary psychological analysis of the field of cognitive psychology. They show how fresh insights into traditional topics—attention, information representation, memory, forgetting, inference, judgment, heuristics, biases, and decision making—can be informed by evolutionary analysis. Reciprocally, they show how advances in cognitive psychology greatly aid evolutionary analyses. Todd, Hertwig, and Hoffrage provide compelling arguments that benefits of the merger flow both ways, since traditional cognitive psychology also has much to offer evolutionary psychology.

David Bjorklund, Carlos Blasi, and Bruce Ellis provide a chapter on evolutionary developmental psychology (Chapter 38). They offer important insights that challenge some traditional assumptions in developmental psychology. For example, one traditional assumption has been that psychological features in childhood are merely preparations for the fully functioning adult form. They argue persuasively that, instead, some adaptations are designed for specific stages of development and are appropriately functional at those times, rather than serving merely as way stations to the development of the adult form. They consider how evolutionary analysis of many topics central to developmental psychology—topics such as theory of mind, children's intuitive mathematics, and social behaviors such as children's aggression and dominance hierarchies—can lead to fresh insights that have been entirely missed by the traditional conceptual frameworks that have guided developmental psychology.

Douglas Kenrick, Jon Maner, and Norman Li also argue persuasively for reciprocal benefits, this time flowing from evolutionary psychology to social psychology, and from social psychology to evolutionary psychology (Chapter 39). They propose that the traditional social psychological emphasis on situation specificity is highly compatible with evolutionary psychological approaches that emphasize domain specificity. They suggest that social psychologists can gain by adding ultimate explanations to their traditional proximate explanations. Finally, Kenrick, Maner, and Li provide an attractive taxonomy of social adaptive problems that could serve as a powerful organizing framework for social psychology.

Aurelio José Figueredo, Michael Woodley, and W. Jake Jacobs (Chapter 40) provide an exciting chapter on evolutionary personality psychology, with a special focus on what has been called "The General Factor of Personality." They focus on an area that tends to be relatively neglected by evolutionary psychologists—stable individual differences. Figueredo and colleagues review empirical evidence, both from human and nonhuman animal studies, which supports the contention that individual differences in personality have been subjected to natural selection, sexual selection, and frequency-dependent selection. They then evaluate a hierarchical model of life history strategy. It is an important chapter, and one that augers well for a greater conceptual integration of individual differences within an evolutionary psychological framework that emphasizes species-typical psychological mechanisms.

Martie Haselton, Daniel Nettle, and Damian Murray present theory and empirical research on the evolution of cognitive biases in social interaction (Chapter 41). As such, their chapter elegantly links two traditional disciplines that historically have been separate—cognitive psychology and social psychology. They provide sound arguments that certain social cognitive biases are in fact designed and functional, resulting in better solutions to adaptive problems than cognitive mechanisms that "accurately" detected social signals. They call for an evolutionary reformulation of the entire "heuristics and biases" literature, which typically casts humans as making illogical and unfounded errors. This new line of work has already led to the discovery of new cognitive biases and offers much promise for the future discovery of additional adaptive biases. It also may lead to the detumescence of decades of work that has cast humans as fundamentally irrational and hopelessly muddled in their judgment and decision making.

Jerome Wakefield provides a penetrating analysis of the concepts of function and dysfunction, which should form the foundation for the field of evolutionary clinical psychology (Chapter 42). He argues that clinical psychology historically has lacked a coherent definition of disorder. Instead, the field has relied on intuitive, conflicting, and usually fuzzy notions of disorder and dysfunction. Evolutionary psychology provides clarification. Wakefield cogently argues that the only sensible definition of disorder requires *the failure of a designed function*. It follows that we need to know the designed function of psychological mechanisms as a prerequisite to understanding when they fail to function as designed. Wakefield also exposes several fallacies in arguments that mental disorders are naturally selected conditions, and draws implications for the DSM classification system of disorders. It is somewhat astonishing to realize that clinical psychology has proceeded for decades without a clear definition of mental disorder. Wakefield's chapter fills the needed lacuna.

In the final chapter in this section (Chapter 43), Randolph Nesse provides a broad analysis of evolutionary psychology and mental health, identifying eight contributions of an evolutionary analysis: It explains why humans are vulnerable to mental disorders, offers a functional understanding of behavior, fosters a deeper and more empathic understanding of individuals, explains how relationships work, provides a way to think clearly about developmental influences, provides a functional approach to emotions and their regulation, provides a foundation for a scientific diagnostic system, and provides a framework for considering how multiple causal factors can explain why some people get mental disorders while others do not. Nesse's compelling chapter should be required reading of everyone in clinical psychology.

Taken together, the chapters in this section provide a set of conceptual tools for evolutionizing each of the major subdisciplines within psychology. To the extent that the subdisciplines retain their inertial institutional boundaries, these chapters are invaluable. Ultimately, however, they may also contribute to the eventual demise of the traditional boundaries and pave the way for a unification of the field of psychology.

CHAPTER 37

Evolutionary Cognitive Psychology

PETER M. TODD, RALPH HERTWIG, and ULRICH HOFFRAGE

INTRODUCTION: SELECTIVE PRESSURES ON COGNITIVE MECHANISMS

TRADITIONAL COGNITIVE PSYCHOLOGY, the study of the information-processing mechanisms underlying human thought and behavior, is problematic from an evolutionary viewpoint: Humans were not directly selected to process information, nor to store it, learn it, attend to it, represent it—nor even, in fact, to think. All of these capacities, the core topics of cognitive psychology, can be seen as by-products arising over the course of the evolution of solutions to the central challenges, survival and reproduction. Moreover, while the subgoals of those two main goals—finding food, maintaining body temperature, selecting a mate, negotiating status hierarchies, forming cooperative alliances, fending off predators and conspecific competitors, raising offspring, and so on—relied on gathering and processing information, meeting the challenges of each of these domains would have been possible only by in each case gathering *specific* pieces of information and processing it in specific ways. This suggests that to best study the faculties of memory, or attention, or reasoning, one should take a goal- and domain-specific approach that focuses on the use of each faculty for a particular evolved function, just the approach exemplified by the other chapters in this handbook.

Cognitive psychology's traditional approach, however, is domain general or domain agnostic, as if cognitive capacities arose in a void and orthogonal to any environment-specific selective pressures. Nonetheless, we believe that even while taking the traditional domain-agnostic approach to studying the mind, cognitive psychology can still benefit from as well as contribute to an evolutionary perspective on thinking and reasoning. This is because in addition to the selective pressures shaping domain-specific mechanisms, there are also a number of important selective forces operating across domains more widely, such as those arising from the costs of decision time and information search. Much as our separate physiological systems have all been shaped by a common force for energy-processing efficiency, individual psychological information-processing systems may all have been shaped by various common pressures for information-processing efficiencies. These broad pressures can in turn lead to common design features in many cognitive systems, such as decision mechanisms that make choices swiftly based on little information.

In this chapter, we show how a set of broad forces operating on multiple domains can impact the design of specific cognitive systems. In particular, we first discuss how the costs of gathering information, and of using too much information, can be reduced by decision mechanisms that rely on very limited information—or even a lack of information—to come to their choices. Next, we explore how the pressures to use small amounts of appropriate information may have produced particular patterns of forgetting in long-term memory and particular limits of capacity in short-term memory. Finally, we show how selection for being able to think about past sets of events can help explain why different representations of the same information, for instance samples versus probabilities, can produce widely varying responses. Throughout, we focus on three topics of central interest to cognitive psychologists—decision making, memory, and representations of information. But at the same time, we also lay out three main theses that will be less familiar to those taking a traditional view of cognition as computation unfettered by external, environmental considerations: First, simple decision mechanisms can work well by fitting environmental structures; second, limited memory systems can have adaptive benefits; and third, experience-based representations of information can enhance decision making. Thus, while we ignore many of the topics typically covered in cognitive psychology, we aim to sketch out some existing questions that we think an evolution-savvy cognitive psychology should explore. (For other views of evolutionary cognitive psychology and consideration of further issues such as individual differences, see Kenrick et al., 2009; Kenrick, Sadalla, & Keefe, 1998.)

DECISION MAKING: PUTTING INFORMATION TO USE

We begin by considering decision mechanisms, which process perceived and stored information into choices leading to action. Because decision processes stand close to behavioral actions, they are also close to the particular functionally organized selective forces operating on behavior. Thus, decision mechanisms may have been strongly affected by individual selective forces to become domain specific, in contrast to more general-purpose perceptual systems. Nonetheless, there are also broad selection pressures operating across domains that, we propose, have shaped a wide range of decision mechanisms in similar directions. Foremost is selection for making an appropriate decision in the given domain. This does not mean making the best possible decision, but rather one that is good enough (a "satisficing" choice, as Herbert Simon, 1955, put it), and on average better than those of one's competitors, given the costs and benefits involved. Good-enough decisions depend on information, and the specific requirements of the functional problem along with the specific structure of the relevant environment will determine what information is most useful (e.g., valid for making adaptive choices) and most readily obtained.

But gathering information also has costs and is subject to selection pressures (Todd, 2001), which cognitive psychologists studying the adaptive nature of inference should attend to. First, there is the cost of obtaining the information itself, in time or energy that could be better spent on other activities. Such costs can arise in both external information search in the environment and internal search in memory (Bröder, 2012). Second, there is the cost of actually making worse decisions if too much information is taken into consideration. Because nobody ever faces exactly the same situation twice, decision makers must generalize from past experience to new situations. Yet, as a consequence of the uncertain nature of the world, some of the features of earlier situations will be noise, irrelevant to the new decision. Thus, by considering too much information, one is likely to add noise to the decision process, and to *overfit* when generalizing to new circumstances—that is, to make worse decisions than if less information had been considered (Gigerenzer & Brighton, 2009; Martignon & Hoffrage, 2002).

Thus, there seem to be two selective pressures shaping decision making in opposite directions: the need to make good choices and the need to use little information. But this apparent accuracy/effort tradeoff can be sidestepped: Many environments are structured such that little information suffices for making good-enough choices, and decision mechanisms that operate in a "fast and frugal" manner can outperform those that seek to process all available information (Gigerenzer, Todd, & the ABC Research Group, 1999; Payne, Bettman, & Johnson, 1993). When these simple heuristics are used in particular environments with a stable information structure that they can exploit, they lead to what has been termed "ecological rationality," emphasizing the important match between mental and social and physical environmental structures in a way that fits closely with an evolutionary perspective (Hertwig, Hoffrage, & the ABC Research Group, 2013; Todd & Gigerenzer, 2007; Todd, Gigerenzer, & the ABC Research Group, 2012). We now briefly survey some of the types of decision heuristics in the mind's "adaptive toolbox" (Todd, 2000) that flourish at the intersection of these selective forces.

Decision Making Using Recognition and Ignorance

Minimal information use can come about by basing decisions on a *lack* of knowledge, capitalizing on one's own ignorance as a reflection of the structure of the environment. If there is a choice between multiple alternatives along some criterion, such as which of a set of fruits is good to eat, and if only one of the alternatives is recognized and the others are unknown, then an individual can employ the "recognition heuristic": Choose the recognized option over the unrecognized ones (D. G. Goldstein & Gigerenzer, 1999, 2002). Following this simple heuristic will be adaptive and ecologically rational, yielding good choices more often than would random choice in particular types of environments—specifically, in those where exposure to options is positively correlated with their ranking along the decision criterion being used. Thus, in our food choice example, the recognition heuristic will be beneficial because those things that we do not recognize in our environment are often inedible; humans have done a reasonable job of discovering and incorporating edible fruits into our diet. (See Pachur, Todd, Gigerenzer, Schooler, & Goldstein, 2012, for analysis of environments in which recognition will lead to adaptive decisions.)

Decision Making Using Few Cues

When the options to be selected among are all known, the recognition heuristic can no longer be applied, and further cues must be consulted. The traditional approach to rational decision making stipulates that all of the available information should be collected, weighted properly, and combined before choosing. A more frugal approach is to use a stopping rule that terminates the search for information as soon as enough has been gathered to make a decision. In the most parsimonious version, "one-reason decision making" heuristics (Gigerenzer & Goldstein, 1996, 1999) stop looking for cues as soon as the first one is found that differentiates between the options being considered. Among the many possible one-reason decision heuristics, *take-the-best* searches for cues in the order of their ecological validity (proportion of correct decisions). *Take-the-last* looks for cues in the order determined by their past decisiveness, so that the cue that was used for the most recent previous decision is checked first during the next decision. The *minimalist* heuristic lacks both memory and knowledge of cue validities and simply selects randomly among those cues currently available.

Heuristics employing this type of one-reason decision making can successfully meet the selective demands of accuracy and little information use simultaneously in appropriately matched environments. For instance, take-the-best is ecologically rational in environments comprising cues that have a *noncompensatory*, or roughly exponentially decreasing, distribution of the importance of cues. By letting the world do some of the work, these heuristics can be simpler and more robust (resistant to overfitting). A similar analysis within the world of linear models was undertaken by Dawes and Corrigan (1974), who pointed out that simplicity and robustness can be two sides of the same coin: Simply ignoring much of the available information means ignoring much *irrelevant* information, which can consequently increase the robustness of decisions when generalizing to new situations (see also Gigerenzer & Brighton, 2009, for a theoretical account of how cognitive systems can achieve robustness through appropriate simplifying "biases").[1]

Moreover, people appear to learn to apply these fast and frugal heuristics that use minimal information in environments that have the appropriate cue structure (Rieskamp & Otto, 2006), and where information is costly or time-consuming to acquire (Bröder, 2012; Newell & Shanks, 2003; Rieskamp & Hoffrage, 1999). Socially and culturally influenced decision making can also be based on a single reason through imitation (e.g., in food choice or mate choice copying), norm following, and employing protected values (e.g., moral codes that admit no compromise, such as never taking an action that results in human death—see Tanner & Medin, 2004). And when a single cue does not suffice to determine a unique choice, people still often strive to use little information, for instance via an *elimination* heuristic (Tversky, 1972) that uses as few cues as needed to eliminate all but one option from consideration (again in food choice, mate choice, or habitat choice).

DECISION MAKING WITH A SEQUENCE OF OPTIONS

When choice options are not available simultaneously, but rather appear sequentially over an extended period or spatial region, different types of decision mechanisms are needed. In cases where a single option is to be chosen, there must be a stopping rule for ending the search for alternatives themselves. For instance, long-term mate choice requires making a selection from a stream of potential candidates met at different points in time, based on some amount of information gathered about each one (Saad,

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[1] Relatedly, Chater (1999; Chater & Vitányi, 2003) has proposed that minds are themselves designed to seek the simplest possible explanation of the environmental structure they encounter, another general principle that applies across multiple cognitive domains, including perception, language processing, and higher-level cognition.

Eba, & Sejean, 2009). Classic economic search theory suggests that one should look for a new mate (or anything) until the costs of further search outweigh the benefits that could be gained by leaving the current candidate. But in practice, performing a rational cost-benefit analysis is typically difficult and expensive in terms of the information needed (as well as making a bad impression on a would-be partner). Instead, a "satisficing" heuristic, as conceived by Simon (1955, 1990), can be adaptive: Set an aspiration level for the selection criterion being used, and search for alternatives until one is found that exceeds that level. In mutual mate choice, for example, aspiration levels can be set by upward adjustment after successful interactions on the mating market and downward adjustment after failures (Beckage, Todd, Penke, & Asendorpf, 2009; G. F. Miller & Todd, 1998; Todd & Miller, 1999).

In other settings, the individual aims to gain benefits from a succession of chosen options and must decide how long to spend exploiting each option before leaving and exploring for a new option. The best-known instance of this kind of exploitation/exploration tradeoff is foraging for food, deciding when to leave a resource patch that has been depleted. Here, simple patch-leaving heuristics can trigger renewed exploration when the time since the last resource item found in the current patch grows too long (e.g., Wilke, Hutchinson, Todd, & Czienskowski, 2009). But these search mechanisms may also have been exapted from their food-domain origins for use in other domains, including the search for information (Hills, 2006; Todd, Hills, & Robbins, 2012). Thus, people appear to employ patch-leaving rules that achieve near-optimal performance both when searching for information among patches of web pages online (Pirolli, 2007) and when searching for concepts in memory (Hills, Jones, & Todd, 2012), in ways that are similar to searches for resources distributed spatially.

ECOLOGICAL RATIONALITY AND EVOLVED DECISION MECHANISMS

The heuristics described above, by ignoring much of the available information and processing what they do consider in simple ways, typically do not meet the standards of classical rationality, such as full information use and complete combination of probabilities and utilities. Furthermore, heuristics may produce outcomes that do not always follow rules of logical consistency. For instance, take-the-best and the priority heuristic can systematically produce intransitivities among sets of three or more choices (Brandstätter, Gigerenzer & Hertwig, 2006; Gigerenzer & Goldstein, 1996). However, when used in appropriately structured environments, whether ancestral or current, these mechanisms can be *ecologically* rational, meeting the selective demands of making adaptive choices (on average) with limited information and time.

Furthermore, different environment structures can be exploited by—and hence call for—different heuristics. But matching heuristics to environment structure does not mean that every new environment or problem demands a new heuristic: The simplicity of these mechanisms implies that they can often be used in multiple, similarly structured domains with just a change in the information they employ. Thus, an evolution-oriented cognitive psychologist should explore both the range of (possibly domain-general) simple decision mechanisms appropriate to a particular adaptive problem, and the domain-specific cues in the environment that will allow those mechanisms to solve that problem effectively.

MEMORY: RETRIEVING AND FORGETTING INFORMATION

The information that decisions are based on can be accessed immediately from the external environment, or from past experience stored internally in some form of memory. Beginning with Ebbinghaus (1885/1964), cognitive psychologists usually focus on three aspects of human memory—its capacity, its accuracy, and its structure (e.g., Koriat, Goldsmith, & Pansky, 2000; Tulving & Craik, 2000)—but pay little attention to how it has been shaped by selective pressures, those costs and benefits arising through its use for particular functions in particular environments. Recently, however, researchers have begun to investigate the relationship between the design of memory systems and how they meet their adaptive functions. In this section, we describe some of the trends toward putting evolutionary thinking into the study of memory.

Memory has "evolved to supply useful, timely information to the organism's decision-making systems" (Klein, Cosmides, Tooby, & Chance, 2002, p. 306). The evolution of memory to serve this function has occurred in the context of a variety of costs, which also shape the design of particular memory systems. Dukas (1999) articulated a wide range of costs of memory, including (a) maintaining an item once it has been added to long-term memory, (b) keeping it in an adaptable form that enables future updating, (c) growing and feeding the brain tissue needed to store the information, and (d) silencing irrelevant information. But taking into consideration the demands of decision mechanisms outlined earlier, the two main selective pressures acting on memory systems (particularly long-term memory) appear to be, first, to produce quickly the most useful stored information, and second, not to produce too *much* information.

These pressures, like the ones we focused on for decision mechanisms, are broad and general—applying to memory systems no matter what domains they deal with. One way to meet these pressures would be to store in the first place just that information that will be useful later. Having limited memory capacity can work to restrict initial storage in this way, as we will see later with regard to short-term memory. In the case of long-term memory, Landauer (1986) estimated that a mature person has "a functional learned memory content of around a billion bits" (p. 491). This is much less than the data storage capacity of a single hour-long music CD, suggesting that we are indeed storing very little of the raw flow of information that we experience. On the other hand, most of what little we do remember is nonetheless irrelevant to any given decision, so our memory systems must still be designed to retrieve what is appropriate, and not more. How can this be achieved? One way is through the very process that at first glance seems like a failure of the operation of memory: forgetting.

LONG-TERM MEMORY: FORGETTING CURVES AND STATISTICAL PROPERTIES OF INFORMATION USE

Anderson (1990) put forward an approach he called the rational analysis of behavior as a method for understanding psychological mechanisms in terms of their functions or goals—equivalent to Marr's (1982) computational level of analysis, and also the level at which evolutionary psychology should be focused (Cosmides & Tooby, 1987). Having in mind a view of evolution as constrained local optimization (or hill climbing), Anderson set out to assess the explanatory power of the principle that "the cognitive system operates at all times to optimize the adaptation of the behavior of the organism" (1990, p. 28). Anderson and Milson (1989) took this approach to propose that memory should be viewed as an optimizing information retrieval system with a database of stored items from which a subset is returned in response to a query (such as a list of key terms). A system of this sort can make two kinds of errors: It can fail to retrieve the desired piece of information (e.g., failing to recall the location of one's car), thus not meeting the pressure of usefulness. But if the system tried to minimize such errors by simply retrieving everything, it would commit the opposite error: producing irrelevant pieces of information (and thus not meeting the pressure of parsimony), with the concomitant cost of further examining and rejecting what is not useful. To balance these two errors, Anderson and Milson propose, the memory system can use statistics extracted from past experience to predict which memories are likely to be needed soon, and keep those readily retrievable. Consequently, memory performance should reflect the patterns with which environmental stimuli have appeared and will reappear in the environment.

This argument can be illustrated with the famous forgetting curve, first described by Ebbinghaus (1885/1964): Memory performance declines (forgetting increases) with time (or intervening events) rapidly at first and then more slowly as time goes on, characterizable as a power function (Wixted, 1990; Wixted & Ebbesen, 1991, 1997). Combining this prevalent forgetting function with Anderson's rational analysis framework yields the following prediction: To the extent that memory has evolved in response to environmental regularities, the fact that memory performance falls as a function of retention interval implies that the probability of encountering a particular environmental stimulus (e.g., a word) also declines as a power function of how long it has been since it was last encountered. Anderson and Schooler (1991, 2000) analyzed real-world data sets to find out whether the environmental regularities match those observed in human memory. One of their data sets, for example, consisted of words in the headlines of the *New York Times* for a 730-day period, and they assumed that reading a word (e.g., "Qaddafi") represents a query to the human memory database with the goal of retrieving its meaning.

At any point in time, memories vary in how likely they are to be needed. According to the rational analysis framework, the memory system attempts to optimize the information-retrieval process by making available those memories that are most likely to be useful. How does it do that? It does so by extrapolating from the past history of use to the probability that a memory is currently be needed—the *need probability* of a particular memory trace. Specifically, Anderson (1990) suggested that memories are considered in order of their need probabilities, and if the need probability of a memory record falls below a certain threshold, it will not be retrieved. Consistent with their view that environmental regularities are reflected in human memory, Anderson and Schooler (1991) found that the probability of a word occurring in a headline of the *New York Times* at any given time is a function of its past frequency and recency of occurrence. In other words, the demand for a particular piece of information to be retrieved drops the less frequently it occurred in the past and the greater the period of time that has passed since its last use. This regularity parallels the general form of forgetting that has so often been observed since the days of Ebbinghaus. From this parallel, Anderson and Schooler concluded that human memory is a highly functional system insofar as it systematically renders pieces of information less accessible when they have not been used for a while. This functionality operates across domains as a response to broad selection pressures for maintaining quick access to information likely to be useful in upcoming situations (and conversely not maintaining access to information less likely to be needed).

THE FUNCTIONS OF FORGETTING

William James, in the *Principles of Psychology* (1890), argued that "in the practical use of our intellect, forgetting is as important a function as recollecting" (p. 679). Contemporary psychologists have begun to specify some of the following particular adaptive functions of forgetting.

Uncluttering the Mind Bjork and Bjork (1996) argued that forgetting is critical to prevent out-of-date information—say, old passwords or where we parked the car yesterday—from interfering with the recall of currently needed information. In their view, the mechanism that erases out-of-date information is retrieval inhibition: Information that is rendered irrelevant becomes less retrievable (see also Schacter, 2001).

Boosting Decision Performance Forgetting may also boost the performance of decision heuristics that exploit partial ignorance, such as the recognition heuristic described earlier. Ignorance can come from not learning about portions of the environment in the first place, or from later forgetting about some earlier encounters. To examine whether human recognition memory forgets at an appropriate rate to promote the use of the recognition heuristic and its close relative, the fluency heuristic (Hertwig, Herzog, Schooler, & Reimer, 2008), Schooler and Hertwig (2005) implemented these heuristics within an existing cognitive architecture framework, ACT-R (Anderson & Lebiere, 1998), built on the rational analysis of memory mentioned earlier; specifically, ACT-R learns by strengthening memory records associated with, for instance, the names of foodstuffs, habitats, or people based on the frequency and recency with which they were encountered in the environment. In Schooler and Hertwig's simulations, both heuristics benefited from (a medium amount of) forgetting, suggesting that another beneficial consequence of forgetting is to foster the performance of heuristics that exploit (partial) ignorance.

Strategic Information Blockage Could forgetting parts of one's autobiography—in particular, traumatic experiences—also be adaptive? Betrayal trauma theory (Freyd, 1996; Freyd & Birrell, 2013) suggests that the function of amnesia for childhood abuse is to protect the child from the knowledge that a key caregiver may be the sexual perpetrator. In situations involving treacherous acts by a person depended on for survival, a "cognitive information blockage" (Sivers, Schooler, & Freyd, 2002, p. 177) may occur that results in an isolation of knowledge of the event from awareness. Betrayal trauma theory yields specific predictions about the factors that will make this type of forgetting most probable—for instance, it predicts that amnesia will be more likely the more dependent the victim is on the perpetrator (e.g., parental vs. nonparental abuse). While controversial (see DePrince & Freyd, 2004; McNally, Clancy, & Schacter, 2001, and Sivers et al., 2002), the theory illustrates how domain-specific forgetting may have unique adaptive functions.

SHORT-TERM MEMORY: FUNCTIONAL EXPLANATION OF ITS BOUNDS

Another key component of memory posited within traditional cognitive architectures is short-term memory (Atkinson & Shiffrin, 1968). This temporary memory store appears quite limited: The classic estimate of its capacity is seven plus or minus two chunks of information (G. A. Miller, 1956), and more recent estimates make it even smaller (Cowan, 2001). Given the traditional view that more information is better, many cognitive psychologists have asked, why is short-term memory so small?

Perhaps the best-studied evolutionarily informed answer to this question denies the premise that bigger is better. Kareev (1995a, 1995b, 2000; Kareev, Lieberman, & Lev, 1997) argued that limited memory capacity can enhance adaptively important inferences of causality by fostering the early detection of covariation between two variables in the environment (e.g., do these tracks mean a predator is nearby?). To the extent that the degree of covariation is derived from the information in one's working (short-term) memory, there will be an upper bound on the size of the information sample that can be considered at one time. Taking Miller's estimate as a starting point, Kareev suggested that using samples of around seven observations of the co-occurrence (or lack thereof) of two events increases the chances for detecting a correlation between them, compared to using a greater number of observations (and assuming that the population correlation is not zero). Specifically, looking at *small* randomly drawn data samples increases the likelihood of encountering a sample that indicates a stronger correlation than that of the whole population (the reason for this lies in the skewedness of the sampling distribution of correlation coefficients, based on small samples of observations). Thus, a limited working memory can function as an *amplifier* of correlations, allowing those present in the population to be detected swiftly. This enhanced ability to detect contingencies seems particularly important in domains in which the benefits of discovering a causal connection outweigh the costs of *false alarms*, which also increase in number with smaller sample sizes (a point highlighted by Juslin & Olsson, 2005—but see Fiedler & Kareev, 2006, and Kareev, 2005, for further considerations). Such domains may be characterized by situations in which missing potential threats would be extremely costly (cf. Haselton & Nettle, 2006).

Of course, overreliance on small samples will exact a price in terms of systematic misperceptions of the world—but the important thing to ask from an evolutionary cognitive psychology perspective is how large that price is compared to the potential benefits accruing to their use. Kareev's analysis can be taken as a challenge to the premise that the more veridical the mental representations of the world, the better adapted the organism; instead, these results support the idea that systematically inaccurate mental models of the world (models with a "bias"—Gigerenzer & Brighton, 2009) can confer functional benefits to organisms whose aim is not to explain the world but to survive and reproduce in it. Other proposals for a functional benefit of limited short-term memory include Hertwig and Pleskac's (2010) related demonstration that small samples amplify the difference between the expected earnings associated with the payoff distributions (e.g., food patches), thus making the options more distinct and facilitating choice, along with MacGregor's (1987) theoretical argument that memory limitations can speed up information retrieval. These and other combinations of a functionalist view with a cost-benefit analysis of particular memory mechanisms, as often employed in evolutionary cognitive ecology (Dukas, 1998), can move us closer to a thorough understanding of the workings of human memory.

REPRESENTATION OF INFORMATION: MODERN PRACTICES MEET EVOLUTIONARY CONSTRAINTS

In the previous section, we discussed memory from an evolutionary point of view. But why do we have memory at all? Why should we be able to recall representations of the past? After all, changes in behavior could arise through learning even without the ability to remember independently any aspects of the events that we learned from. Being able to store and retrieve information about what happened in the past, however, lets us process that information further in the light of new information and experience. It also allows us to communicate the information to others (as well as to ourselves at later points in time) and combine it with information from them in turn. Ultimately, recalled information from the past enables us to form expectations about the future which can guide behavior in the present.[2]

Internal memories, our focus in the previous section, are not the only innovation over the course of evolution for representing past events. Paintings of animals in Pleistocene caves, for instance, demonstrate one step in the development of representations that have been used to externalize internal states—here, memories of what the early artists had previously experienced outside the cave. During the evolution of culture, such external representations were complemented by symbols that became standardized and gradually reached greater and greater levels of abstraction (such as alphabets and number systems—Schmandt-Besserat, 1996). As a consequence, the sources of information that could be used as a basis for judgments and decisions have increased over the course of human evolution, from individual experiences (a source that we share with even the lowest animals), through reports from family or group members (a source that social animals have, and that humans have in greatly developed form, including across generations), to modern statistics (a source that has been added only very recently during our cultural evolution). Does it make a difference, in terms of individual decision making, what form the information takes as a consequence of its source? Adopting an evolutionary point of view, one would hypothesize that the answer is "yes," because our cognitive systems have been exposed to different forms and sources of information for different amounts of time. In particular, forms that have been created during our most recent cultural development may pose a bigger challenge to our information-processing capacities than those to which the human species had much more time to adapt, as the next two examples demonstrate.

DECISIONS FROM EXPERIENCE VERSUS DECISIONS FROM DESCRIPTION

Much of decision making can be understood as an act of weighing the costs against the benefits of the uncertain consequences of our choices. Take the decision of whether to engage in short-term mating: Although casual sex has obvious evolutionary benefits (e.g., Trivers, 1972), it can cause one to contract a sexually transmitted disease or suffer violence at the hands of a jealous partner (Buss, 2004). Each of these consequences is uncertain, and choosing to have casual sex is thus like rolling a die, each side of which represents one or more possible consequences of that choice.

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[2] See Freyd (1983, 1990) for a theory of how pressures for shareability of information between and within individuals can, in conjunction with pressures from natural selection on cognitive systems, shape the representations of information that we use.

The metaphor of life as a gamble (see W. M. Goldstein & Weber, 1997) has exerted a powerful influence on research on behavioral decision making, giving rise, for example, to the ubiquitous use of monetary lotteries in laboratory experiments. Studies that employ such lotteries typically provide respondents with a symbolic—usually written—description of the options, for example:

A: Get \$4 with probability .8, or *B*: Get \$3 for sure.
\$0 with probability .2

The most prominent descriptive theory of how people decide between such lotteries is *prospect theory* (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992). One of its central assumptions is this: Relative to the *stated* probabilities with which an outcome can be expected to occur (e.g., .8 and .2 in option A above), people make choices as if small-probability events receive more weight than they deserve and as if large-probability events receive less weight than they deserve. This assumption can explain why, for instance, most people are inclined to choose lottery *B* over *A* above, though *A* has the higher expected value: The rare outcome in *A*, receiving \$0, receives more weight than it deserves, reducing the perceived value of *A*.

But are choices between options like *A* and *B* representative of the gambles that life presents us? Hertwig, Barron, Weber, and Erev (2004) argue that we rarely have complete knowledge of the possible outcomes of our actions and their probabilities. When deciding whether to have a one-night stand, for instance, we do not make a *decision from description*, consulting a written list of the possible consequences and their stated likelihoods. Instead, we rely on the experience that we (or others) have accumulated over time. Hertwig and colleagues referred to this kind of choice as a *decision from experience*. (Note that because animals do not share humans' ability to process symbolic representations of dicey prospects, all their decisions are decisions from experience—see also Weber, Shafir, & Blais, 2004.)

Do people behave differently when they learn about outcomes and probabilities from written descriptions as opposed to experience? To find out, Hertwig et al. (2004) created an experimental paradigm in which decision makers started out ignorant of the outcomes and the outcome probabilities associated with pairs of lotteries. Respondents saw two buttons on a computer screen and were told that each button was associated with a payoff distribution (for instance, option A vs. B). When they clicked on a button, an outcome was randomly sampled from its distribution (e.g., \$3 if they chose *B* above, or \$0 on 20% of clicks and \$4 on 80% of clicks if they chose *A*). Respondents could sample from either distribution as many times as they wished. After they stopped sampling, they were asked which lottery they wanted to play for real payoffs.

Comparing choices made in this experience-based paradigm with choices made in the usual, structurally identical description paradigm revealed dramatic differences (Hertwig et al., 2004): Across six problems, the average absolute difference between the percentage of respondents choosing the option with the higher expected value (e.g., *A* above) in the experience and description groups was 36 percentage points. Moreover, in every problem, this difference was consistent with the assumption that rare events (e.g., \$0 in *A*) had more impact than they deserved (given their objective probability) in decisions from description—consistent with prospect theory—but had less impact than they deserved in decisions from experience.

Since its original demonstration, this *description-experience gap* has been shown to be robust across numerous investigations and experimental paradigms (Hertwig, in press; Hertwig & Erev, 2009). A number of factors have been identified as contributing to the description-experience gap, including reliance on small samples (Hertwig et al., 2004), recency (Hertwig et al., 2004), the search policy people apply to explore the payoff distributions (Hills & Hertwig, 2010), their aspiration levels (short-term vs. long-term maximization; Wulff, Hills, & Hertwig, 2014), and the cognitive processes used to gauge the value of payoff distributions based on the stated or experienced outcome and probability information (Gonzalez & Dutt, 2011).

The implication of the robust description-experience gap is that representations that are identical mathematically can be different psychologically—because they differ in form. Furthermore, the two types of information also differ in the length of evolutionary time that they have exerted a pressure on our cognitive abilities to understand and process them appropriately. Throughout the course of human evolution, we have experienced events in our interactions with the environment, but only very recently have we begun to aggregate such information and communicate it in the form of statistical descriptions.[3] Thus, one might speculate that our cognitive strategies for making decisions under risk and uncertainty are more likely tuned to experienced frequencies than to described probabilities. This assertion is also supported by research done in the domain of Bayesian reasoning.

INFERENCES BASED ON NATURAL FREQUENCY VERSUS PROBABILITY REPRESENTATIONS

How should a Pleistocene hunter update his belief regarding the chance of finding prey at a particular location after he has seen some unusual movements in the grass there? Humans have been facing the task of updating beliefs for a long time, and there should have been sufficient selective pressure to produce a mechanism able to perform such inferences. At first glance, however, empirical results have been inconclusive: Whereas research by Gallistel (1990) and Real (1991) suggests that other animals can be adept at such Bayesian inferences (updating of beliefs in light of new evidence), humans often seem to lack this capability: "In his evaluation of evidence, man is apparently not a conservative Bayesian: he is not a Bayesian at all" (Kahneman & Tversky, 1972, p. 450). Are animals really better at making Bayesian inferences than humans?

As in the previous section, the answer lies in the different ways that information can be represented. Animals encounter the statistical information about environmental features on a trial-by-trial basis, that is, by sequentially experiencing cases. Experiments with human participants in which cases are sequentially presented have shown that people are well able to estimate the probability of observing the criterion given the presence of the predictor (Christensen-Szalanski & Beach, 1982).

In contrast, those studies leading to the conclusion that people are *not* able to reason in a proper Bayesian fashion have presented participants with descriptions given in terms of probabilities. For example, Eddy (1982, p. 253) presented 100 physicians with the following information: The probability of breast cancer is 1% for a woman at age 40

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[3] The further questions of how people use *non*scientific language (as opposed to statistics) to communicate subjective likelihoods, via words such as "often," "sometimes," and "rarely," and how these words are understood by the audience, is a large research area in itself; see, for example, Dhami and Wallsten (2005) and Hertwig and Gigerenzer (1999).

who participates in routine screening. If a woman has breast cancer, the probability is 80% that she will have a positive mammography. If a woman does not have breast cancer, the probability is 9.6% that she will also have a positive mammography.

The physicians were then asked to imagine a woman in this age group who had a positive mammography in a routine screening, and to state the probability that she actually has breast cancer. Out of those 100 physicians, 95 judged this probability to be about 75%, whereas the Bayesian solution, which is usually seen as the normatively correct answer, is actually about 8%.

By considering what kinds of representations our minds evolved to deal with, Gigerenzer and Hoffrage (1995) created an effective compromise between sequential acquisition of information and descriptions in terms of probabilities: They presented participants with descriptions in which the probabilities were translated into natural frequencies. Natural frequencies result from natural sampling (Kleiter, 1994) in which cases are randomly drawn from a specified reference class. Eddy's task, with probability information converted into natural frequencies, reads as follows: Out of 10,000 women, 100 have breast cancer. Out of those 100 women with breast cancer, 80 have a positive mammogram. Out of the remaining 9,900 women without breast cancer, 950 nonetheless have a positive mammogram.

Asking for the probability that a woman has breast cancer given a positive mammogram now becomes "How many of those women with a positive mammogram have breast cancer?"—and now the answer is much easier: 80 out of 1,030.

Across 15 tasks like this, when participants were presented with the information as probabilities, they reasoned the Bayesian way only 16% of the time, but when the information was presented as natural frequencies, this percentage rose to 46% (Gigerenzer & Hoffrage, 1995). Similar results were obtained with physicians (Hoffrage & Gigerenzer, 1998), medical students (Hoffrage, Lindsey, Hertwig, & Gigerenzer, 2000), and lawyers (Lindsey, Hertwig, & Gigerenzer, 2003).

Gigerenzer and Hoffrage (1995) proposed two explanations to account for the facilitating effect of natural frequencies: computational simplification and evolutionary preparedness for (natural) frequencies. Further studies (e.g., Brase, 2002) showed that computational simplification alone cannot account for the increased performance of people using natural frequencies. The overall conclusion of this research is that reasoning performance increases substantially when information is presented in terms of the natural frequencies that correspond to the way organisms have acquired information through much of evolutionary history—that is, by naturally sampling (and tallying) events observed in the natural environment.

CONCLUSIONS: THE ADVANTAGES OF LIMITED COGNITIVE SYSTEMS

Cognitive psychologists have long studied the limitations of human thought, and with good reason. Despite Hamlet's exhortation that we humans are "noble in reason . . . infinite in faculty" (Act 2, Scene 2), we struggle to keep more than a half dozen things in mind at once, we quickly forget what we have learned, we ignore much of the available information when making decisions, and we find it difficult to process deeply what information we do consider. But in focusing on the negative implications of these limitations, cognitive psychology may have grabbed the wrong end of the stick. The limited human mind is not just the compromised result of running up against constraints that can little be budged, such as the current birth-canal-limited size of the skull; rather, it is a carefully orchestrated set of systems in which limits can actually be beneficial *enablers* of functions, not merely constraints (Cosmides & Tooby, 1987). A less limited mind might fare worse in dealing with the adaptive problems posed by the structured environment. As Guildenstern later responded to Hamlet, presciently summing up modern psychology's computationally intensive theories of cognition, "There has been much throwing about of brains." In many cases, throwing less brains at a task might do the trick. More is by no means always better (and indeed, recent pharmaceutical attempts to enhance properties of the cognitive system may exact enormous detrimental side effects, including by compromising the beneficial effects of limits—see Hertwig & Hills, in press; Hills & Hertwig, 2011).

Considering the widespread selective pressures and attendant costs and benefits that have acted over the course of evolution on our cognitive mechanisms can help us to uncover these surprising instances when limitations are beneficial (and help us understand the design and functioning of those mechanisms even when their limits are constraining). As we have seen in this chapter, limited information use can lead simple heuristics to make more robust generalizations in new environments. Forgetting in long-term memory can improve the performance of recall, and can protect individuals from harmful reactions at vulnerable periods in their lives. And limited short-term memory can amplify the presence of important correlations in the world. (See Hertwig & Todd, 2003, for more on how cognitive limits can even enable functions that may not be possible otherwise.)

These potential benefits of cognitive limitations compose one of the main themes we believe should be addressed within an evolution-inspired cognitive psychology. We have portrayed the importance of considering how general selective pressures—those arising in multiple task domains—can shape adaptive cognitive mechanisms, in addition to the shaping forces of domain-specific task requirements and environment structure (as covered in other chapters in this handbook). But much of the picture remains to be sketched in. Here are few of the important questions open for further exploration: How does the mind's adaptive toolbox of cognitive mechanisms get filled—that is, what are the processes through which heuristics and other strategies evolve, develop, are learned individually, or are acquired from others (Hertwig et al., 2013)? How do people select particular cognitive strategies in particular situations or environments? What role do noncognitive and social factors—for instance, social emotions such as shame, guilt, and empathy as well as social norms—play in heuristics? What selective pressures have shaped other limited cognitive capacities we have not touched upon, such as attention, categorization, and planning (e.g., Hullinger, Kruschke, & Todd, 2014)? What selective pressures (if any) have shaped how cognitive aging affects our cognitive strategies and processes? How does the use of particular cognitive strategies actually shape the environment itself (e.g., Hutchinson, Fanselow, & Todd, 2012; Todd & Kirby, 2001)? And what methods are most appropriate for studying the action of selective forces on cognitive adaptations?

Taking an evolutionary perspective can help introduce new ideas and hypotheses into cognitive psychology. But the benefits of bringing the cognitive and evolutionary approaches to psychology together do not flow solely from the latter to the former. Cognitive psychology is also a salutary approach for evolutionary psychologists to engage with: It points to the importance of information, hence of the environment that it reflects, and the structure of the environment must be a central aspect of any evolutionary explanation of behavior. The field's experimental methodology is an important component of supporting and revising evolutionarily inspired hypotheses regarding human cognition and action. Finally, cognitive psychology also reminds us of the crucial role that processing information with specific algorithmic mechanisms plays in the generation of adaptive behavior. This step—cognition—is often the "missing link" in nonpsychological approaches to investigating the evolution of behavior (Cosmides & Tooby, 1987), and is still too often missing within evolutionary psychology studies, as in those that merely assert correlations between environmental cues and behavioral outcomes. By cross-fertilizing these two traditions, evolutionary and cognitive, a more vigorous hybrid psychology will arise, espousing the rigorous analysis of the functional aspects of human cognition.

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CHAPTER 38

Evolutionary Developmental Psychology

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Developmental psychology is concerned with changes in behavior, emotions, and cognition over the lifespan of an individual. Our ancient ancestors also developed, and features of infants, children, and adolescents, as well as the course of human ontogeny itself, have been shaped by the forces of natural selection as surely as have features of adulthood (Bjorklund & Ellis, 2014). This evolutionary perspective has been increasingly recognized by developmental psychologists, despite strong criticism of evolutionary-psychological viewpoints by some in the field (e.g., Spencer et al., 2009). For example, special issues devoted to topics in evolutionary-developmental psychology have been published in many journals, including *Developmental Psychology*, *Development and Psychopathology*, *Journal of Experimental Child Psychology*, *Developmental Review*, *Anuario de Psicología*, *Psicothema*, *Infancia y Aprendizaje,* and *Evolutionary Psychology.* Edited volumes and book-length monographs have appeared on the topic, both in the professional literature (e.g., Burgess & MacDonald, 2005; Ellis & Bjorklund, 2005; Tomasello, 2009) and the popular press (e.g., Bjorklund, 2007; Principe, 2011). And most child-development textbooks now include at least a discussion of evolutionary theory, with several including an explicit evolutionary perspective (Bjorklund & Hernández Blasi, 2012; Smith, Cowie, & Blades, 2011).

Although many developmental psychologists seem to have discovered evolution, many mainstream evolutionary psychologists have yet to discover development. Darwin's main thesis was that individuals who were better adapted to local environments were more likely to survive and reproduce and to pass those features associated with "success" to their offspring than less fit individuals. From this perspective, it is understandable that evolutionarily-minded psychologists would focus on adaptations of adulthood where "the real show of humanity" emerges. However, to assume that natural selection plays its trump cards only during adulthood is ignoring the perilous trials and tribulations involved in reaching maturity and the role that natural selection must have played in solving the problems of surviving the early stages of life.

Table 38.1
Some Assumptions of Evolutionary Developmental Psychology

1. All evolutionarily influenced characteristics in the phenotype of adults develop, and this requires examining not only the functioning of these characteristics in adults, but also their *ontogeny*.
2. All evolved characteristics develop via continuous and bidirectional gene-environment interactions that emerge dynamically over time.
3. Infants and children are prepared by natural selection to process some information more readily than others.
4. Development is constrained by genetic, environmental, and cultural factors.
5. Infants and children show a high degree of developmental plasticity and adaptive sensitivity to context.
6. An extended childhood is needed in which to learn the complexities of human social communities.
7. Many aspects of childhood serve as preparations for adulthood and were selected over the course of evolution, termed *deferred adaptations*.
8. Some characteristics of infants and children were selected to serve an adaptive function at specific times in development and *not* as preparations for adulthood, termed *ontogenetic adaptations*.

Source: Adapted from Bjorklund and Pellegrini, 2002; Hernández Blasi and Bjorklund, 2003.

In this chapter, we explore the field of *evolutionary developmental psychology*, the application of the basic principles of evolution to explain contemporary human development. It involves the study of the genetic and environmental mechanisms that underlie the universal development of social and cognitive competencies and the evolved epigenetic (gene-environment interactions) processes that adapt these competencies to local conditions (Bjorklund & Ellis, 2014; Bjorklund & Pellegrini, 2002; Geary & Bjorklund, 2000). We present some of the basic assumptions of evolutionary developmental psychology along with a sample of some of the research findings in this rapidly growing discipline. We argue that "development matters" and that mainstream evolutionary psychology can benefit from adopting a developmental perspective. Table 38.1 presents some of the basic assumptions of evolutionary developmental psychology, many of which are discussed in the remainder of this chapter.

NATURAL SELECTION WILL HAVE ITS GREATEST EFFECTS ON EARLY STAGES OF DEVELOPMENT

From an evolutionary perspective, child development might be described as a bridge joining two shores: conception and reproductive age. Crossing it in terms of survival is a must, not an option. In humans, such a bridge is particularly long, taking about 15 years to traverse (Poirer & Smith, 1974); requires considerable resources in terms of parental and in-group investment (Hrdy, 2009; Trivers, 1972); and is associated (or was for our ancestors) with increased risk of dying before reproducing relative to species with a less-prolonged developmental pathway.

Fetal development, infancy, and childhood are not for the faint of heart. In fact, the challenge to stay alive begins shortly after conception. A fertilized egg has only about a 40% chance of surviving the first 6 weeks of life (Wang et al. 2003), after which its chances of making it to birth improve greatly. Although the probability of dying prior to adolescence in developed countries is less than 1%, that rate is closer to 50% in traditional cultures today and for all human cultures in the not-too-distant past, and was at least as high for our hunter-gatherer ancestors (Volk & Atkinson, 2013). Thus, selection is strong for traits that promote survival in young animals. The mortality bottleneck of infancy and childhood has served to maintain those characteristics that promote survival and reproductive success, and adaptations whose sole purpose is to ensure successful passage through childhood will be retained.

DEVELOPMENT IS CONSTRAINED BY BIOLOGICAL AND ENVIRONMENTAL FACTORS

Animals inherit not only a species-typical genome but also a species-typical (adaptively relevant) environment. As discussed by Tooby and Cosmides (1990), this environment "is not a place or a habitat, or even a time period. Rather, it is a statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and fitness-consequences" (pp. 386–387). These adaptively relevant environments start at conception, with the cellular machinery in the zygote (inherited directly from the mother). They continue prenatally, with mammals, for example, developing in a womb and being nourished through the placenta, and they persist postnatally, including a lactating mother in mammals, intestinal bacteria, and a social structure for many species that may include parental care. In addition, a species-typical environment includes certain characteristics of the physical surroundings, such as light, gravity, and air, among many others.

To the extent that individuals grow up in environments similar to those of their ancestors, development should follow a species-typical pattern. Although most animals (including humans) did not evolve in a single, narrowly defined environment, they have evolved to "expect" certain adaptively relevant experiences. For humans, this would include 9 months in a sheltered womb; a lactating, warm, and affectionate mother (though variation in parental investment is part of the adaptive landscape); kin to provide additional support; peer groups; and so forth.

As an example of the coordination between a species-typical genome and a species-typical environment, consider Turkewitz and Kenny's (1982) proposal that the maturation of the various sensory systems is coordinated with perceptual experience, so that early-developing systems (e.g., audition) do not compete for neurons with later-developing systems (e.g., vision). This is nicely demonstrated in research that altered the perceptual experiences of precocial birds (e.g., ducks, bobwhite quail) while still in the egg, either depriving them of expected sensory stimulation (e.g., preventing ducks from hearing conspecific vocalizations; Gottlieb, 1976) or providing earlier-than-usual perceptual experience (e.g., patterned light while still in the egg; Lickliter, 1990), and assessed its consequences on species-typical behavior after hatching. In general, species-atypical sensory experiences produce species-atypical post-hatching behavior. For example, several days before hatching, Lickliter (1990) removed the shell over the heads of bobwhite quail embryos and presented them with patterned light, something they would not normally experience until after hatching. When subsequently tested for auditory imprinting, the birds exposed to visual stimulation while still in the egg failed to approach the maternal bobwhite quail call and were just as likely to approach the call of a chicken, whereas control bobwhite quail chicks that had the ends of their shells removed but were not exposed to pattern light consistently approached their species maternal call. This and other studies (see Bjorklund, 1997, for a review) demonstrate that when animals receive species-*atypical* patterns of stimulation, the choreographed dance between gene-influenced neural maturation and perceptual experience is interrupted, disrupting the typical course of development.

Due to the highly structured organism-environment relationship during the course of ontogeny, humans are "prepared" by evolution to process some information more readily than others (language and faces, for instance, compared to numerals or written words); they are constrained in how they make sense of their world, with such constraints making it easier to process certain types of information (*enabling constraints*; Gelman & Williams, 1998). Such constraints are the result of selectively structured gene × environment × development interactions that emerge in each generation, are influenced by prenatal as well as postnatal environments, and reflect the inheritance of developmental systems, not just genes. Consistent with this idea is the concept of *evolved probabilistic cognitive mechanisms*. These are:

> information-processing mechanisms that have evolved to solve recurrent problems faced by ancestral populations; however, they are expressed in a probabilistic fashion in each individual in a generation, based on the continuous and bidirectional interaction over time at all levels of organization, from the genetic through the cultural. These mechanisms are universal, in that they will develop in a species-typical manner when an individual experiences a species-typical environment over the course of ontogeny. (Bjorklund, Ellis, & Rosenberg, 2007, p. 22)

Evolved probabilistic cognitive mechanisms are reflected in the phenomenon of *perceptual narrowing*. For example, faces have special processing priority for people, as they should, being perhaps the most socially significant stimulus in one's environment. In fact, adults process upright and inverted faces differently, as reflected by differences in speed of processing and patterns of brain activation. However, they show this pattern only to faces of conspecifics; when shown upright and inverted monkey faces, they process them similarly, reflecting a species-specific bias. A similar bias is found for 9-month-old infants (Pascalis, de Haan, & Nelson, 2002). This bias is not observed, however, in newborns (Di Giorgio, Leo, Pascalis, & Simion, 2012) and 6-month-old infants (e.g., Pascalis et al., 2002), who process upright and inverted faces differently for *both* fellow humans and monkeys. This pattern suggests that cortical processing of human faces becomes more specialized with age and experience. Based on these and related findings, Pascalis et al. proposed "that the ability to perceive faces narrows with development, due in large measure to the cortical specialization that occurs with experience viewing faces. In this view, the sensitivity of the face recognition system to differences in identity among the faces of one's own species will increase with age and with experience in processing those faces" (p. 1321). These findings are consistent with the position that human infants are born with perceptual constraints and that the resulting biases become modified with experience.

ADAPTATIONS OF INFANCY, CHILDHOOD, AND ADOLESCENCE

In order to traverse the bridge between conception and reproductive age, natural selection has shaped a series of adaptations of infants, children, and adolescents, some specific to the early stages of development. In this section, we discuss two broad types of adaptations of infancy, childhood, and adolescence: deferred and ontogenetic. A third type, conditional adaptations, will be discussed separately in the section entitled "Developmental Plasticity and Adaptive Individual Differences."

DEFERRED ADAPTATIONS

Developmental psychologists usually make the implicit assumption that experiences in infancy and childhood serve as preparations for adulthood (e.g., learning the conventions of one's social group). In fact, some aspects of infancy and childhood that play this role may have been selected over the course of evolution, referred to as *deferred adaptations* (Hernández Blasi & Bjorklund, 2003). Such adaptations likely function throughout life, adapting children to the niche of childhood, but also preparing them for the life they will likely lead as adults. This is most apt to occur when ecological or social conditions remain relatively stable over time, as would likely be the case, for example, of children from hunter-gatherer groups interacting with the same set of peers both as juveniles and as adults.

Some sex differences are good candidates for deferred adaptations. Males and females have different self-interests, often focused around mating and parenting. Following parental investment theory (Trivers, 1972), females of most mammals invest more in offspring than do males, and, as a consequence, are more cautious in selecting a mate and consenting to sex than are males. Males, as the less-investing sex, tend to compete more vigorously over access to females than vice versa. As a result, men and women have evolved different psychologies, which develop over the course of childhood. Many experiences during childhood seem to promote and even exaggerate these sex differences (e.g., play styles), serving to prepare boys and girls for the roles they will play (or would have played in the environment of evolutionary adaptedness) as adults.

Sex differences in play serve as good examples. Although there is no type of play that is the exclusive purview of one sex or the other, boys and girls show different patterns and styles of the major types of play, and some theorists have argued that such sex-differentiated play served to prepare children for adult roles in ancient environments (Geary, 2010). For example, rough-and-tumble play (R&T) is observed in most mammals and usually accounts for about 10% of their time and energy budgets (Fagen, 1981). Males engage in R&T more frequently than females in all human cultures and in many mammal species. Some have argued (Geary, 2010; Smith, 1982) that R&T is a classic example of play serving deferred benefits to juvenile males, especially in terms of practice for adult fighting skills, important in traditional environments. Boys' position in a social hierarchy is more often based on physical skills than that of girls' (Hawley, 1999), and the high incidence of R&T among boys may facilitate their ability to encode and decode social signals (Pellegrini & Smith, 1998), which is important at all stages of life.

Sex differences are also found in fantasy play, although less in the frequency in which boys and girls engage in such play, and more in the content of their pretending. For example, beginning around age 6, girls engage in more play parenting than boys (see Geary, 2010). This pattern is seen across cohorts in the United States (Geary, 2010) and in traditional cultures (Eibl-Eibesfeldt, 1989), making it unlikely that it reflects recent Western social norms. From infancy, girls are more socially responsive than boys (e.g., Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992), and social responsivity involves paying attention to family roles and relationships. Such play might have prepared girls to perform the traditional roles that women played over our species' evolutionary history (and continue to play in most cultures today). In contrast, boys' fantasy play is more likely to focus on aggression, power, and dominance and is often part of R&T. When dolls are used in boys' play, they more typically serve the role of combatants rather than nurturers. Thus, the patterns of fantasy play displayed by boys and girls can be viewed as antecedents for the roles (e.g., parenting, male–male competition) they will have as adults, or would have had in ancestral environments (see Pellegrini & Bjorklund, 2004).

As children grow into adolescents, the distinction between the immediate and deferred benefits of adaptations becomes increasingly blurred, as adolescents begin to "try out" adult behaviors. From an evolutionary perspective, a major function of adolescence is to attain reproductive status. Both sexual promiscuity and the intensity of sexual competition peak during adolescence and early adulthood (Weisfeld, 1999), when most people have not yet found a stable partner and the mating market is maximally open. Indeed, an important function of self-organized peer groups in adolescence may be to position oneself in a social context to be sexually active, pulling away from adult supervision and engaging in reinforcing activities with peers (Dishion, Ha, & Véronneau, 2012). To achieve success at the critical adolescent transition, natural selection has favored a coordinated suite of rapid, punctuated changes—puberty—across multiple developmental domains, including new drives and motivations and a wide array of social, behavioral, and affective changes (Table 38.2). These puberty-specific processes function to build reproductive capacity and increase sociocompetitive competencies in boys and girls (Ellis, Del Giudice, et al., 2012).

Table 38.2

Puberty-Specific Morphological and Biobehavioral Changes (Independent of Age)

1. *Sexual development*. Maturation of primary and secondary sexual characteristics. Growth spurt in height and weight. Each stage of pubertal development moves the adolescent toward greater physical reproductive capacity.
2. *Sleep*. Circadian shift in sleep timing preference, with later onset of sleep and morning rise times, occurs in midpuberty. Increased sleepiness, which may indicate increased need for sleep, is linked to more advanced pubertal development.
3. *Appetite and eating*. Total caloric intake increases over the stages of pubertal development, with approximately a 50% increase from prepuberty to late puberty. Sharpest increases occur from pre- to midpuberty in girls and mid- to late puberty in boys, corresponding to the periods of most rapid growth in females and males, respectively.
4. *Sexual motivation*. Each stage of pubertal development increases the probability of being romantically involved (e.g., dating), being sexually active, sexually harassing members of the other sex, and being "in love." Effects generally apply to both boys and girls.
5. *Sensation seeking* (wanting or liking high-sensation, high-arousal experiences). Boys and girls with more advanced pubertal development display higher levels of sensation seeking and greater drug use.
6. *Emotional reactivity*. Boys and girls with more advanced pubertal development (pre- to early vs. mid- to late) display greater reactivity of neurobehavioral systems involved in emotional information processing.
7. *Aggression/delinquency*. Progression through each Tanner stage is associated with increasing levels of aggression and delinquency in both boys and girls.
8. *Social dominance*. During pubertal maturation, higher levels of testosterone are associated with greater social dominance or potency in boys. This relation appears to be strongest in boys who affiliate with nondeviant peers.
9. *Parent–child conflict*. Parent–child conflict/distance increases and parent–child warmth decreases over the course of pubertal maturation. Some research suggests a curvilinear relation, with conflict/distance peaking at midpuberty. Effects generally apply to both boys and girls.
10. *Depression and anxiety*. More advanced pubertal maturation, as well as underlying changes in pubertal hormone levels, are associated with more symptoms of depression and anxiety and greater stress perception in girls.

Source: Adapted from Ellis, Del Giudice, et al., 2012; see supporting citations therein.

Heightened sexual desire increases motivation to pursue, attract, and maintain mating relationships. Increased sensation seeking and emotional responsivity promote novelty seeking and exploration and may increase pursuit of socially mediated rewards. Higher levels of aggression and social dominance both facilitate and reflect the higher-stake competition that is occurring in adolescence over sex, status, and social alliances. Delinquent and risky behaviors (e.g., crime, fighting, reckless driving, drinking games) often signal bravery and toughness and can leverage position in dominance hierarchies, especially for males. Increasing levels of anxiety and depression in girls may reflect heightened sensitivity to negative social evaluations at a critical time for alliance formation.

The peak in these high-risk, high-stakes behaviors during adolescence suggests that this phase of the lifespan had substantial effects on fitness over human evolutionary history and, therefore, underwent strong selection. Ellis, Del Giudice, et al. (2012) have hypothesized that natural selection favored especially strong emotional and behavioral responses to social successes and failures during the adolescent transition, including heightened reactivity to peers. This hypothesis is consistent with fMRI data showing that in adolescents, but not adults, the presence of peers during a simulated driving task amplifies activity in reward-related brain regions, including the ventral striatum and orbitofrontal cortex (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011). This heightened brain activity predicts subsequent risky decision making while driving. In total, there may be an evolved nexus between the adolescent brain's incentive-processing system, peer contexts, and risky behavior. At the same time, however, adolescence is a key period of opportunity to impact developmental trajectories in positive directions. It is a time when youth develop healthy habits, interests, skills, and inclinations and align their motivations and inspirations toward positive goals (Dahl, 2004).

ONTOGENETIC ADAPTATIONS

Not all aspects of childhood serve to prepare individuals for life as an adult. Many features of infancy and childhood serve to adapt individuals to their *current* environment, and not to an anticipated future one. These have been referred to as *ontogenetic adaptations* (Bjorklund, 1997; Oppenheim, 1981) and can be easily recognized in some prenatal mechanisms in mammals and birds. For example, before birth, fetal mammals get their nutrition and oxygen through the placenta, but immediately after birth these systems become obsolete and infants must eat and breathe on their own. These are not immature forms of adult adaptations that become gradually shaped to mature forms, but are structures or mechanisms that have a specific function at a particular time in development and are discarded when they are no longer necessary.

Such adaptations are not limited to the prenatal period, nor to mechanisms associated with physiological functioning, but may also be found in infant and child behavior and cognition. For instance, Bjorklund (1987) proposed that newborns' tendency to imitate facial gestures (e.g., tongue protrusion) may be an ontogenetic adaptation. Meltzoff and Moore (1977) argued that such neonatal imitation reflects "true" imitation and involves the same underlying cognitive mechanisms as does the imitation seen more readily in older infants. Yet, imitation of the most frequently studied gesture of tongue protrusion can be elicited by a looming pen, small ball, or flashing stimuli (Jacobson, 1979; Jones, 1996; Legerstee, 1991), declines to chance levels by 2 months of age (Jacobson, 1979), and is not reliably seen again until about 10 to

12 months. One interpretation of this decline is that neonatal imitation serves a different function than does imitation in older infants. For example, it may be functional in nursing (Jacobson, 1979), serve as a form of prelinguistic communication (Legerstee, 1991), or facilitate mother–infant interaction at a time when infants cannot easily control their head movements and gaze in response to social cues (Bjorklund, 1987; Byrne, 2005). Byrne (2005) proposed that such matching behavior helps the neonate to stay "in tune" with his or her mother, fostering and consolidating the social interaction. Consistent with this hypothesis, Heimann (1989) reported that infants who displayed high levels of imitation as neonates later showed greater levels of social interactions with their mothers at 3 months of age. These findings are consistent with the interpretation that neonatal imitation has a specific function at that time in development only—fostering mother–infant communication and social relations—and when infants are better able to control their own social and communicative behaviors, it disappears. Although it has a similar surface structure to the behavior of older infants, the two sets of behaviors have different functions (fostering infant–mother interaction and social learning) and were presumably selected for these specific functions over evolutionary time.

Other examples of ontogenetic adaptations can be found in the behavior of older children. For example, earlier we proposed that aspects of children's play serve to prepare them for adult roles in traditional cultures. In addition to these preparatory roles, play may also serve more immediate functions. For example, rough-and-tumble play may serve as a way for children to learn and practice social signaling, with exaggerated movements and a play face indicating playful intent (Pellegrini & Smith, 1998). Such play also provides opportunities for vigorous exercise, important in skeletal and muscle development (Pellegrini & Smith, 1998).

Natural selection provided children with sets of adaptations to cross the bridge connecting conception to young adulthood. Some of these adaptations were unique to particular times in development, adapting the young organism to the niche of childhood and disappearing when they were no longer needed. Others served not only to adapt children to current environments but also to prepare them for future ones. Although many of these adaptations served to facilitate children's understanding of the physical world (e.g., folk physics; Geary, 2005; Spelke & Kinzler, 2007), perhaps the most important adaptations, from the perspective of the evolution of *Homo sapiens*, concerned navigating the social world, which we examine briefly in the next section.

HUMANS ARE AN INHERENTLY SOCIAL SPECIES BEGINNING AT BIRTH

There has been no lack of proposals about the pressures most responsible for the evolution of human intelligence. The currently popular *social brain hypothesis* focuses on the complex social environment that humans and our ancestors lived in and proposes that it was the need to deal with conspecifics that, more than any other single force, was the primary selective pressure in the evolution of the modern human mind (Dunbar, 2003). Human social complexity is also associated with a large brain and an extended juvenile period, and it was the confluence of these three factors, we propose, acting synergistically, that produced the human mind (e.g., Bjorklund & Pellegrini, 2002). In fact, several theorists have proposed that humans uniquely evolved (or at least greatly expanded) new developmental stages, specifically childhood (about 2 to

6 years in humans) and adolescence (Bogin, 2001), and that the stage of childhood was necessary for the evolution of advanced forms of social learning (Nielsen, 2012). An extended childhood provides more time for brain development and increased opportunity to learn the social norms and complexities of one's group prior to reproducing. A sophisticated intelligence is required to deal with problems of relating to conspecifics, and the skills needed to traverse the social landscape take a long time to acquire. At the transition to the reproductive phase of the human lifespan, individuals who have better mastered their social world reap the benefits in terms of increased access to resources and mating opportunities.

Human infants and young children have a suite of adaptations devoted to orienting to and processing social stimuli, some of which they share with other animals, and others that seem to be unique to or exceptionally developed in humans, and we examine several of them here.

ORIENTATION TO SOCIAL STIMULI AND VIEWING OTHERS AS INTENTIONAL AGENTS

Human infants' orientation to social stimuli begins at birth. For example, neonates preferentially look at lights depicting biological motion (Bardi, Regolin, & Simion, 2011), selectively attend to face-like stimuli (Mondloch et al., 1999), and look longer at the faces of their mothers than those of other women (Bushnell, Sai, & Mullin, 1989). Young infants are particularly attentive to eyes, especially a direct gaze (Farroni, Csibra, Simion, & Johnson 2002).

Beyond the neonatal period, infants are able to exert greater intentional control of their actions, as neural control is shifted from subcortical to cortical brain areas (Nagy, 2006). Infants are now able to engage in sustained eye contact and social smiling, which is not frequently and unambiguously seen until about 3 months (Reilly, Harrison, & Klima, 1995). These positive social cues are seen universally and were described by the ethologist Eibl-Eibesfeldt (1970) as "flirting." Such behaviors promote repeated social interaction with their caretakers, fostering infant–mother attachment and thus survival. These cues also serve as reinforcements to caregivers, promoting a mother's feeling of competence, which may serve to increase the quantity and quality of maternal care infants receive (see Murray & Trevarthen, 1986).

Despite infants' improved abilities to facilitate social interaction with their caregivers, human social interaction requires, at its most basic, the ability to view other people as *intentional agents*—individuals who *cause* things to happen and whose behavior is designed to achieve some goal (Tomasello, 1999). Although infants are highly attentive to social stimuli from birth, it is not until the latter part of the first year that they seem to appreciate that other people behave in purposive ways. This is seen in *shared attention*, which involves a triadic interaction between the infant, another person, and an object, such as when a parent points to an object for infant's attention (Carpenter, Akhtar, & Tomasello, 1998; Tomasello & Carpenter, 2007). Although parents begin engaging in shared attention early on, infants only begin to hold up their end of the shared interaction beginning around 9 months of age, when they look in the direction adults are looking or pointing, engage in repetitive give-and-take with an adult and an object, and point or hold up objects for another person to see (Carpenter et al., 1998). These abilities continue to improve over the next year (Tomasello, 1999; Tomasello, Carpenter, & Liszkowski, 2007). Although the responsiveness of the caregiver influences infants' shared attention (Deák, Walden, Kaiser, & Lewis, 2008), shared attention is highly canalized and is expressed similarly in diverse cultures (Callaghan et al., 2011).

On the surface, sharing a perceptual experience does not seem to be a great cognitive accomplishment, but it is one that is seemingly not observed in the great apes. For instance, although chimpanzees point to objects in some contexts (Leavens, Hopkins, & Bard, 2005) and will follow the gaze of another in other contexts (Bräuer, Call, & Tomasello, 2005), most researchers concur that there is little evidence of shared attention in great apes (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Russell, Lyn, Schaeffer, & Hopkins, 2011; but see Leavens et al., 2005), with the exception of enculturated apes that have been reared much as human children are (for a review, see Bjorklund, Causey, & Periss, 2010).

Social Learning

The ability to view others as intentional agents plays an important role in learning from one another. Although chimpanzees and the other great apes display impressive social-learning abilities, permitting the transmission of nongenetic information across generations (Whiten et al., 1999), the fidelity with which humans achieve this is unmatched in the animal world and afforded by their social learning abilities, which develop over an extended prereproductive period. In fact, an extended juvenile period is necessary not only for understanding the intricacies of human social relations and organization, but also for mastering the products that result from complex human culture. As new ways of thinking about fellow members of our species evolved, they resulted in new or more effective ways of transmitting information between individuals and generations. These new forms of social learning led to new technologies that no longer needed to be discovered or invented anew by each generation, but could be taught or acquired via observation. As the contents and complexity of culture increased, each generation had more to learn than the previous generation about dealing with their physical and social environments, requiring an extended childhood to master them (Nielsen, 2012).

Although there are many aspects of children's developing social learning abilities, one that has caught the attention of evolutionarily-minded psychologists is *overimitation*—the copying of all components of a model's behavior, even those not relevant to solving the task. Most 2-year-old children, like most chimpanzees, will copy only the relevant actions of a model or will sometimes use means not demonstrated by a model to achieve a goal (termed *emulation*). However, beginning at about 3 years of age, children frequently copy all behaviors of a model, even those that are clearly irrelevant to solving a task (Lyons, Young, & Keil, 2007; Nielsen, 2006). Such overimitation is not limited to Western cultures but has been observed in 2- to 6-year-old Kalahari Bushman children (Nielsen & Tomaselli, 2010) and persists into adulthood (McGuigan, Makinson, & Whiten, 2011), and its prevalence and persistence has resulted in some researchers proposing that it reflects an evolved adaptation (Csibra & Gergely, 2011; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Children seem to believe that the actions of a model are normative, correcting a puppet, for example, that failed to copy irrelevant actions of a model (Kenward, 2012). There is no evidence of overimitation in chimpanzees (see Nielson, 2012).

Overimitation may be especially adaptive for human children, who must learn to use thousands of artifacts. An economical way to learn to use cultural inventions might be to assume that all modeled behaviors related to the artifact are relevant. Although this will result in the acquisition of some irrelevant behaviors, these can be "weeded out" with individual learning.

PROSOCIALITY: HELPING

Humans are not just a social species, but a prosocial one, engaging in behaviors that benefit other group members. Prosociality begins early in life and is as much a part of human-typical behavior as aggression, preference for attractive mates, and endearing feelings toward baby-faced infants. Tomasello (2009) proposed several reasons to believe that prosociality is part of humans' evolved nature, among them that it is mediated by empathy, it is observed relatively early in development, it is not increased by parental rewards, and rudiments of such behavior are seen in humans' closest living relatives, chimpanzees.

One early demonstration of prosocial behavior is helping. For example, in one experiment, 18- and 24-month-old toddlers sat across from an adult who was having difficulty performing a task (Warneken & Tomasello, 2006). For instance, in a "reaching" task, a person accidentally dropped an object on the floor (e.g., a marker) and reached unsuccessfully for it. This was contrasted with a control condition in which the person intentionally threw the marker on the floor. In a "wrong-result" task, a book slipped off as the person attempted to place it on top of the stack, versus a control condition in which the person placed the book beside the stack. The children helped the adult (e.g., retrieved the marker, placed the book on top of the stack) more in the experimental than the control condition on 6 of 10 tasks. In other research, 2-year-olds demonstrated the same sympathetic arousal when they helped a person as when they watched a person being helped by a third party, suggesting that from an early age children have a genuine concern for the welfare of others (Hepach, Vaish, & Tomasello, 2012).

Enculturated (human-reared) chimpanzees also provided "help" in some of these contexts, although only when the adult was reaching unsuccessfully for an object, not for other types of tasks (Warneken & Tomasello, 2006). Evidence of helping using a similar procedure was reported for a group of semi-free-ranging and nonenculturated chimpanzees (Warneken, Hare, Melis, Hanus, & Tomasello, 2007). Thus, although human preschool children generally display greater prosociality than chimpanzees, Warneken et al. (2007, p. 1418) concluded that "the altruistic tendency seen in early human ontogeny did not evolve in humans de novo. The roots of human altruism may go deeper than previously thought, reaching as far back as the last common ancestor of humans and chimpanzees."

DEVELOPMENTAL PLASTICITY AND ADAPTIVE INDIVIDUAL DIFFERENCES

In addition to species-typical developmental adaptations, natural selection maintains individual differences in developmental processes; indeed, theory and research in evolutionary biology have acknowledged that in most species, single "best" strategies for survival and reproduction are unlikely to evolve. Instead, the locally optimal strategy varies as a function of three overarching parameters. First, the expected costs and benefits of different strategies depend on the physical, economic, and social parameters of an organism's environment (e.g., food availability, mortality rates, quality of parental investment, social competition). This context dependency means that a strategy that promotes success in some environments may lead to failure in others. Second, the success and failure of different strategies depends on an organism's relative competitive abilities in the population (e.g., age, body size, health, history of wins and losses in agonistic encounters). Third, an organism's sex often has important implications for the range of available strategies and their relative costs and benefits.

In this section, we discuss how developmental processes increase adaptation by matching an organism's phenotype to local environmental conditions and individual characteristics. We begin by reviewing the general concepts of plasticity and conditional adaptation. We then introduce life history theory and show how it provides a general framework for adaptive plasticity, as well as an integrative understanding of the development of individual differences in physiology, growth, and behavior.

Developmental Plasticity and Conditional Adaptations

Because the viability of different survival and reproductive strategies is so context and condition dependent, natural selection tends to maintain *adaptive developmental plasticity*: biological systems that reliably guide the development of alternative phenotypes (including anatomy, physiology, and behavior) to match an organism's internal condition and external environments (see West-Eberhard, 2003). Importantly, adaptive developmental plasticity is a nonrandom process; it is the outcome of structured interplay between the organism and its environment, shaped by natural selection to increase the capacity and tendency of individuals to track both their internal condition and external environments and adjust the development of their phenotypes accordingly. Developmental plasticity is ubiquitous throughout the animal world (see reviews in DeWitt & Scheiner, 2004; West-Eberhard, 2003).

Developmental plasticity is critically important for enabling organisms to adapt to stress, which has always been part of the human experience. From an evolutionary-developmental perspective, stressful rearing conditions, even if those conditions engender sustained stress responses that must be maintained over time, should not so much impair neurobiological systems as direct or regulate them toward patterns of functioning that are adaptive under stressful conditions (see Ellis et al., 2012; Frankenhuis & de Weerth, 2013).

Developmental plasticity involves durable change, and therefore it is inherently forward-looking; that is, it involves predicting—and preparing—for future experiences. Boyce and Ellis (2005) make this explicit in their definition of *conditional adaptation*: "evolved mechanisms that detect and respond to specific features of childhood environments, features that have proven reliable over evolutionary time in predicting the nature of the social and physical world into which children will mature, and entrain developmental pathways that reliably matched those features during a species' natural selective history" (p. 290). During fetal development and infancy, important features of the environment are communicated to the child via the placenta and lactation in nutrients, metabolites, hormones, growth factors, and immune factors that reflect the mother's current and past experiences (Kuzawa & Quinn, 2009). Beyond these molecular signals from the mother, relevant features of the environment are detected and encoded through the child's ongoing experiences.

TRADE-OFFS IN DEVELOPMENT OF LIFE HISTORY STRATEGIES

A major framework in evolutionary biology for explaining patterns of developmental plasticity and individual differences is *life history theory* (see Kaplan & Gangestad, 2005; Stearns, 1992). All organisms live in a world of limited resources; for example, the energy that can be extracted from the environment in a given amount of time is intrinsically limited. Time itself is a limited good; the time spent by an organism looking for mates cannot be used to search for food or care for extant offspring. Due to these structural and resource limitations, organisms cannot maximize all components of fitness simultaneously and instead are selected to make trade-offs that prioritize resource expenditures, so that greater investment of time and/or resources in one domain occurs at the expense of investment in competing domains.

For example, resources spent on mounting a robust inflammatory response to fight infection cannot be spent on reproductive effort. Thus, the benefits of inflammatory response are traded off against the costs of lower ovarian function in women and reduced musculoskeletal function in men (Clancy et al., 2013; Muehlenbein & Bribiescas, 2005). Trade-offs between reproductive effort and health go in the opposite direction as well, as early reproductive maturation is linked to more physical health problems in adulthood (Allsworth, Weitzen, & Boardman, 2005). Each trade-off constitutes a decision node in allocation of resources, and each decision node influences the next decision node (opening up some options, foreclosing others) in an unending chain over the life course (Ellis, Figueredo, Brumbach, & Schlomer, 2009). This chain of resource-allocation decisions—expressed in the development of a coherent, integrated suite of physiological and behavioral traits—constitutes the individual's life history strategy.

Life history strategies are adaptive solutions to fitness trade-offs within the constraints imposed by social conditions, physical laws, phylogenetic history, and developmental mechanisms. An organism's life history strategy coordinates morphology, physiology, and behavior in a way that maximizes expected fitness in a given environment (Braendle, Heyland, & Flatt, 2011; Réale et al., 2010). At the most basic level, the resources of an organism must be distributed between *somatic effort* and *reproductive effort*. Somatic effort can be further subdivided into growth, survival and body maintenance, and developmental activity (Geary, 2002). Developmental activity includes play, learning, exercise, and other activities that contribute to building and accumulating *embodied capital*—strength, coordination, skills, knowledge, and so forth (Kaplan & Gangestad, 2005). Reproductive effort can be subdivided into *mating effort* (finding and attracting mates, conceiving offspring), *parenting effort* (investing resources in already conceived offspring), and *nepotistic effort* (investing in other relatives, for example, siblings and grandoffspring).

The critical decisions involved in a life history strategy can be summarized by the fundamental trade-offs between current and future reproduction, between quality and quantity of offspring, and between mating and parenting effort (see Ellis et al., 2009; Hill, 1993; Kaplan & Gangestad, 2005). By delaying reproduction, an organism can accumulate resources and/or embodied capital, thus increasing the quality and fitness of future offspring; however, the risk of dying before reproducing increases concomitantly. When reproduction occurs, the choice is between many offspring of lower quality and fewer offspring of higher quality. Although intensive parental investment is a powerful way to increase the embodied capital (and long-term prospects) of one's descendants, the fitness gains accrued through parenting must be weighed against the

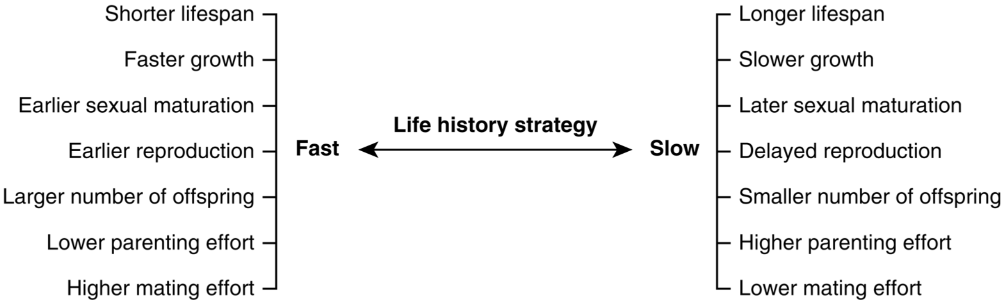

Figure 38.1 The Fast-Slow Continuum of Life History Variation.

corresponding reduction in mating opportunities. Different life history strategies solve these problems in different ways by determining how organisms allocate effort among fitness-relevant traits.

At the broadest level of analysis, life history traits covary along a dimension of *slow* versus *fast* life history strategies. Variation along the slow-fast continuum is observed both among related species and among individuals of the same species (see Ellis et al., 2009; Réale et al., 2010). Slow growth and late reproduction correlate with long lifespan, high parental investment, fewer offspring of higher quality, and low juvenile mortality. Conversely, fast growth and early reproduction correlate with high juvenile mortality, short lifespan, larger numbers of offspring and reduced parental investment in each (Figure 38.1). Fast life history strategies are comparatively high risk, focusing on mating opportunities, reproducing at younger ages, and producing a greater number of offspring with more variable outcomes.

Environmental Determinants of Life History Strategies

Developmental calibration of slow versus fast life history strategies is a prototypical case of developmental plasticity. Key dimensions of the environment that regulate the development of life history strategies include energy availability, extrinsic morbidity-mortality, and predictability of environmental change (Ellis et al., 2009; Kuzawa & Bragg, 2012). Energetic resources—caloric intake, energy expenditures, and related health conditions—set the baseline for many developmental processes. Energy scarcity slows growth and delays sexual maturation and reproduction, resulting in a “slow” life history strategy. However, when bioenergetic resources are adequate to support growth and development, then proximal cues to extrinsic morbidity-mortality and unpredictability generally promote faster life history strategies.

Extrinsic morbidity-mortality refers to external sources of disability and death that are relatively insensitive to the adaptive decisions of the organism. Environmental cues indicating high levels of extrinsic morbidity-mortality cause individuals to develop faster life history strategies. Faster strategies in this context—a context that devalues future reproduction—function to reduce the risk of disability or death prior to reproduction. Moreover, high extrinsic morbidity-mortality means that investing in parental care has quickly diminishing returns, which favors reduced parental investment and offspring quantity over quality. Accordingly, exposure to environmental cues indicating extrinsic morbidity-mortality (i.e., observable cues that reliably covaried with morbidity-mortality risks during evolutionary history) can be expected to shift life history strategies toward current reproduction by anticipating maturation and onset of sexual activity. In humans, these cues may include exposure to violence, harsh child-rearing practices, premature disability and death of other individuals in one's local ecology, and so forth.

In addition to extrinsic morbidity-mortality, environmental unpredictability—stochastic changes in ecological and familial conditions—also regulates development of life history strategies (Ellis et al., 2009). In humans, cues of unpredictability may include erratic neighborhood conditions, frequent residential changes, fluctuating economic conditions, changes in family composition, and so forth. In environments that fluctuate unpredictably, long-term investment in development of a slow life history strategy does not optimize fitness; all of the energy invested in the future is wasted if the individual matures into an environment where life expectancy is short. Instead, individuals should detect signals of environmental unpredictability and respond to them by adopting faster life history strategies.

Belsky, Steinberg, and Draper (1991) were the first to hypothesize that harsh parenting, conflictual family relations, and insecure attachment would predict early sexual maturation, precocious sexuality, unstable couple relationships, impulsivity, reduced cooperation, and exploitative interpersonal styles—the expected correlates of a fast life history strategy in humans. Empirical studies have confirmed these associations (see the special section of *Developmental Psychology*; Ellis & Bjorklund, 2012). Other key psychological mediators of fast life history strategies include present orientation (the inability to delay gratification and/or wait for larger rewards in the future) and a short subjective life expectancy (reviewed in Belsky, 2012; Del Giudice, 2014). At the level of personality traits, slow life history strategies are robustly associated with agreeableness and conscientiousness (Del Giudice, 2014). Taken together, these results strongly support the existence of a fast-slow dimension underlying a broad spectrum of individual differences in humans.

Because extrinsic morbidity-mortality and unpredictability are distinct, developmental exposures to each of these environmental factors should uniquely contribute to variation in life history strategy (Ellis et al., 2009). Longitudinal analyses of the National Longitudinal Study of Adolescent Health, the National Institute of Child Health and Human Development (NICHD) Study of Early Child Care and Youth Development, and the Minnesota Longitudinal Study of Risk and Adaptation (MLSRA) support this prediction (Belsky, Schlomer, & Ellis, 2012; Brumbach, Figueredo, & Ellis, 2009; Simpson, Griskevicius, Kuo, Sung, & Collins, 2012). For example, in the NICHD and MLSRA studies, exposures to environmental unpredictability in the first 5 years of life (e.g., parental changes, residential changes) uniquely predicted faster life history strategies in adolescence and emerging adulthood, independent of the effects of unpredictability in later childhood and indicators of extrinsic morbidity-mortality.

THE CENTRALITY OF THE PHENOTYPE AND DIFFERENTIAL SUSCEPTIBILITY

All developmental processes are ultimately the product of structured organism–environment interplay. Development is always modulated by the organized phenotype, which is initially provided by the parents in the form of a zygote and then changes during ontogeny in response to both genetic and environmental influences.

Consider a central life history trait: timing of sexual maturation. Sexual maturation is regulated by energetic conditions, so that (on average) individuals in well-fed populations experience early puberty and individuals in poorly fed populations experience late puberty (Ellis, 2004). The effects of energetic conditions, however, are modulated by the organized phenotype. For example, food-getting ability (a behavioral phenotype), metabolic efficiency (a physiological phenotype), and energy stores in the form of body fat (a morphological phenotype) all contribute to regulation of puberty; that is, these phenotypic traits modulate the effects of the critical environmental factor (energy availability) on maturation and functioning of the reproductive axis. The same logic applies to genetic effects: Genes provide templates for the production of particular molecules that become incorporated into the phenotype, depending on the responsivity of the phenotype to those molecules and the presence of the necessary environmental building blocks (substances from outside the organism) to support gene expression (West-Eberhard, 2003). The effects of genes, environments, and phenotypes are hierarchically organized: The preexisting phenotype is the transducer of both genetic and environmental sources of information. Specifically, genetic and environmental effects depend on the phenotype being organized to accept them, and the modified phenotype retains these effects as development proceeds. In this sense, the phenotype embodies one's own particular history of genetic and environmental effects.

An important phenotypic characteristic that moderates the effects of environmental conditions on the timing and tempo of puberty is *biological sensitivity to context*, which Boyce and Ellis (2005) defined as neurobiological susceptibility to both cost-inflicting and benefit-conferring features of the environment. Enhanced biological sensitivity to context increases developmental receptivity to the environment, with more neurobiologically susceptible individuals experiencing more developmental change in response to environmental conditions (Ellis, Boyce, Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2011). Boyce and Ellis (2005) operationalized biological sensitivity to context as heightened autonomic or adrenocortical reactivity to environmental challenge (see Obradovic, 2012; Sijtsema et al., 2013, for reviews of empirical evidence and limitations). In a longitudinal study of children from preschool to high school, lower-quality parent–child relationships forecasted faster initial tempo of puberty and earlier pubertal timing, but only among children showing biological sensitivity to context in the form of heightened sympathetic nervous system or adrenocortical reactivity (Ellis, Shirtcliff, Boyce, Deardorff, & Essex, 2011). Thus, consistent with bidirectional models of person-environment interactions, environmental effects on regulation of puberty depended on the extant phenotype being organized to accept them, with heightened stress reactivity increasing the child's susceptibility to familial conditions.

Although we do not have detailed information on gene-environment interactions in human sexual development, there is emerging evidence that genetic effects on puberty are also conditioned by environmental context, and vice versa. The first molecular genetic study to investigate this question focused on variation in the estrogen receptor gene *ESR1* (Manuck, Craig, Flory, Halder, & Ferrell, 2011). Consistent with past research, women who reported being raised in families characterized by distant interpersonal relationships and high levels of conflict tended to reach menarche earlier than women raised in close families with little discord. However, this effect was moderated by *ESR1* variation. Among women who were homozygous for minor alleles of the two *ESR1* polymorphisms examined in the study, a childhood history of low-quality family relationships (−1 *SD*) was associated with a 1-year decrease in age of menarche compared with a childhood history of high-quality family relationships (+1 *SD*); no such effect was found among women with other *ESR1* genotypes. These data demonstrate moderating effects, in which environmental influences on regulation of puberty depend on genotypic variation.

* * *

The organized phenotype incorporates and biologically embeds environmental and genetic inputs throughout the life course. This ongoing process translates into individual differences in such critical traits as body size, energy reserves, metabolic efficiency, susceptibility to environmental influence, immune function, fecundity, mate value, and fighting ability. Differences between individuals in these phenotypic traits influence the cost-benefit trade-offs of different life history strategies and thus play a central role in regulating the development of these strategies. Life history concepts can be used to make remarkably accurate predictions about the structure of individual differences in physiology, growth, and behavior and the environmental factors that shift development along alternative trajectories (Del Giudice & Ellis, in press). In particular, life history theory delineates basic dimensions of environmental stress and support that underlie the multitude of *risk and protective factors* described in mainstream developmental psychopathology—resource availability, morbidity-mortality risk, and unpredictability.

CONCLUDING REMARKS

Development matters, and this should be reflected in how evolutionary psychologists theorize about what is inherited and how. Infants are not born as blank slates; evolution has prepared them to "expect" certain types of environments and to process some information more readily than others. But prepared is not preformed (Bjorklund, 2003). It is the constant and bidirectional interaction between various levels of organization, which changes over the course of development, that produces behavior. Although contemporary evolutionary psychologists clearly state that "environment" interacts with genetic dispositions to produce adaptive behavior, *how* this occurs (i.e., how phenotypes develop) is rarely addressed. This is a major contribution that a developmental perspective can have for evolutionary psychology, along with the realization that natural selection has impacted human thought and behavior not only during adulthood, but also during infancy and childhood. A developmental perspective does not lessen the role of genetics in explaining contemporary human behavior, but rather helps to clarify how genes interact over time with environments, broadly defined, to produce adaptive patterns of thought and behavior, including individual differences. Such a perspective can go a long way, we believe, to bringing evolutionary thought to a wider range of behavioral scientists.

Paraphrasing Dobzhansky, we believe that nothing in *development* makes sense except in the light of evolution. An evolutionary perspective affords a deeper understanding of human ontogeny, as it does all aspects of human functioning. However, an evolutionary perspective by itself is not sufficient to "explain" development, but must be integrated with other causal factors, including also sociohistorical and current contextual influences (from genes through contemporary culture) (Bjorklund & Hernández Blasi, 2012).

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CHAPTER 39

Evolutionary Social Psychology

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SOCIAL PSYCHOLOGY HOLDS a central place in human evolution. Indeed, we are here today because our ancestors were intuitive masters of social psychological principles. The engine driving evolution by natural selection is differential reproduction. As a minimum, reproduction in any sexually reproducing species involves negotiating at least one critical social interaction. But successful reproduction involves much more than sexual intercourse. To reproduce successfully, our ancestors were required to master a diverse array of social tasks: making friends, negotiating status hierarchies, maintaining long-term relationships, and taking care of one's children.

Although the first social psychology textbook adopted an explicitly evolutionary perspective (McDougall, 1908), the perspective was ignored by social psychologists for most of the 20th century (Kenrick, 2011). However, many of the field's leaders have begun incorporating evolutionary perspectives into their research (Kenrick & Cohen, 2012).

Adaptationist reasoning—bolstered by cognitive, behavioral, cross-cultural, and neurophysiological evidence (Bugental, 2000; Buss, 1999; Fiske, 1992; Kenrick, Li, & Butner, 2003; Panksepp, 1982; Plutchik, 1980)—suggests that much of human behavior may be organized around a relatively small set of fundamental motives, each linked to a major adaptive challenge posed by ancestral environments. We organize this chapter around seven key motivational domains of social life—coalition formation, self-protection, disease avoidance, status, mate choice, mate retention, and parental care (Kenrick, Griskevicius, Neuberg, & Schaller, 2010; Kenrick, Neuberg, Griskevicius, Becker, & Schaller, 2010). For each domain, we consider some cognitive and behavioral decision rules that may have evolved to allow people to achieve fundamental motives.

COALITION FORMATION

For most of human history, our ancestors lived in small, highly interdependent groups (Caporael, 1997; Sedikides & Skowronski, 1997). Successful cooperation among group members greatly increased each person's probability of surviving, prospering, and eventually reproducing. This was particularly true during times of need (e.g., food shortages) (Hill & Hurtado, 1996).

PROXIMATE BENEFITS OF ALLIANCE FORMATION

Social psychologists have focused primarily on proximate functions of participating in cooperative alliances. For example, other members of our groups provide us with several valuable types of social support (Reif & Singer, 2000). Emotional support from friends and family is linked to a vast array of positive health outcomes: People with a support network are more resistant to disease, less upset by stressful events, and live longer (e.g., Buunk & Verhoeven, 1991). Second, group members share information, which is especially valuable in uncertain or ambiguous situations (Orive, 1988). Third, group members exchange material goods and resources. Social psychologists have delineated different types of exchange rules (e.g., equity versus communal sharing) that commonly guide patterns of social exchange (e.g., Clark & Chrisman, 1994; Fiske, 1992; Kenrick & Griskevicius, 2013).

Cooperative alliances have costs as well as benefits: It requires time and resources to provide support for others, and raises dangers of being exploited in one-sided exchanges. Alliances also involve direct competition for food, social status, mates, and other resources (Alcock, 2013; Hill & Hurtado, 1996). From an evolutionary perspective, the trade-offs are more favorable to the extent that one forms alliances with others who share one's genes, or who share a history and expected future of reciprocal exchanges.

ALLIANCES WITH KIN

Social psychologists traditionally focused relatively little attention on the differences between interactions among kin versus nonkin (Daly, Salmon, & Wilson, 1997). However, cooperative relationships in traditional societies have most frequently involved individuals who were genetically related. From the perspective of Inclusive Fitness Theory (Hamilton, 1964), it is easy to see why people align themselves with their kin: Benefits shared with a kin member implies indirect genetic benefits to oneself, and costs exacted on the self by kin are also indirect costs to them (Kenrick, Sundie, & Kurzban, 2008). Consistently, research with humans and other species suggests lower thresholds for engaging in various types of cooperative behavior among neighbors who are closely related (Burnstein, Crandall, & Kitayama, 1994; Essock-Vitale & McGuire, 1985; Neyer & Lang, 2003; Segal & Hershberger, 1999). Indeed, people are more likely to cooperate with someone is if his or her morphological features make the person merely appear to be genetically related (DeBruine, 2002; Rushton, 1989).

ALLIANCES WITH NONKIN

Given the importance of investing energy in relationships with kin, why would people form coalitions with nonkin? Theories of reciprocal altruism provide one answer (Axelrod & Hamilton, 1981; Cosmides & Tooby, 1992; Trivers, 1971). According to these theories, our ancestors would have benefited from cooperating with others to the extent that those other people were likely to reciprocate. In this way, each member of a reciprocal exchange relationship reaps benefits over the long term. Indeed, whereas cooperation is less contingent on past history of reciprocation among close kin, sharing between progressively less related individuals becomes more linked to a history of reciprocal sharing (Fiske, 1992; Trivers, 1971).

Because people cannot see into the future, they cooperate with group members based on the *probability* that those group members will someday reciprocate. Hence, it pays to attend to signs that a member of one's group is not a good bet for future reciprocation or is likely to draw more resources from the group than he or she is willing to give back. Indeed, evidence suggests that people are quite vigilant to potential deceit and evidence of cheating (Cosmides & Tooby, 1992; Delton, Cosmides, Robertson, Guemo, & Tooby, 2012; Mealey, Daood, & Krage, 1996). People are generally more likely to trust friends, and women in particular are generally more cooperative toward friends (Ackerman, Kenrick, & Schaller, 2007). Activating concerns about group competition, though, increases men's cooperativeness with members of their groups (van Vugt, de Cremer, & Jannsen, 2008).

Social Exclusion

Given the importance of maintaining strong relationships with kin and nonkin, people are very vigilant to cues signaling that they might be at risk for being excluded from their group. Ostracism, rejection, and other forms of social exclusion can be highly aversive (Williams & Nida, 2011).The pain of social exclusion can produce a range of destructive consequences, including depression and aggressive behavior (Twenge & Campbell, 2003). However, when given the opportunity, people who feel rejected also sometimes try hard to reconnect with others, acting prosocially and turning optimistically toward others as sources of social affiliation (Maner, DeWall, Baumeister, & Schaller, 2007). Such responses are consistent with evolutionary logic. Being part of a group has been essential for survival throughout most of human history, and thus the threat of being excluded heightens people's interest in shoring up their bonds with other people. Consistent with this logic, research with hunter-gatherers suggests that people living under ancestral conditions are especially inclined to form alliances with others who cooperate with them, and to exclude those who do not cooperate (Apicella, Marlowe, Fowler, & Christakis, 2012).

SELF-PROTECTION

Ancestral humans frequently confronted threats from members of other groups (Baer & McEachron, 1982), and through competition over status and material resources, from ingroup members (Daly & Wilson, 1988). Decades of research in social psychology has demonstrated that people often behave aggressively as a means of countering perceived threats (Berkowitz, 1993). People with a defensive attributional style—a tendency to perceive others as threatening—are generally more likely to react aggressively toward others (Dodge, Price, Bachorowski, & Newman, 1990).

Besides increasing aggressive behavior, threats also enhance affiliative motivation in adaptive ways (Mikulincer, Florian, & Hirschberger, 2003; Taylor et al., 2000). For example, thoughts about death lead to increased affiliative tendencies, suggesting that the tendency to affiliate under threat is based in adaptive design: People are safer in groups, and threats lead people to seek the security of a crowd (Wisman & Koole, 2003). Physiological and behavioral evidence suggest that females' primary response to stress is "tend and befriend" rather than "fight or flight." Fighting or running would have increased risks to dependent offspring (Taylor et al., 2000). Propensities to tend and befriend with group members under threat were also adaptive for males (Geary & Flinn, 2002). As we discuss below, different social consequences of threat-induced affiliative motivation, more than other affiliative goals, may lead to the formation of larger groups (Kenrick et al., 2003).

Self-protective goals lead people to selectively process signals of potential physical threat, especially in males and members of outgroups. People are very quick to detect angry expressions, especially on a man's face (Becker, Kenrick, Neuberg, Blackwell, & Smith, 2007). They are also likely to misperceive men, rather than women, as angry when they are not (Neel, Becker, Neuberg, & Kenrick, 2012). Self-protective goals also elicit cognitive vigilance toward outgroup members. For example, self-protective goals can lead people to see anger in the faces of outgroup members, even when those faces are perceived as neutral in other contexts (Maner et al., 2005). Furthermore, ambient darkness (a context ancestrally associated with increased vulnerability to physical harm) increases people's reports of threat-related prejudices against groups who are heuristically associated with physical danger (Schaller, Park, & Mueller, 2003). Such responses may have evolved to protect humans in particularly precarious contexts.

DISEASE AVOIDANCE

Exposure to disease-causing pathogens has been a major cause of illness and death throughout human history (Anderson & May, 1991). Consequently, pressures to avoid disease facilitated the evolution of processes that promote avoidance of sources of contagion (Schaller & Park, 2011). Research in evolutionary social psychology suggests that people possess two interdependent systems that help protect them against disease. In addition to a physiological immune system, which is designed to neutralize pathogens that have entered the body, people also possess a behavioral immune system, a psychological-behavioral system that helps people avoid coming into contact with pathogens in the first place (Neuberg, Kenrick, & Schaller, 2011).

A growing literature suggests that when they are concerned about disease, people become highly vigilant to cues in the environment signaling the possible presence of disease (S. L. Miller & Maner, 2012; Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010). Some cues, such as rashes and lesions, represent actual physical manifestations of illness. However, the behavioral immune system errs on the side of caution and categorizes as disease cues even some characteristics that are not reliably associated with disease (e.g., old age, obesity). Old age, for example, is associated with a weakened immune system, and thus a higher likelihood of carrying diseases, but the relationship is a weak one, and many older people are quite healthy. When people are concerned about disease, however, they attend carefully to such cues and are biased toward seeing them even when they are not reliably connected with disease (e.g., S. L. Miller & Maner, 2011).

In women, the threat of disease becomes particularly pronounced during the luteal phase of the menstrual cycle (which occurs immediately following ovulation) and during pregnancy. During these periods a woman's body downregulates her natural immune response so as to not treat a growing fetus as an intruding pathogen. To compensate for this temporary immune suppression, women display a host of adaptive responses, such as increased disgust sensitivity, avoidance of potentially dangerous foods, and even avoidance of ethnic outgroup members (Navarrete & Fessler, 2006) who could carry foreign pathogens (see Fincher & Thornhill, 2012).

STATUS

Social status is a ubiquitous regulator of social interaction (Barkow, 1989; Eibl-Eibesfeldt, 1989). Even in face-to-face interactions between complete strangers, relative status differences emerge quickly and spontaneously, often on the basis of very limited social information (Fisek & Ofshe, 1970). Around the world, "dominant" versus "submissive" is one of the two primary dimensions with which people categorize members of their groups (G. M. White, 1980; Wiggins & Broughton, 1985). Many people are highly motivated to achieve and hold on to positions of high status over others (Maner & Mead, 2010).

PROXIMATE FUNCTIONS OF STRIVING FOR STATUS

Social psychological perspectives have focused on direct consequences of a person's status. Indeed, possessing high status is associated with a variety of important cognitive and emotional outcomes (Keltner, Gruenfeld, & Anderson, 2003). For example, high-status individuals tend to have relatively high self-esteem (Steele, 1988; Tesser, 1988) and be particularly persuasive and successful at influencing the behavior of others (A. G. Miller, Collins, & Brief, 1995). They tend to be desired as friends (Nakao, 1987) and enjoy a relatively great degree of respect and attention, as well as other social benefits and material resources (Cummins, 1998). And, high-status individuals tend to be happier, pay more attention to potential social rewards than punishments, and engage more in automatic cognitive processing (Keltner et al., 2003).

GENDER DIFFERENCES IN FITNESS PAYOFFS FOR STATUS-STRIVING

From an evolutionary perspective, males gain an additional set of benefits from status-striving. This follows because females, whose high parental investment predisposes more selectivity about mates, are more likely to use male status as a cue for mate selection (Gould & Gould, 1989; Li, Bailey, Kenrick, & Linsenmeier, 2002; Sadalla, Kenrick, & Vershure, 1987). Dominant men are able to offer their mates relatively greater protection and access to resources, both of which were useful in caring for offspring. Consequently, males are, compared with females, more motivated to seek high levels of social dominance (Hill & Hurtado, 1996) and more likely to pay attention to possible loss of status relative to neighbors (Daly & Wilson, 1988; Gutierres, Kenrick, & Partch, 1999).

Eagly and Wood (1999) argued that differences in status-striving may stem from the male social role's emphasis on power and status, versus the female role's relative emphasis on nurturance. These authors believe that these role assignments for men and women differ across societies because of fundamental evolved differences:

Women carry and nurse the offspring, and men are physically larger. Thus, they posit an interaction between evolved mechanisms and the development of cultural norms and are in this way squarely in line with modern evolutionary psychological models of gender role norms (Kenrick, 1987; Kenrick, Trost, & Sundie, 2004; Kenrick & Luce, 2000). However, where they differ from evolutionary models is their claim that evolutionary processes responsible for sex differences ended with the physical differences between men and women. Thus, we believe that Eagly and Wood's biosocial model is too limited and domain general in positing a simple causal link between parental role assignment and various sex differences in social behavior (Kenrick & Li, 2000). It does not, for example, take into account comparative research, including studies suggesting that testosterone is linked to dominance and competitiveness in humans as well as other species (Mazur & Booth, 1998).

MATE CHOICE

Given that differential reproduction is central to natural selection, decisions about mating have significant adaptive consequences. Such decisions can be broadly categorized into two main areas: relationship selection and mate selection.

RELATIONSHIP SELECTION

Individuals in all societies engage in long-term bonding (Daly & Wilson, 1983) and, in many cultures, uncommitted sexual relations (Marshall & Suggs, 1971). Decisions about which type of relationship to enter depend on a person's sociosexual orientation, or tendency to engage in uncommitted sex (Gangestad & Simpson, 2000; Simpson & Gangestad, 1991). Men are more inclined to be sociosexually unrestricted, requiring less commitment, whereas women tend to be restricted, requiring more commitment. Although social psychologists cite differences in social norms for men and women (Eagly & Wood, 1999), evolutionary theorists attribute this difference to differences in minimum obligatory parental investment (Trivers, 1972). Women, like other female mammals, are biologically required to make a much larger investment of time and resources than men if a pregnancy occurs. Thus, the cost-to-benefit ratio of casual sex is higher for women than men, who can invest as little as a teaspoon of seminal fluid. As such, men may have evolved to be more eager than women for casual sex opportunities (Buss & Schmitt, 1993; Kenrick, Groth, Trost, & Sadalla, 1993; Kenrick, Sadalla, Groth, & Trost, 1990; Li & Kenrick, 2006).

However, not all men seek short-term relationships, and not all women seek long-term relationships. There is significant intrasexual variation in sociosexuality, which depends on numerous factors, including one's developmental environment and mate value. For instance, socially dominant (Sadalla et al., 1987) and bilaterally symmetrical men tend to be sexually attractive to women (Thornhill & Gangestad, 1994). Such men start having sex earlier and have more casual sexual partners (Gangestad & Thornhill, 1997; Thornhill & Gangestad, 1994). Women's sociosexuality varies not with their attractiveness but with factors such as their masculinity (Mikach & Bailey, 1999) and father absence (Ellis, 2004), which are both associated with more unrestricted orientations.

A more complete account of sociosexuality should take into consideration how individuals interact with each other (Gangestad & Simpson, 2000). We constructed a dynamical model simulating a network of individuals and found that relatively small sex differences in sociosexual orientation (i.e., decision rule criteria for whether to be restricted or unrestricted) were sufficient to account for observed real-world patterns, where the large majority of people enter long-term relationships, and smaller pockets of people engage in unrestricted relationships. As we discuss later, dynamical models can help psychologists understand how diverse social norms can emerge from small variations in (evolved) decision rules at the individual level (Kenrick et al., 2003).

Long-Term Partner Selection

For marriage partners, women prefer status and resources more than men do, and men prefer physical attractiveness and youth more than women do (Buss, 1989; Kenrick & Keefe, 1992: Sprecher, Sullivan, & Hatfield, 1994). To explain these preferences, social psychologists have invoked sociocultural (Eagly & Wood, 1999) and social exchange models (Hatfield, Utne, & Traupmann, 1979; Homans, 1961). However, a number of features of mate preferences violate simple cultural normative accounts (Kenrick, Gabrielidis, Keefe, & Cornelius, 1996; Kenrick & Gomez-Jacinto, 2014). A more ultimate explanation is that men and women evolved psychological mechanisms to solve different adaptive problems that each sex faced in the ancestral past (Buss, 1989; Symons, 1979). Because female fertility drops off rapidly after 30, men looking for long-term partners may be especially drawn to physical markers of sexual maturity and youth, including full lips, smooth skin (Symons, 1979), and a low waist-to-hip ratio (Singh, 1993). Consistent with this reasoning, teenage boys prefer relatively older females, whereas older men prefer relatively younger females (Kenrick & Keefe, 1992; Kenrick et al., 1996). Male long-term reproductive value, on the other hand, is constrained more by the ability to provide resources (Symons, 1979). Thus, women may be especially attentive to cues relating to a man's status and ability to provide resources (Buss, 1989; Sadalla et al., 1987). Activating mating motives leads men to become more competitive, place higher value on economic gains, and publicly display their creativity and wealth (Griskevicius, Cialdini, & Kenrick, 2006; Griskevicius et al., 2009; Li, Kenrick, Griskevicius, & Neuberg, 2012; Sundie et al., 2011).

Evolved psychological mechanisms for mate selection, however, are more complex than simple preferences for physical attractiveness and status. Because maintaining a long-term relationship and raising offspring are complex tasks, a wide variety of personal qualities are key, including kindness, creativity, energy level, and so on. Nevertheless, in the evolutionary past, infertile females or destitute males, if chosen as partners, would have been reproductive dead ends. To solve this adaptive problem, men may have evolved to prioritize having a moderate level of physical attractiveness (over other traits) in a long-term mate, and women may have evolved to prioritize having a moderate level of social status (Li et al., 2002; Li, Valentine, & Patel, 2011). Once these "necessities" are acquired, then other traits—"luxuries"—are sought after. Indeed, the sex-differentiated prioritization is reflected in people's preferences when considering potential long-term mates (Li et al., 2002) and thinking about themselves as potential long-term mates (Li, 2007). Furthermore, in live-interactive mate-selection contexts, men (more than women) reject partners who are low on physical attractiveness, whereas women (more than men) reject those who are low on social status (Li et al., 2013).

Short-Term Partner Selection

As the intended duration of a relationship decreases, a man's resources become less relevant and the risk of father absence increases. As such, offspring survival, in the ancestral past, became increasingly dependent on a man's genetic quality (Gangestad & Simpson, 2000). Thus, for short-term relationships, women may have evolved to prioritize having moderate physical attractiveness to indicate genetic quality (Li & Kenrick, 2006). For men, women's fertility is even more singular in importance in a short-term context. Thus, men may have evolved to prioritize physical attractiveness even more in short-term mates than long-term mates.

Consistent with this reasoning, numerous studies have found physical attractiveness to be valued more greatly in short-term relationships than long-term ones (Buunk, Dijkstra, Fetchenhauer, & Kenrick, 2002; Regan & Joshi, 2003). Furthermore, both sexes prioritize having physical attractiveness over other traits not only when considering hypothetical potential short-term mates (Li & Kenrick, 2006) but also when encountering and selecting actual ones in live-interactive contexts, where unattractive individuals are shunned by both sexes (Li et al., 2013).

MATE RETENTION

Because human infants are helpless and slow to develop, the continued inputs of both parents are often essential to ensure the offspring's survival (Geary, 1998; Hrdy, 1999). Hence, a key adaptive problem for both sexes is to maintain mating bonds with desirable partners (Buss, 1999; Hazan & Diamond, 2000).

Decisions to maintain or end a relationship involve a dynamic consideration of new information as it becomes available. Relevant information includes the existence of offspring, availability of resources to each parent within and outside the relationship, presence and quality of same-sex interlopers, and the sex ratio of the mating pool (Dijkstra & Buunk, 1998; Guttentag & Secord, 1983; Kenrick & Trost, 1987). Psychological mechanisms may exist to process such inputs and to adaptively weigh the costs and benefits of staying in a relationship. For example, having offspring raises the threshold for leaving a relationship (Essock-Vitale & McGuire, 1985; Rasmussen, 1981). Local availability of desirable alternatives lowers the decision threshold for both sexes (Guttentag & Secord, 1983; Kenrick, Neuberg, Zierk, & Krones, 1994). Also, a partner's breach of fidelity may greatly reduce the benefit-to-cost ratio of staying in the relationship for both sexes (Buss, Larsen, Westen, & Semmelroth, 1992).

PREVENTING A PARTNER FROM STRAYING

People are often highly motivated to guard their long-term partner from same-sex romantic competitors (Buss et al., 1992; Maner, Miller, Rouby, & Galliot, 2009). The threat of intrasexual rivalry evokes strong feelings of jealousy, which is more likely to occur when one perceives one is putting more effort into a relationship than one's partner (G. L. White, 1981) or is singularly dependent on the relationship for happiness (Bringle & Buunk, 1986).

Some evidence suggests sex differences in jealousy such that men are more prone to jealousy when their partner appears to be sexually attracted to others, whereas women are relatively more sensitive to emotional infidelity (Clanton & Smith, 1977). This difference has been attributed to societal norms of men sexually controlling women and women being more attuned to the emotional quality of relationships (G. L. White, 1981).

On the other hand, evolutionary theorists (Buss, 2000; Buss et al., 1992) attribute these differences to factors such as internal gestation and different types of resources contributed to offspring (females contribute bodily resources, males contribute indirect resources such as food and shelter). Because of internal gestation, only females can be certain that offspring carry their genes—males with unfaithful partners risk investing in offspring that are not their own. On the other hand, females confronted with reproductive competitors risk losing all or part of their partners' resources. Thus, jealousy may have evolved to solve each sex's adaptive problem of ensuring their partners' key reproductive resources are not diverted to others (Buss et al., 1992). Though jealous reactions occur in response to actual third-party interference with one's relationship, they also can occur in the absence of infidelity. The traditional view of seemingly unsubstantiated reactions is that they are self-delusional and pathological, but evidence indicates that they often accurately reflect covert infidelity or eventual affairs (Buss, 2000). Thus, jealousy may serve not only to deter ongoing infidelity, but also to preemptively warn of a possible infidelity. Although social psychologists have raised various methodological issues regarding these sex differences, a recent meta-analysis suggests that the sex difference is robust (Sagarin et al., 2012).

KEEPING ONESELF IN THE CURRENT RELATIONSHIP

There may also be mechanisms to prevent oneself from wandering. Such mechanisms might involve having a positive bias toward one's partner and a negative bias against potential mates. For instance, people who are committed to their partners underrate the desirability of alternative mates, especially when the alternatives are made salient (Johnson & Rusbult, 1989). Compared with people who are not in relationships, those currently in relationships tend to consider viable alternatives as less physically and sexually desirable (Maner, Gailliot, & Miller, 2009; Simpson, Gangestad, & Lerma, 1990). Indeed, evidence shows that those who are committed to and well invested in a relationship are much less attentive to potential alternatives than those who are not committed to and invested in a relationship (R. S. Miller, 1997).

The desire to stay in a relationship is probably not purely altruistic, but ultimately was likely to serve our ancestors' reproductive success. First, couples in the ancestral past who did not stay together very long may not have produced any offspring, or at least ones that survived (Geary, 2000). Second, there is more uncertainty associated with new partners than with existing ones. Thus, from an evolutionary perspective, biases account for the time needed to produce and raise offspring and offset risks associated with starting new relationships.

PARENTAL CARE

As noted earlier, parental care has been critical to the survival of human offspring (Geary, 2000; Hrdy, 1999). Yet, motivation to nurture offspring can vary considerably. Evolutionary theorists have posited that decisions about caring for any particular offspring depend on various factors that affect the payoffs for their parental investment (Alexander, 1979; Daly & Wilson, 1980; Hrdy, 1999). In this section, we summarize the underlying evolutionary logic and some research findings associated with the following factors: perceived genetic relatedness to the parent, ability of parental investment to be converted to reproductive success, and opportunity costs.

INVESTING WHERE THERE ARE SHARED GENES

Because a given offspring shares 50% of each parent's genes, and offspring themselves can someday reproduce, evolution has selected for behaviors that promote the survival and reproductive success of one's offspring. However, consider the following: Fathers tend to invest less in their offspring than mothers do. Maternal grandparents tend to invest more than paternal grandparents do (Laham, Gonsalkorale, & von Hippel, 2005). Compared with biological parents, stepparents invest less in their children and are 40 times more likely to abuse and up to several hundred times more likely to kill them (Daly & Wilson, 1988).

From an evolutionary perspective, these differences in investment reflect differences in genetic relatedness: Women are 100% sure which offspring are theirs, but men face a degree of uncertainty. Thus, investments made by a mother and through the maternal line are more likely to be channeled to genetically related individuals than those made by a father and through the paternal line. And, because investing in other men's offspring is unlikely to be selected for, we can expect the behavior of stepparents toward stepchildren not to be on par with that of biological parents towards their own children.

HIGHER RATES OF RETURN

Parents also prefer investing in offspring who are more likely to channel resources into reproductive success (Alexander, 1979). Compared with normally developing children, those with serious congenital disease have a much lesser likelihood of finding a mate and reproducing. Accordingly, many such children who have Down's syndrome or other serious impediments to mainstream life are sent off to institutions and effectively abandoned (Buss, 2000) or are subjected to high rates of abuse at home (Daly & Wilson, 1980).

Parental investment in male offspring may be riskier than investment in female offspring (Daly & Wilson, 1988; Trivers & Willard, 1973). While there is rarely a shortage of males willing to mate with a female, a male typically needs to compete successfully against other males to get mates. Also, whereas females are physically limited to having children at a relatively slow rate across a shorter reproductive lifespan, males are not constrained by internal gestation and menopause. Rather, male reproductive success differs greatly, ranging from those at the bottom of a status hierarchy with no mates to those at the top, who have been known to sire up to several hundred children (e.g., Betzig, 1992; Daly & Wilson, 1988).

Because of this difference in risk and return, it may pay for a family with abundant resources to invest in sons, but for poor families to allocate what they have to daughters (Trivers & Willard, 1973). In support of this reasoning, a study of families in North America (Gaulin & Robbins, 1991) found that low-income mothers were significantly more likely to breastfeed their daughters than their sons, whereas the opposite pattern was true for mothers of affluent families. Low-income mothers also had another child sooner if the first was a son, whereas high-income mothers had another child sooner if the first was a daughter. In a similar vein, other research suggests that wealthier families leave more of their wealth to their sons, whereas poorer families leave proportionally more to their daughters (Smith, Kish, & Crawford, 1987).

Finally, parental investment makes sense when alternative uses of such time and resources are not more lucrative. For example, because men are not physiologically constrained to childbearing and nursing, extrapair mating is a more viable option to them than it is for women. Indeed, among the Aka pygmies of Africa, high-status men have more wives and spend less time on parenting than low-status men do (Hewlett, 1991). People may also be more willing to pull out of any given investment when their investment time horizon is long versus short. Infanticide records show that women are more likely to kill their infants when the women are younger and when they are unwed with no men acknowledging fatherhood (Daly & Wilson, 1988).

Evolutionary theories, most notably Life History Theory (e.g., Ellis, 2004), suggest that an individual's reproductive timing often is adaptively calibrated to help that individual produce the largest possible number of surviving offspring. At any point in time, a person faces a trade-off between investing in current reproduction (faster life history strategy) versus future reproduction (slower life history strategy). Many factors determine how a person navigates this trade-off. One key factor identified by recent research is a person's childhood socioeconomic status (SES; Griskevicius, Delton, Robertson & Tybur, 2011; Simpson, Griskevicius, Kuo, Sung, & Collins, 2012).

When confronted with circumstances that signal threats to their reproductive potential (e.g., mortality cues or signs of economic uncertainty or instability), people high versus low in childhood SES respond in very different ways. Because their childhood environment signaled that payoffs associated with long-term investments are uncertain and unpredictable, people from low SES backgrounds are sensitized at an early age to the possibility of poor long-term reproductive prospects. Consequently, people from low SES backgrounds tend to respond to forms of threat (e.g., economic threat, stress, or uncertainty) by focusing on short-term gains associated with reproducing quickly (Griskevicius et al., 2011). Individuals from wealthier backgrounds, in contrast, are sensitized to the presence of strong long-term reproductive prospects and learn that those prospects are relatively positive and predictable—that they can afford to invest in building somatic resources now so that they can attract a desirable long-term partner and care for offspring more effectively in the future. People from high SES backgrounds, thus, tend to respond to environmental threat by "weathering the storm"—by focusing more on long-term investments likely to enhance the reproductive quality and welfare of their offspring over the lifespan. Thus, the overall pattern emerging from the literature suggests that salient signs of environmental unpredictability or uncertainty lead adults with a low childhood SES background to speed up their reproductive timing, whereas those same signs of unpredictability or uncertainty lead those with a high childhood SES background to slow down their reproductive timing.

DYNAMIC EMERGENCE: FROM DECISION RULES TO CULTURAL NORMS

McDougall's evolution-based *Social Psychology* was actually not the only book with that title published in 1908. In the same year, E. A. Ross (1908) published a text with the same name. But Ross adopted a very different theoretical approach. Ross was a sociologist who saw the wellsprings of social behavior as residing not in the individual but in the social group. He argued that people were carried along on "social currents," such as "the spread of a lynching spirit through a crowd . . . [or] an epidemic of religious emotion" (Ross, 1908, pp. 1–2). Ross looked at the group as a whole rather than at the psyche of the individual group member. He viewed crazes and fads as products of "mob mind . . . that irrational unanimity of interest, feeling, opinion, or deed in a body of communicating individuals, which results from suggestion and imitation" (Ross, 1908, p. 65).

Since 1908, there has been a basic disagreement between sociologically oriented social psychologists who focus on groups as determinants of social behavior and psychologically oriented social psychologists who focus on determinants within the individual. In recent years, advances in theory and research on complex dynamical systems have offered the promise of bridging these formerly discrepant views of the social world (Latané, 1996; Vallacher, Read, & Nowak, 2002). Dynamic models have begun to unravel the formerly mysterious processes by which patterned societal norms emerge from seemingly random interactions between individuals, each acting on the basis of simple and proximately focused decision rules.

We have argued elsewhere that a truly comprehensive model of behavior needs to incorporate insights from evolutionary psychology along with the insights of dynamical systems theory (Kenrick, Li, & Butner, 2003; Kenrick et al., 2002). Consistent with work in evolutionary psychology, the dynamical evolutionary model assumes that human psychological mechanisms can be conceived as a set of conditional decision rules designed to serve fundamental motivations associated with key problem areas confronted by human ancestors. It assumes further, in line with our arguments above, that qualitatively different decision rules are associated with different problem domains, as summarized in Table 39.1. The model further assumes that individuals differ in decision rules as a function of adaptive design and random variation. Men and women, for example, have different rules for choosing mates, and individual men and women may

Table 39.1
Domains of Adaptive Problems Associated With Social Life in Human Groups, Fundamental Goals, and Possible Examples of Evolved Decision Constraints Associated With Each Domain

Domain of Social Behavior	Fundamental Goal	Some Evolved Decision Constraints Associated With This Domain
Coalition Formation	To form and maintain cooperative alliances.	Cooperation is more likely to the extent that others (a) are close relatives or (b) have shared resources in past.
Self-Protection	To protect oneself and alliance members against threats to survival or reproduction.	Male outgroup members are heuristically associated with threat; males are more involved in intra- and intergroup exchanges of threats.
Disease Avoidance	To reduce the chances of contracting communicable illnesses.	People will be cautious about unnecessary interactions with (a) people who manifest overt symptoms (coughing, sores) or (b) people from exotic, faraway places. Females will especially avoid strangers during the first trimester of pregnancy, when teratogenic effects of disease are highest.
Status	To gain or maintain respect from, and power over, other group members.	The cost-benefit ratio of striving for status is more favorable for males because females emphasize male status in choosing mates.

Mate Choice	To obtain a partner or partners who will enhance one's own fitness.	Trade-offs for long vs. short-term relationships differ for men and women and depend on sex ratios; males and females emphasize somewhat different features in long-term mates.
Mate Retention	To maintain a mating bond with a desirable partner.	Males will be inclined to break a bond if a partner is sexually unfaithful or if there are physically attractive alternatives available. Females will be inclined to break a bond if a partner compromises resources or if a high-status alternative is available.
Parental Care	To promote survival and reproduction of individuals carrying one's genes.	More care is invested in others who share one's genes and who have relatively high reproductive value.

differ from the "average" members of their sex as a function of genetic variation, developmental experiences, or local ecological factors (sex ratios, for example).

Consistent with research and theory on dynamical systems, our model assumes that decision mechanisms within given individuals unfold in dynamic interplay with decision mechanisms of others in the social network. As we noted earlier, an individual man's decision rule regarding sexually unrestricted versus restricted behavior interacts with those of other men and women in the vicinity to result in a group-level norm that becomes self-maintaining. The different decision rules operating in each domain lead to different sociospatial social geometries associated with different social goals—hierarchical for status, expansive for self-protection, narrower for cooperation between friends, still narrower for mate choice, and lopsided for parent–child interactions (see Kenrick et al., 2003).

CONCLUSION

These are exciting times for social psychology. The insights of modern evolution-inspired theory and research have opened up connections with other subdisciplines of psychology and with the other social and life sciences (Kenrick, 2011). The insights added by a dynamical perspective have opened up the possibility of integrating the psychology of the selfish individual and the sociology of the collective self. Although we now have a much better road map for progress, most of the empirical findings that will serve as landmarks on the new intellectual terrain are still awaiting discovery.

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CHAPTER 40

The General Factor of Personality: A Hierarchical Life History Model

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IN THIS CHAPTER, we first review the theoretical orientation, content, and conclusions of a previous chapter that our group contributed to the first edition of this *Handbook* (Buss, 2005). The previous version of this chapter contained three major theoretical threads of reasoning that provided form and substance to our review of personality theory from an evolutionary perspective: (1) personality traits are systematically related to fitness-relevant life outcomes, and are thus subject to various selective pressures; (2) the persistence of individual differences in personality in the face of these selective pressures can be attributed to intraspecific character displacement as a consequence of the splitting of individual micro-niches under conditions of sociality; and (3) the evolutionary significance of the fitness-relevant life outcomes in these contexts, and therefore of the corresponding personality traits themselves, can best be understood within the theoretical framework of life history theory.

Anchored in a body of literature that has arisen primarily over the past 10 years or so, we now extend these approaches to consider the evolutionary significance of a newly documented phenomenon, the so-called *General Factor of Personality* (GFP). We review the history of the concept and most of the recent empirical literature on the topic. Finally, we review and evaluate several recent attempts to test a hierarchical model of life history strategy designed to encompass and account for the dynamics of the GFP.

EVOLUTIONARY THEORIES OF PERSONALITY REVISITED

Our chapter in the first edition of this *Handbook* described three classes of theory accounting for the evolution of personality and individual differences in humans. The first, *theories of selective neutrality,* are best exemplified by Tooby and Cosmides (1990), who suggested that humans have an innate and universally evolved psychology, and that individual differences in personality result from essentially random ontogenetic variations in the expression of universals, whereas cultural-group differences result from the specific evocation of human universals given geographic variation in evolutionarily familiar challenges (i.e., variations in parasite-load evoke different levels of collectivism-individualism as an adaptive response). In the environment of evolutionary adaptedness, psychological adaptations are complex and coordinated with one another as part of a larger integrated functional design. Tooby and Cosmides suggest that evidence for the heritability of personality supports this theory, and as such, personality variation is a result of the environment.

The second class, *theories of adaptive significance*, includes theories proposed by Buss (1991) and G. F. Miller (2000b) and extended by others. Buss (1991) proposed that personality is central to social interactions and individual differences in personality; specifically, the Five-Factor Model (FFM) of personality reflects distinct adaptive strategies. G. F. Miller (2000b) extended Buss's theory and suggested that individual differences in personality require both natural selection *and* sexual selection to explain their existence. Weiss, King, and Enns (2002) extended G. F. Miller's (2000b) theory by pointing to research indicating that fitness-enhancing characteristics are correlated with one another, the combination of which they named *covitality*, and suggesting that potential mates use the presence of one fitness-enhancing trait to indicate the presence of others. MacDonald (1998) proposed that individual differences in personality are based on a "continuous distribution of phenotypes that matches a continuous distribution of viable strategies" (p. 142), and assuming relative levels of fitness are equal, these differences allow individuals to occupy a variety of environmental niches.

The third class of theory, *theories of frequency dependence*, includes theories proposed by Wilson (1994) and Figueredo and King (2001). Wilson (1994) proposed that there are two types of individuals: *generalists*, individuals who can moderately adapt to a variety of niches, and *specialists*, those who are adapted to do well in a specific niche. Wilson suggested that individuals evaluate and choose niches based on the presumed adaptive benefit those niches offer and that an individual's fitness depends on (a) the number of individuals simultaneously occupying one's niche and (b) the traits those individuals exhibit. Figueredo and King (2001) proposed that social competition further leads to individual differences in personality, which they explained through four points. First, each of the five dimensions of the FFM has a pole (e.g., high extraversion) that enhances fitness and thus, through directional selection, leads towards an "ideal." Frequency-dependent selection disrupts this process, however, because an overabundance of individuals at the ideal end of the pole creates a niche for individuals at the opposite end on that pole (e.g., low extraversion). Second, frequency-dependent selection pressures vary across personality dimensions depending on the traits expressed by individuals in a particular niche, leading to increased personality variation. Third, interactions between the FFM dimensions within individuals might finally lead to further observed individual differences in personality. Finally, environments with dense social interactions amplify these pressures (see Figueredo, Sefcek, et al., 2005).

ATTEMPTED EMPIRICAL TESTS OF EVOLUTIONARY PERSONALITY THEORIES

Although limited, research regarding personality in nonhuman animals indicates the existence of personality dimensions, similar to the FFM observed in humans, in many species (e.g., Gosling & John, 1999). In addition, some comparative research (e.g., between chimpanzees and humans; King & Figueredo, 1997) indicates similar personality factor structures as well. The extent to which personality traits remain stable across time and situations is debated; much of the research (e.g., Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980a, 1980b), however, suggests personality traits are relatively stable across the lifespan. Finally, the empirical evidence indicates the majority of those species in which personality has been documented are social, supporting the *coral reef model* of intraspecific character displacement based on niche splitting for the disruptive social selection of individual differences in personality proposed first by Figueredo (1995) and further elaborated by Figueredo and King (2001; see also Figueredo, Sefcek, et al., 2005, for a more fully developed treatment of the quantitative-ecological foundations of this theory). This association of personality with sociality was generally supported by the published data then available, with the notable exception of certain species of cephalopods, such as the octopus.

More recently, the researcher who first documented the existence of substantial individual differences among octopus personalities reported new data suggesting that intraspecific trophic specialization occasioned by social competition for resources might cause such systematic variation in individual behavior (Mather et al., 2012). Generalist species (such as *Octopus vulgaris*, *Octopus cyanea*, and *Enteroctopus dofleini*) appear to be composed of specialist individuals, each of whom concentrates upon a limited variety of prey, whereas the population in the aggregate is spread out ecologically over a broad range of prey. Thus, cephalopod behavioral differentiation may also serve the ultimate adaptive function of *competitive release*, and, as such, no longer constitutes the principal exception to this theory.

In humans, the preponderance of empirical results support the inference that personality is related to both (a) actual and completed *survivorship* (i.e., life expectancy) and (b) actual and completed *fecundity* (i.e., expected fertility). For example, regarding the relation of personality to survivorship, various studies have found that individuals higher on conscientiousness are more likely to experience increased longevity (e.g., Friedman, 2000), presumably because these individuals are more likely to engage in health-enhancing behaviors. Moreover, a meta-analysis of the literature (Friedman & Booth-Kewley, 1987) found that depression and anxiety (associated with high neuroticism) as well as anger and hostility (associated with low agreeableness) and many health problems, including coronary heart disease and asthma, are statistically related. Another such example, this time regarding the relation between personality and fecundity, was found by Eaves, Martin, Heath, Hewitt, and Neale (1990), who studied 1,000 postmenopausal women and found that highest reproductive success was associated with either high neuroticism and low extraversion or high extraversion and low neuroticism, and by Hellhammer, Hubert, Phil, Freischem, and Nieschlag (1985), who found that higher levels of self-confidence, extraversion, and social assertiveness correlate negatively with male fertility.

In addition, sexual selection affects the evolution of personality traits. Sexual selection can be divided into intrasexual competition and mate choice. The dearth of evidence regarding relations between personality and intrasexual competition precludes its discussion here, so instead we focus on evidence specific to mate choice.

There are two approaches to the relation between mate choice and personality. The first approach defines preferences as *absolute* and *consensual*, suggesting preferences are similar for all individuals. For example, across nations men and women rate kindness and understanding (possibly associated with agreeableness) and intelligence as the first and second most desired characteristics in a romantic partner, respectively (Buss, 1985, 1989). The second approach views preferences as *relative* to one's own personality, and individuals either *positively assortatively mate*, by selecting a partner who is similar, or *negatively assortatively mate*, by selecting a partner who is dissimilar or complementary to their own personality. Positive assortative mating has been found for a variety of characteristics, both those typically considered desirable, such as affectivity, emotional expression, and personality (Gonzaga, Carter, & Buckwalter, 2010) and those typically considered undesirable, such as Machiavelliansim (Novgorodoff, 1974). In addition, evidence for disassortative mating has been found for mating effort, intentions towards infidelity, and self-monitoring (Olderbak & Figueredo, 2012). In one recent naturalistic observational study (Figueredo et al., in press), statistically significant and generally equivalent positive assortative mating coefficients among social and romantic partners have been documented in four Western cultures on several reproductively relevant traits, including life history (LH) strategy; in a quasi-experimental follow-up (Olderbak, Wolf, & Figueredo, 2014), absolute and relative partner preferences were compared with one another and found each to be simultaneous predictors of perceived relationship satisfaction.

To be consistent with the frequency-dependent selection model of personality traits, the personality phenotype must vary inversely with its relative frequency in the population, such that rarer phenotypes have higher fitness (Tooby & Cosmides, 1990). Indirect evidence of this phenomenon can be found under circumstances where personality variation and reproductively relevant traits are related *and* subject to frequency-dependent selection. To demonstrate frequency-dependent selection, however, requires the explicit consideration of the fitness gains and losses of the behavioral manifestation of personality traits.

PERSONALITY TRAITS AS RESOURCE ALLOCATIONS

LH theory proposes that different traits are desirable depending on the environmental circumstances, with individuals from stable and predictable environments more likely to develop a slow LH strategy, characterized by long-term romantic relationships, few children, and long-term planning, whereas individuals from unstable and unpredictable environments are more likely to develop a fast LH strategy, characterized by many short-term romantic relationships, many children with different partners, and short-term planning (Figueredo, Vásquez, et al., 2006). Multiple studies demonstrate the predicted relation between personality and LH strategy (e.g., Figueredo, Sefcek, et al., 2005), suggesting that the various selective pressures on personality traits might be generated as a consequence of LH evolution. This immediately raises the question of how and why personality traits should be governed by LH strategy.

Personality traits all require the expenditure of bioenergetic and material resources on the part of the individual to behaviorally enact. For example, extraversion is not just a passive “trait” that one possesses or does not possess; extraversion reflects an identifiable pattern of behavior that entails one engaging in elevated levels of social verbal and nonverbal behaviors, highly proactive social interactions, and (at least according to Eysenck, 1976) frequent sexual “philandering.” All of this “extraverted” behavior requires energy to implement. Similarly, agreeableness is not just a passive “trait” that one either has or does not have; agreeableness reflects an equally identifiable pattern of behavior that entails that one engage in elevated levels of verbal and nonverbal socially altruistic behaviors, as well as highly proactive interpersonal engagement and perception for determining the needs and desires of others to optimize the strategic allocation of one's altruistic efforts to maximally "please" and ingratiate oneself with other individuals. All of this "agreeable" behavior requires energy to implement. We can go on, but our point is made.

LH strategy regulates the allocation of the bioenergetic and material resources available to the individual, not only the level of total effort to be expended socially, but also the *specific budget* for allocating relative amounts of social investment across the various competing adaptive domains (as can be taxonomically partitioned by various models of personality structure, such as the FFM). Moreover, the optimality of such resource allocations must, according to evolutionary theory, ultimately serve to maximize fitness. This understanding situates the latent structure of personality solidly within the nomological network of LH strategy, providing a much-needed alternative to the mostly empirically based (rather than theoretically grounded) taxonomies that have been prevalent historically in personality psychology. This understanding also implies that an explicitly *hierarchical* model of both personality in specific and LH strategy in general is required.

THE PRINCIPLE OF BRUNSWIK-SYMMETRY

Recall that both higher-order and lower-order personality factors are *latent hypothetical constructs* (also known as latent *variables* when operationalized) that psychometricians typically operationalize as *multivariate common factors*. Hence, latent constructs are not directly observable; instead, we *infer* their existence from the covariance structure of their observable consequences (called *manifest indicators* or *manifest variables*, because psychometricians reconstruct the presumably underlying latent causes from the measurable effects of these hypothetical latent constructs).

As latent constructs are theoretical entities, the relations among them have historically been matters of great controversy. Personality theorists have even debated their number as well as the optimal levels of data aggregation that should be used to construct them.

One appealing solution to this conundrum is the principle of Brunswik-Symmetry (Brunswik, 1952; Wittmann, 2012), which presumes that at a deep level, all biological structures are hierarchically organized. Given that psychological phenomena must be viewed as a subset of biological phenomena, the hierarchical principle of Brunswik-Symmetry is a necessary component of personality theory. For example, the anatomical and physiological structure of the brain shows unmistakable evidence of hierarchical organization. It should therefore not be surprising if behavioral output that the brain organizes also reflects this inherently hierarchical structure. Mayr (1982) best expressed this general principle:

> In such a hierarchy the members of a lower level, let us say tissues, are combined into new units (organs) that have unitary functions and emergent properties. . . . At each level there are different problems, different questions to be asked, and different theories to be formulated. Each of these levels has given rise to a separate branch of biology; molecules to molecular biology, cells to cytology, tissues to histology, and so forth, up to biogeography and the study of ecosystems. (p. 65)

In fact, the hierarchical principle also extends downwards through even lower levels of organization because nonliving matter also shows similar patterns of aggregation downwards through molecules, to atoms, to subatomic particles, to quarks, to (possibly) strings, to (even more speculatively) quantum-relativistic fields, and who knows what else that is even smaller.

The obvious implication of this reasoning renders moot the question of what is the "true" number of personality factors that underlie the latent structure of the empirical data. The answer depends on the level of data aggregation desired, because the structure resembles that of a Christmas tree to which one can take one's psychometric chainsaw at any of various key points along the major axis. Thus, the "true number of personality factors" construction of the problem becomes a meaningless question and is replaced by what is the *optimal* level of data aggregation for a particular application. This does not mean that the answer to this better-formulated question is an arbitrary or whimsical one, because the principle of Brunswik-Symmetry outlines a pragmatic strategy for specifying precisely which level of data aggregation is optimal for any given problem.

Simply put, both a predictor variable (putative cause) and a criterion variable (putative effect) in any problem are necessarily embedded in a particular level of aggregation for the construct indicated by those measures. The principle of Brunswik-Symmetry involves a mathematical proof that any given level of aggregation will optimize the correlation between predictor and criterion, as long as the level of aggregation of the given criterion matches that of its predictor. Any discrepancy between these levels inevitably reduces the magnitude of the association between predictor and criterion. Therefore, to predict a specific set of behaviors, a lower-order personality construct is optimal; to predict a more general pattern of behavior, a higher-level personality construct is optimal. Thus, the practical application of this metatheoretical principle is actually quite simple.

It is reasonable to ask if higher-order personality constructs might predict outcomes that differ from the lower-order outcomes already reviewed, or at least those outcomes themselves to different degrees. Our next section introduces several new ideas regarding the putative hierarchical structure of personality, the historical origins of the idea, and the dynamics of the theoretical and empirical links among the higher-order and the lower-order constructs, as well as the theoretical and empirical links among the lower-order constructs and each other.

A HIERARCHY OF TRAITS: THE GENERAL FACTOR OF PERSONALITY

The research reviewed above casts most of the results in terms of traditional factor models, such as the FFM, which generally decompose human personality traits into anywhere between three and six common factors. Since the writing of the first edition of this *Handbook*, however, a new body of data has accumulated, delineating a so-called *General Factor of Personality* (GFP), which some have technically defined as the first unrotated principal factor extractable from among a large array of seemingly different personality measures. GFPs have been isolated from more than 25 different personality scales and across different instruments, accounting for roughly 30% of the variance (Rushton & Irwing, 2011). A number of studies have shown that these method-independent GFPs generally correlate among themselves, indicating they are not independent or idiosyncratic with respect to specific personality inventories (Irwing, 2013; Just, 2011).

There is considerable speculation about what the GFP might be. Theories range from the idea that it is an artifact of uncontrolled social desirability bias and self-esteem, or even a statistical artifact (see Irwing, 2013, for a thorough overview of competing theories), to the idea that it corresponds to a continuum characterized by low social functioning and personality disorders at one pole and high social functioning or high social and emotional intelligence at the other (Rushton, Bons, & Hur, 2008). Evolutionary models of personality, such as those based in life history theory, have gone further by integrating the GFP into a broader life history super-factor termed *Super-K*, which encompasses behavioral manifestations of life history strategy and global measures of physical and mental health (this being the aforementioned covitality factor; Figueredo, Vásquez, Brumbach, & Schneider, 2004, 2007; Figueredo, Sefcek, et al., 2005; Weiss et al., 2002). The life history model posits that the high-functioning pole of GFP relates to prosocial or altruistic orientations necessary for optimum fitness under conditions of low extrinsic mortality and morbidity where organisms exist at the carrying capacity of their environment and conspecific densities are high (Figueredo & Rushton, 2009).

Before we recount the relatively brief history of the GFP in modern psychological literature, it is worth noting several of its historical antecedents; these antecedents are potentially informative regarding the reality of the GFP.

THE GFP IN HISTORICAL PERSPECTIVE

Here we summarize four major historical and contemporary ways of thinking about personality (humoral, lexical, psychoanalytical, and archetypal), and in so doing, present evidence for the vestiges of the GFP in the early writings of all of these schools. We close this section with a discussion of the possible implications of this research for thinking about the reality of the GFP construct.

Hippocrates's Humoral Approach

The history of the GFP goes as far back as recorded thinking about temperament and personality itself. The ancient Greek physician Hippocrates (460–370 BC) proposed a "four factor" humoral model of personality based on observation and introspection, which decomposed the temperament domains into four biologically mediated archetypes: angry (choleric—associated with yellow bile), cheerful (sanguine—associated with blood), phlegmatic (stoical—associated with phlegm), and gloomy (melancholic—associated with black bile). Disequilibria among these various humors was seen as the cause of certain temperamental disorders that could be treated only by bringing the humors back into balance with one another (Garrison, 1966).

So-called good temperament was not formally operationalized as a higher-order factor, but as an optimal balance among humoral dispositions. Nevertheless, this conceptualization remarkably presages modern ideas regarding the GFP as a regulator of the public presentation of personality (e.g., Rushton et al., 2008).

Galton's Lexical Approach

The 19th century saw the origins of what could be termed the trait approach to the study of personality and cognitive ability. This approach, inaugurated by Sir Francis

Galton, was predicated upon the idea that variation in personality and intelligence was associated with the existence of individual and group differences in measurable lexical (i.e., natural language) or physiological outcomes. Galton was the first to develop lexical questionnaires to probe variation in what he termed "character":

> I tried to gain an idea of the number of the more conspicuous aspects of the character by counting in an appropriate dictionary the words used to express them. . . . (Galton, 1884, p. 181)

It is interesting to note the sophistication of Galton's conceptualization of character, and also how poorly known and regarded his scientific intuitions are today. In the same work, he goes on to qualitatively describe a hierarchical structure among the various "shades of meaning" among lexicania, culminating with what might well be the first explicit description of a GFP-like higher-order personality factor:

> I examined many pages of its index here and there as samples of the whole, and estimated that it contained fully one thousand words expressive of character, each of which has a separate shade of meaning, *while each shares a large part of its meaning with some of the rest.* (Galton, 1884, p. 181; italics added for emphasis)

Inspired by the work of his half-cousin Charles Darwin, especially in relation to his development of the theory of *modification by descent* (Darwin, 1859/1968), Galton became especially interested in the possibility that national character, far from being a fixed quantity, was in fact variable in response to selection and furthermore played a significant role, along with intelligence and vitality (general health), in determining the fates of civilizations (Galton, 1869).

Although so-called good character was not formally operationalized as a higher-order factor, either, the large proportions of shared "meaning" among the lexical items describing "character" suggest that such a common factor might exist and might be of some interpersonal utility.

FREUD'S PSYCHOANALYTIC APPROACH

Although it is true that the trait-centered or *differential* school of psychology instigated by Galton developed in the late 19th and early 20th centuries—most notably with the advent of the method of *factor analysis* (Spearman, 1904), which permitted the measurement of true trait dimensions—the psychological zeitgeist worked against this tendency. The rise of Freudian psychology saw a retreat from the trait-centered model, with its conceptual emphasis on the idea that personality is a source of behavior, toward the idea that manifestations of personality are instead contingent upon interactions between exposure to specific types of environments and various instincts and "race memories" (acquired characteristics transmitted in a Lamarckian fashion from parent to child; Freud, 1930). The Freudian approach rejected the idea that there is any intrinsic structure to personality beyond certain environmental regularities, although a minority of differential and evolutionary psychologists have sought to link Freud's notions of primal psychic drives (*eros, thanatos, id, ego*) and the suppressive urge (*superego*) with the dimensions contained within more conventional trait-centered models of personality (e.g., Brand, 1994; Nesse, 1990).

It also rejected the idea of personality as a measurable and quantitative source of behavioral variation. To the Freudian, strong manifestations of personality were often regarded as deviant, the products of trauma or failed attempts to sublimate basal desires, and could only be known via a process of ultimately amelioratively guided introspection. Despite this, and following in the consilient footsteps of Freudian-sympathetic differential and evolutionary psychologists, there are some interesting parallelisms between Freud's concept of the superego—or the idea that in suppressing the "baser" urges, especially the id, which encompasses an animalistic and short-term oriented urge towards hedonic-pleasure and destruction (Freud, 1930), while simultaneously enhancing self-esteem and other emotionally satisfying mind-states, the motivation towards better and more socially desirable behavior ensues (Nesse, 1990).

Again, although the Freudian "superego" was not formally operationalized as a higher-order factor, there is a basic resonance between this Freudian aspect of the psyche and the GFP. In some contemporary theories of personality and clinical neuropsychology, this latent faculty functions as a governor or central executive in behavioral expression, regulating impulsivity and permitting socially desirable and effective manifestations of personality (Rushton et al., 2008).

JUNG'S ARCHETYPAL APPROACH

The Jungian school, which was sharply deviant with respect to the differential-psychology tradition, was another major influence on 20th-century personality psychology. Carl Gustav Jung, a one-time acolyte of Freud, proposed a major theory of personality that decomposed the psyche into three distinct domains: the *ego*, the *personal unconscious*, and the *collective unconscious*. The ego was synonymous with the conscious mind, whereas the personal unconscious embodied all memories, and the collective unconscious contained the collective "race memory" of mankind. Jung claimed that we processed the world via the use of archetypes, or sign systems that embodied specific systems of meanings, and proposed a number of major archetypes, the most relevant of which to the current discussion is the *self*, which represents a unification among different elements of the psyche, and the integration of various aspects of personality into an *individuated whole* (Jung, 1964).

Again, although the Jungian "self archetype" was not formally operationalized as a higher-order factor, it is interesting to note how this particular archetype is nonetheless consilient with modern conceptualizations of the GFP as a locus of integration among personality traits, and also as an effortful and conscious regulatory system regimenting the more basic components of personality in socially effective ways (Rushton et al., 2008). These parallels are evident despite the fact that Jungian thought traveled in an entirely separate direction from differential psychology in the 20th century.

THE INTUITIVE APPEAL OR "FACE VALIDITY" OF THE GFP

These historical observations illustrate how the modern GFP was presaged across many previous attempts to define character, temperament, and personality, even when the proponents of those approaches might vehemently disagree with one another about the fundamentals. These theoretical antecedents have bearing on the potential face validity of the GFP, as they imply that the GFP is an intuitive construct, perhaps part of our "implicit personality theory," and one that we have perhaps evolved to innately recognize as a desirable life history trait for the purposes of sexual and social selection (Figueredo, Sefcek, & Jones, 2006).

MODERN DIFFERENTIAL PSYCHOLOGY CONSTRUCTS THE GFP

Within the differential psychology tradition, the lexical approach to the measurement of personality slowly grew in popularity throughout the 20th century, until it reached ascendancy with Costa and McCrae (1992) developing the FFM of personality. The FFM had to compete with alternative ways of measuring personality, such as the physiological-centered three-factor Psychoticism, Extraversion, Neuroticism (PEN) model, which assumes personality dimensions and physiological processes relate fundamentally (e.g., Eysenck & Eysenck, 1976).

In the latter half of the 20th century and the first decade of the 21st, the debates revolved primarily around the "correct" structure of personality, with many proposing models that decomposed personality into different and alternative personality domains (e.g., 16 factors—Cattell, 1946; 7 factors—Cloninger & Gilligan, 1987; and 6 factors—Ashton et al., 2004; Brand, 1994). Debates about higher-order personality factors rarely entertained the idea of a general factor of personality, although Digman (1997) proposed a model that reduced personality to two correlated higher-order factors (DeYoung, Peterson, & Higgins, 2002).

Rushton (1985) was among the earliest modern thinkers to take the idea of a GFP seriously. In his paper, which introduced the idea of life history to the study of individual and group differences, Rushton stated:

> An exciting, if open-ended possibility is that one basic dimension—K—underlies much of the field of personality psychology. (Rushton, 1985, p. 445)

In subsequent work, Rushton explicitly described this common variance among personality domains as the General Factor of Personality, and proposed that it evolved as a source of individual differences in an underlying prosocial personality, permitting individuals to tolerate one another and to behave cooperatively. He and his colleagues explicitly likened the GFP to social and emotion intelligence (Rushton et al., 2008). Rushton also acknowledged Darwin's (1871) writings as inspiration for this insight, crediting Darwin as the first to identify a need for altruistic personality to harmonize individual relations in a way that enhances group-level evolutionary effectiveness (Rushton & Irwing, 2011). More recently, Rushton corroborated another important prediction of a life history-anchored theory of personality, namely that the low-functioning pole of the GFP relates to certain extreme manifestations of personality, which shade into recognized clinical disorders. This includes various personality disorder assessment scales, which seem to share common variance giving rise to a "dark" or low-functioning GFP (Rushton & Irwing, 2009).

Immediately subsequent to Rushton's (1985) published insights, little progress was made towards testing predictions from the GFP until the 1997 Spearman Symposium on Intelligence and Personality, in which Hofstee proposed the existence of a *p*-factor, or general personality factor. He suggested an evolutionary function for this factor much along the lines of that proposed by Rushton—namely, that it embodied a suite of socially desirable traits including competence, emotional steadiness, and reality orientation. Importantly, Hofstee's model encompassed the idea that socially desirable responding is in fact an integral or primordial component of *p*, rather than a social-perception artifact (Hofstee, 2001, 2003).

Perhaps the most substantial empirical and theoretical developments with respect to understanding the nature of the construct occurred in a series of papers stemming from the Ethology and Evolutionary Psychology Laboratory at the University of Arizona. In these papers (Figueredo et al., 2004; Figueredo, Sefcek, et al., 2005; Figueredo, Vásquez, et al., 2007), several important theoretical and empirical advances were made. First, the GFP was successfully isolated from respondent data in the America at Midlife Survey, which comprises a large and representative sample of the midlife population of the United States. In the original paper (Figueredo et al., 2004), this factor was termed the higher-order personality construct (the term *GFP* had not yet been coined). Second, the GFP was shown to be substantially heritable ($h^2 = .50$; Figueredo et al., 2004). Third, two other substantially heritable factors, one encompassing behavioral and attitudinal scales capturing slow life history or high-*K* behavior (termed the *K*-Factor), and a second encompassing physical and mental health (Covitality; Weiss et al., 2002), were extracted from the same data set, where it was found that a higher order *Super-K* factor accounted for the preponderance of the variance among the three subfactors. The Super-K factor is itself substantially heritable ($h^2 = .68$). Subsequent analyses revealed genetic correlations among both the subfactors of Super-K and also the subcomponents of each factor (Figueredo, Vásquez, et al., 2007; Figueredo & Rushton, 2009). These developments should be considered significant because they strongly validate Rushton's (1985) notion of a unitary life history core to personality, which extends well beyond personality into other psychophysical domains as well.

Subsequent to this seminal work was that of Musek (2007), who (apparently unaware of Rushton's, Hofstee's, or Figueredo and colleagues' research) termed the GFP the "Big One." Musek was the first to extract the GFP from three large samples. Musek also identified a hierarchy among personality factors, with the Big Two traits of plasticity (encompassing openness and extraversion in the Big Five) and stability (encompassing conscientiousness, agreeableness, and emotional stability in the Big Five) being subordinate to the GFP and the Big Five subordinate to the Big Two. He also considered the "Big One" to be related to the evolution and genetics of social effectiveness.

Musek's (2007) paper can be rightly considered to have opened the floodgates of research into the GFP. Since its publication, dozens of papers have been published both debating and describing the construct, in addition to exploring the large nomological net of associations with life outcomes (Just, 2011; Rushton & Irwing, 2011). A landmark event occurred in 2011 when the International Society for the Study of Individual Differences devoted an entire symposium to the GFP. Recently, the GFP was even examined in the context of primate personality, where it was found to be almost entirely absent (Weiss, Adams, & Johnson, 2011). This has potentially major ramifications. The existence of a GFP in humans, but not in other anthropoid primates, may stem from the complexity and intensity of sociality—even though primates, compared to most other mammals, live in larger groups, devote more time to social grooming, and form more complex cliques. Hominin and especially modern humans have an even more complex sociality system, with a much larger average functional group size, and use their time devoted to social interactions even more efficiently (Dunbar, 2001; Hill & Dunbar, 2003).

CONTROVERSIES REGARDING THE INTERPRETATION OF THE GFP

Ultimately, few ideas in psychology have proven to be as controversial as the notion that there exists a common source of variance latent in the various diverse measures of personality. As has been mentioned, many have raised objections to its putative psychological function; others have raised objections to its very existence (see Irwing, 2013, and Just, 2011, for an overview of these theories, which we discuss more thoroughly below). Despite this, and perhaps like a moth to a flame, psychometricians, and increasingly evolutionists too, are being drawn towards the study of this parsimonious construct. As we have seen, Just's (2011) broad systematic review indicates a major upswing in interest in this construct after 2007. Major headway has been made in the past decade toward a better understanding of both the behavioral genetic and the evolutionary underpinnings of this construct. Previous reviews of the GFP have not, however, seriously considered the idea that some prominent and even ancient theories of personality presaged aspects of the GFP, incorporating analogous concepts into their own distinct theoretical bodies of work. We contend that the reader should take this as evidence that the GFP exhibits *intuitive* or *face validity*, perhaps congruent with its potential evolutionary role as an indicator of underlying life history strategy aiding in sexual and social selection (Figueredo, Sefcek, & Jones, 2006).

In addition, the most important challenge to the status of the GFP as a valid theoretical construct, as reflecting a personality characteristic that exists independently of observer bias rather than an artifact of measurement, stems from the observation that the personality indicators of the GFP are all oriented in the "socially desirable" direction (Anusic, Schimmack, Pinkus, & Lockwood, 2009; Ashton, Lee, Goldberg, & de Vries, 2009; Bäckström, Bjorklund, & Larsson, 2009), suggesting that the common source of variance might be *method* rather than *trait* variance (Campbell & Fiske, 1959). However methodologically sophisticated, this argument is evolutionarily uninformed.

One fundamental misconception is that self-presentation bias exists only in responding to questionnaire items and does not reflect a real pattern of behavior. Aside from the fact that responding to test items itself constitutes *verbal* behavior, and not some ethereal activity, a growing body of literature supports the observation that socially desirable verbal behavior is highly correlated to socially desirable nonverbal behavior. In fact, a growing number of social psychologists now consider "social desirability" to represent a behavioral *trait* rather than a response *bias* (e.g., Fleming, 2012). This is because the fundamental motivation that drives socially desirable verbal and nonverbal behavior is the same: obtaining what Darwin (1871) called "approval of one's fellows." It is therefore not surprising that these two behavioral manifestations tend to co-occur within the same individuals, and this logic implies that the allegedly biased self-reports of prosocial behavior are, more often than not, reasonably veridical. In contrast, this state of affairs does not hold symmetrically with respect to self-reports of socially undesirable behavior because antisocial individuals avoid revealing their own antisocial acts (for obvious reasons), while not necessarily fabricating false accounts of their own prosocial behavior.

Second is the misconception that what is socially desirable is somehow subjective or idiosyncratic. In fact, there is a high degree of agreement among both individuals and cultural groups regarding what constitutes prosocial behavior, although there might occasionally exist some differences in detail. Third is a direct consequence of the second misconception, and that is that there is no relation between a preference for certain traits and the possession of those traits. As originally proposed by Fisher (1930) for sexual selection, and extended by Nesse (2007) to social selection in general, a population preference for a certain trait inevitably creates selective pressures for the possession of that trait. Furthermore, these selective pressures also automatically produce *genetic correlations* among the preference and the possession of the given socially or sexually desirable trait over evolutionary time. This logical implication further supports the general veridicality of prosocial self-report. We may therefore link all the evidence associating the common factor variance underlying the GFP directly with the original conceptualization of the GFP (Rushton et al., 2008; Figueredo & Rushton, 2009) as a shared dimension of prosocial personality that extends to both the verbal and nonverbal domains of behavior.

Fourth are the increasingly numerous demonstrations that the GFP does not survive what has frequently been referred to as “multitrait-multimethod analysis” (MTMM; e.g., Riemann & Kandler, 2010); although the mathematical methods being applied are the same as those often applied to MTMM data, the different “methods” used in all these cases are comparison of *self*-report to *peer* report. Nevertheless, these are neither completely equivalent nor completely independent “methods” of assessment, because self-report is based on personal experience and introspection (which are themselves fallible) and the corresponding descriptions by “peers” that (almost by definition) are working with incomplete information and detailed knowledge of the person being rated, and have their own distinctive biases that are not due to any *measurement error* but to different *experiential histories*.

The broader understanding of the problem that we are proposing provides direct links to the evolutionary theories of personality that we have considered. In the sections that follow, we therefore seek to reconcile the entire corpus of results and the growing body of evidence for the existence of higher-order factors of personality structure than have been previously considered.

COGNITIVE AND STRATEGIC DIFFERENTIATION-INTEGRATION THEORY

A more recent empirical development in the application of life history theory to understanding personality concerns the idea that in addition to higher levels of the GFP, conative integration is associated with faster life history (low *K*-selected) populations and is adaptive given unstable and unpredictable environmental contexts where the ability to contingently switch among transient social-ecological niches leads to increased fitness (Figueredo, Woodley, Brown, & Ross, 2013). In contrast, slower life history (high-*K*) populations exhibit more highly differentiated GFPs, which account for the generally lower correlations among lower-order personality factors in slower life history strategists than appear among the less differentiated GFPs characteristic of faster life history (high-*r*) populations, which account for the generally higher correlations among lower-order personality factors in slower life history strategists. This is termed the *Strategic Differentiation-Integration Effort* (SD-IE) theory, and it is based on the idea that conative (social cognitive and psychosocial behavioral) differentiation permits more efficient niche splitting where conspecific densities and interindividual competition are high, and where there is more variation between individuals in terms of personality specialization.

The observation of these systematic individual differences in either the integration or the differentiation of the GFP, presumably in response to the adaptive demands of the environment, opened up a whole new way for us to view the evolved structure of personality as controlled by mechanisms that are exquisitely shaped by selective pressures for either the articulation or the coordination of life history resource allocations in general, as required by the contingencies of survival and reinforcement across the multifaceted adaptive landscape of more specific contexts and domains.

To test this theory empirically, as applied to the evolution and development of individual differences in personality, one needs to demonstrate that the contingent differentiation and integration of personality constructs (and of life history traits in general) is also *systematic*, *predictable*, and adaptively *strategic*, as specified by the relevant evolutionary theory, and by means of the specific mechanisms that we have proposed. We now turn our attention to the growing number of critical tests of this theory that have been done in the elucidation of the *strategically contingent nature* of the differentiation and integration of cognitive and conative individual difference factors in differential evolutionary psychology.

EMPIRICAL TESTS OF SD-IE THEORY

The realization that those individual lineages exhibiting slow life histories must be capable of cognitive and conative differentiation in response to heightened environmental stability sparked a new development in the area of life history research (Woodley, 2011). This is because slower life-history populations rapidly grow to the limits of their environmental carrying capacity, which produces greatly increased interindividual competition. Thus, cognitive and conative differentiation encourages *prosocial competition*, which is competition over narrow sociocultural microniches. Prosocial competition, in its turn, encourages intraspecific *character displacement*, giving each individual a *comparative advantage.* A comparative advantage then raises the environmental carrying capacity by increasing the aggregate efficiency of the diversified population of high-*K* specialists (as originally predicted by the *coral reef model* of personality evolution and development proposed in Figueredo, Sefcek, et al., 2005). In contrast, those with faster life histories are cognitive and conative generalists. Being a generalist advantages individuals coping with unstable environments because they can *contingently switch* between a variety of different sociocultural microniches, and thus they invest little in any single microniche at any given time, but over time can come to occupy many in response to spatiotemporal heterogeneity.

The theory was originally developed to resolve an anomaly in the individual-differences literature—namely, why it is that the speed of life history correlates positively with general intelligence when population-level aggregates are considered (Rushton, 2004), but not at all when the dimensions are considered at the individual-differences level (Woodley, 2011). This anomaly has been termed "Rushton's Paradox" (Meisenberg & Woodley, 2013). One possible solution involved the idea that even though there is no individual-level main effect of *K* on *g* (the general intelligence factor), *K* might nonetheless control the amount of effort that goes into reinforcing the positive manifold of *g* during development, such that those with high *K* tend to exhibit a more specialized ability profile and weaker *g* than those with low *K*. In this model, the *level* of *g* functions as a fitness indicator, as per G. F. Miller's (2000a) Fitness Indicators Theory and is thus genetically uncorrelated with *K*.

This *Cognitive Differentiation-Integration Effort* (CD-IE) hypothesis was tested using the *Continuous Parameter Estimation Method* (CPEM; Gorsuch, 2005), which permits individual differences in the level of trait covariance to be measured via the use of the individual-level cross-products between the common factor and component scores (Woodley, Figueredo, Brown, & Ross, 2013). CD-IE effects were tested using four individual-level samples (two student samples and two nationally representative ones) totaling 12,374 individuals. Statistically significant CD-IE effects were detected in all four samples, in the expected negative direction, indicating that the covariance among convergent indicators weakens as a function of increasing levels of the latent common factor (*K*). The *Strategic Differentiation-Integration Effort* (SD-IE) hypothesis derived from research into the CD-IE phenomenon (Woodley et al., 2013). As was mentioned previously in the section reviewing the history of the GFP, SD-IE tradeoffs occur among the conative and behavioral fitness domains of life history itself, with slower life history individuals exhibiting more specialized profiles of behavior and personality and faster life history ones showing the opposite tendency.

Bronfenbrenner's (1979) *ecological systems theory* defined a series of concentric circles defining the social influences surrounding any developing individual, using Greek praefices to describe the relative ranks of each concentric circle, characterizing their relative inclusiveness within this hierarchically nested system: *microsystem*, *mesosystem*, *exosystem*, and *macrosystem*. This basic framework has been applied within evolutionary psychology (Figueredo, Brumbach, et al., 2007) for understanding the various pressures of social selection that these systems generate by (a) adapting the theoretical framework to conform to more evolutionarily informed levels of social organization and (b) generalizing the principle from applying exclusively to phenomena occurring over developmental time to encompass phenomena occurring over evolutionary time. Consistent with this evolutionary application of ecological systems theory, wherein similar but nonidentical selective pressures (including developmental influences) exist across the hierarchically nested levels of social organization, the predictions of SD-IE theory have been subjected to empirical tests across a wide array of different levels of organization. The results of these various empirical tests of the theory, including the original CD-IE results described above, are summarized in Table 40.1.

As with CD-IE effects, *individual-level* tests of the predicted SD-IE effects were conducted using two student samples and two nationally representative samples totaling $n = 7{,}749$. The effect sizes across all samples were statistically significant, substantial in magnitude, and in the expected negative direction, thus confirming the presence of SD-IE. SD-IE effects were found for both the convergent indicators of lower-order and the higher-order latent common factor of life history strategy, where the magnitudes of the effects were appreciably larger in absolute value for the higher-order factor. It was predicted that the positive manifold of life history traits should be the locus of SD-IE effects, because the phenomenon involves a fundamental reconfiguration of the ways in which individuals allocate effort into specific life history domains. A final note on these two large individual-differences-level studies is that the effects are *not* confounded with sex differences, this having been measured via the construction of a dimorphic sex indicator, which was used as a moderator in regression analysis. Thus, CD-IE and SD-IE constitute *sex-universal* sources of individual differences.

More recently, the heritability of the SD-IE effect on the components of Super-K has been estimated using twin data from the U.S. MIDUS (316 monozygotic and 274 dizygotic twin dyads) and the Swedish STAGE (863 monozygotic and 475 dizygotic

Table 40.1

CD-IE and SD-IE Effects at Increasing Hierarchically Nested Levels of Social Organization

Scale	Effect Type	Average Effect Size (β)	Sample Size (*N*)	Reference
Individual Level	CD-IE[1]	−.10	12,374 individuals	Woodley, Figueredo, Brown, and Ross (2013)
	SD-IE (Super-K, Sweden)	−.36	1,726 twin-singletons	Woodley of Menie, Figueredo, Cabeza de Baca, Fernandes, Madison, and Black (2015)
	SD-IE (Super-K, United States)	−.32	7,749 individuals	Figueredo, Woodley, Brown, and Ross (2013)
	SD-IE (K-Factor, United States)	−.31		
	SD-IE (GFP, United States)	−.25		
	SD-IE (Covitality, United States)	−.38		
	Sociosexual SD-IE (Brazil)	−.25	448 individuals	Fernandes, Woodley, Kruger, and Hutz (2014)
	Sociosexual SD-IE (United States)	−.29	318 individuals	
	Sociosexual SD-IE (Multinational)	−.37	112 individuals	
Regional Level	CD-IE (Italy)	−.43	18 counties	Armstrong, Fernandes, and Woodley (2014)
	CD-IE (Spain)	−.78	18 provinces	
	SD-IE (Italy)	−.49	18 counties	
	SD-IE (Spain)	−.56	18 provinces	
	SD-IE (Japan)	−.22	47 prefectures	Woodley, Fernandes, and Madison (2014)
	SD-IE (United States)	−.44	50 states	Fernandes and Woodley (2013)
National Level	CD-IE	−.23	76 countries	Woodley and Fernandes (2014)
	SD-IE	−.43		
Continental Level	CD-IE[1]	−.17	107 observations	Woodley, Figueredo, Brown, and Ross (2013)
Species Level (Primates)	SD-IE	−.32	120 species	Fernandes, Figueredo, and Woodley (2014)

[1] CD-IE effects were obtained either in the absence of a *g*/*K* correlation, or where a preexisting correlation had been eliminated.

twin dyads) cohorts. It was found that the heritabilities of the SD-IE effects ranged from .3 to .64 in the U.S. sample, and from .55 to .61 in the case of the Swedish sample. The specific h^2 of the SD-IE effect on the GFP was .3 in the U.S. and .61 in the Swedish sample (Woodley of Menie et al., 2015).

Cross-culturally, individual-level SD-IE effects have also been detected among sexual strategy indicators in Brazilian ($n = 448$), American ($n = 318$), and multinational ($n = 112$) samples (Fernandes, Woodley, Kruger, & Hutz, 2014). Scores on sociosexual behavior, attachment anxiety and avoidance, factors of postcoital emotions, and mate value appear to be more integrated among themselves in those with faster life histories. A considerably higher range of strategic differentiation and integration was found in the multinational sample compared to the nation-specific samples, which might partly be due to the higher population stratification in this sample, as it was composed of individuals originating from various continents and ethnic-genetic clusters that have been demonstrated to vary in their aggregates of both life history speed (Rushton, 2000) and strategic integration and differentiation (Woodley & Fernandes, 2014).

At the level of entire populations, a potentially significant theoretical innovation in Woodley and Fernandes (2014) is the idea of *group-level character displacement*. It was argued that the ecological regimes favoring individual-level character displacement also favor this process at the group level; specifically, the presence of both group-level and individual-level competition offers opportunities for *multilevel selection* among aggregately specialized groups.

To test this more extended theory, the phenomenon of *group-level SD-IE* has been replicated using *regional-level* aggregate data in several other national samples. In Fernandes and Woodley (2013), U.S. state-level data on five life history variables were used to construct a *Super-K Factor*. Across the states of the United States, statistically significant SD-IE effects were detected that were substantial in magnitude and in the expected negative direction. Another test of group-level SD-IE has been conducted using aggregate-level data on eight life history salient indicators collected among the 47 prefectures of Japan (Woodley, Fernandes, et al., 2014). This analysis revealed a significantly trifurcated factor structure among these indicators, suggesting considerable levels of underlying differentiation consistent with the observation that Japan has one of the slowest aggregate life history speeds of any country (Woodley & Fernandes, 2014). Attempts to quantify SD-IE therefore focused on the five indicators, which loaded on the first principal axis factor because these were considered to constitute the "primary *K* factor." Across the 47 prefectures of Japan, statistically significant SD-IE effects were detected that were substantial in magnitude and in the expected negative direction.

Armstrong, Fernandes, and Woodley (2014) conducted the most recent test of group-level SD-IE using regional-level data for both Spain and Italy. In this analysis, six aggregate life history indicators were collected for 18 Spanish counties and 10 such indicators were collected for 18 Italian provinces. In addition to these, data on five different cognitive ability indicators were collected for the Italian sample and data on four were collected for the Spanish sample. Across the 18 Spanish counties and the 18 Italian provinces, both CD-IE and SD-IE effects were detected that were substantial in magnitude and in the expected negative direction.

At an even higher level of population structure, Woodley and Fernandes (2014) found SD-IE effects on 10 aggregate *national-level* life history measures comprising a *K* Super-Factor (Templer, 2008), using a sample of 76 Old-World countries. At the even higher *continental-level* of genetic population clusters, another recently published analysis of group-level SD-IE (Dunkel, Cabeza de Baca, Woodley, & Fernandes, 2014) used data from populations in the United States dating back to the 1960s taken from Project Talent. These data were split into three major groups based upon geographical region of ancestral origin: Africa (n = 6,533), Europe (n = 147,355), and Asia. A GFP was constructed using the 10 personality subscales of a student activities inventory and data on general intelligence were obtained from a 16-subtest cognitive ability measure.

Although molecular genetic research has shown that continental-level population clusters account for only about 10% of the variance in global-level human genetic biodiversity as measured by the relative frequencies of individual alleles (as opposed to those of latent clusters of alleles or of entire haplotypes), these three continental-level population clusters have been shown to have statistically significant differences in averaged life history speed (e.g., Rushton, 1985). Thus, in spite of the preponderance of interindividual variance within each of them (e.g., Figueredo, Vásquez, Brumbach, & Schneider, 2004, 2007), the large amount of extant data on these continental-level classifications makes it possible to use the groupings as convenient *proxies* for aggregate mean differences in life history, because when aggregated across literally hundreds of millions of individuals, these average differences inevitably achieve any desired level of statistical significance. The relative rankings of these continental population clusters, by average differences in life history speed, are ordered as follows, from faster to slower: Africa>Europe>Asia (Rushton, 2000). Based on both CD-IE and SD-IE theories, it was therefore hypothesized that the within-group correlation between the GFP and g would vary in strength based on the aggregate life history speed of the three groups, and the results were found to be consistent with these predictions.

Finally, at the higher taxonomic level of the primate order, it appears that SD-IE theory applies beyond human individual and group-level differences; SD-IE effects have been detected among a large number of primate species with six life history traits (Fernandes, Figueredo, & Woodley, 2014). A statistically significant and negative SD-IE effect was detected across 120 primate species, after controlling for any effects of phylogeny (as distinct from effects of adaptation; see Tinbergen, 1963), such as phylogenetic inertia (higher similarity among closely related clades than among distantly related ones; Felsenstein, 1985) and faster evolutionary rates in faster life history species due to differences in generation time and in DNA repair mechanisms (e.g., Bromham, 2009). Importantly, species endocranial volume also positively predicted life history differentiation ($\beta = -.25$); however, K fully mediated the effect. Sociality, in turn, did not have a direct SD-IE effect that was statistically significant, but instead had an indirect effect on life history differentiation through its significant direct effect on endocranial volume (Dunbar, 2010; Fernandes, Woodley, et al., 2014).

Although it might be a seeming contradiction that a weaker GFP should be found both in nonhuman primates and in slower LH humans, the presence of a weaker GFP in slow LH humans is in no way equivalent to the complete absence of a GFP in the subset of other primates that have been assessed for it (mainly other apes and not monkeys). In one case, we contend that the GFP has not even evolved, or at least not sufficiently to be detectable. This is the case of species like gorillas and chimpanzees. In the other case, we contend that not only does the GFP exist as a mental structure, but a mechanism has evolved for adaptively integrating or differentiating its components in response to environmental contingencies. This other case is that of humans, seemingly exclusively (to our present knowledge), and represents a much more sophisticated set of psychological mechanisms that the mere absence or presence of the structure, involving not only the possession of a developmental program for constructing a GFP, but also a controlling epigenetic mechanism with developmental switches in place for accomplishing that function. Interestingly enough, the recent work documenting SD-IE in nonhuman primates strongly suggests that this latter mechanism evolved for differentiating LH traits prior to the emergence of the GFP. This implies that SD-IE effects upon the GFP arose when personality became more fully integrated into LH strategies in our own hominan lineage.

THEORETICAL INTERPRETATIONS OF EMPIRICAL TESTS OF SD-IE

We claim this accumulating corpus of evidence demonstrates that differentiation and integration of personality constructs, and of life history traits in general, is *strategically contingent* upon the overall *speed* of life history (the fast-slow or "*r-K*" continuum), and therefore, ultimately, upon the well-documented ecological conditions known to govern its selection over evolutionary and developmental time—an effect that occurs across a wide array of species of nonhuman animals and plants (for a more comprehensive review, see Ellis, Figueredo, Brumbach, & Schlomer, 2009). The main selective pressures shaping the speed of life history are the relative degrees of environmental *stability* and the organism's ability to *predict* and *control* it as afforded by that environment. The controllability aspect is particularly essential, although the other two dimensions are logical prerequisites for it, because high levels of *extrinsic* morbidity and mortality preserve *faster (r)* life histories—that is, high levels of hazards of disease and death that cannot be controlled by any evolvable physiological or psychological mechanism select against slow life history strategies. The opposite, called *intrinsic* morbidity and mortality, are parameters that *can* be brought under at least partial control by biologically evolvable mechanisms, and high levels of this instead selectively favor *slower (K)* life history strategies.

The explicit conditions for theory falsification that we offered above involved demonstrations that the contingent differentiation and integration of personality constructs (and of life history traits in general) are *systematic*, *predictable*, and adaptively *strategic*, as specified by the relevant evolutionary theory. We identified evolutionary life history theory as the relevant interpretive framework, based on our previous psychometric work examining the hierarchical latent structure of life history traits, encompassing both higher-order and lower-order personality constructs. Thus, we assert that we have met at least some of the critical testing conditions and that our integrative theory survived multiple repeated and nontrivially severe attempts at falsification.

Of course, all that philosophy of science will support in such a case is the claim that we have "supported," not "proven," our integrative theory. There are other conditions that future research needs to meet to help develop this conceptualization of the problem. It is to various proposals for these additional tests that we now turn.

We propose that to become more conclusive, future research in personality needs to apply what can be referred to as *vertical integration*, which involves integrating knowledge relevant to personality theory from those disciplines considered to be fundamental to psychology, specifically physiology, anatomy, and genetics, and those to which psychology is a fundamental discipline, specifically, evolutionary biology, evolutionary anthropology, ecology, and ethology. In addition, research should use multiple methods, ranging from controlled experiments to naturalistic observation, in what is referred to as *horizontal integration* (e.g., Jacobs, 1994; Jones, Wenner, & Jacobs, 2005). This is particularly important because personality research is based on methods, each of which has specific inherent flaws, such as observer drift and reactivity associated with observation (Jacobs et al., 1988; Klahr & Simon, 1999; Repp, Nieminen, Olinger, & Brsca, 1988).

The specific phylogenetic and ontogenetic mechanisms necessarily involved in the organic implementation or *proximate mediation* of the strategically contingent differentiation and integration of cognitive and conative individual difference factors has yet to be demonstrated. For example, it is not sufficient to demonstrate that in unstable, unpredictable, and uncontrollable environments, life history traits (such as personality constructs) are more integrated, and that in stable, predictable, and controllable environments, life history traits (such as personality constructs) are more differentiated. These are mere descriptions. We also need to show that the differentiation is strategically *adaptive*, and not just strategically *contingent*. In other words, the allocation of resources to life history and personality domains that increase or decrease relative to one another must correspond to the fitness gains and losses afforded by any given environment in which trait differentiation occurs. Specifically, trait-specific adaptive domains associated with higher fitness gains must receive higher resource allocations, and trait-specific adaptive domains associated with lower fitness gains must receive lower resource allocations.

To substantiate this empirically, it might be fruitful to conduct studies using mixed quasi- and true-experimental designs that relate measured prior traits of different individuals and then predict what their allocations of behavioral effort should be within different environmental contexts (which could be manipulated in the laboratory). Afterwards, one would expose a variety of such individuals to these same conditions and try to match their observed behavioral effort allocations to the predicted patterns. This is similar to what Sherman, Figueredo, and Funder (2013) have already done retrospectively by comparing theoretically expected patterns of behavior for fast and slow life history individuals (produced by an expert panel) to the self-reported patterns of behavior of research participants matching the prototypical trait ratings obtained for fast and slow life history individuals.

To accomplish this, one might administer pretests for the life history traits (or general constructs) of interest, in a way that has adequate Brunswik-Symmetry to the expected outcome of the mixed-design experiment. The reason that this portion of such a study is necessarily a mixed design is that life history speed is a trait that is quite stable over time and is also highly heritable in adults (h^2 ca. .65; Figueredo et al., 2004; Figueredo & Rushton, 2009); thus, it is unlikely that any experimental manipulation will change it dramatically. More importantly, life history speed cannot be randomly assigned, which is a prerequisite for true experimental designs. We expect (based on our stated theory), however, that environmental contexts influence behavioral expression of life history traits in proximal time. If the so-called person-situation interaction can be specified as systematic and predictable (as required by our theory), we should therefore obtain the specified patterns of differential and context-specific behavior predicted by theory.

For example, if participants are prescreened (by questionnaires) on fast or slow life history strategy, then are brought into the laboratory to perform a delay-of-gratification task, we expect that the faster life history strategists will favor shorter-term fitness gains over longer-term fitness gains, and may not be willing to incur shorter-term fitness losses (or defer short-term gains) for longer-term fitness gains. Conversely, we expect that the slower life history strategists will favor longer-term fitness gains over shorter-term fitness gains, and may be willing to incur shorter-term fitness losses (or defer shorter-term fitness gains) for longer-term fitness gains.

Mischel and Ebbesen (1970; see also Mischel, Shoda, and Rodriguez, 1989), for example, applied a true-experimental design to examine delay of gratification in children using the now-famous "marshmallow task," and were able to discriminate between children that were favorably disposed to defer gratification and those that were not on the basis of their observable behavior. Mischel, a well-known critic of trait theory in personality, did not attempt to predict this differential responding by matching them to any preexistent traits that these children might have possessed. In our proposed reexamination of the phenomenon, we expect differential responding based primarily on pretask assessment of life history strategy. Similarly, we predict that fast life history strategists would be more likely to "defect" in a Prisoner's Dilemma task than slow life history strategists, who are generally more invested in maintaining longer-term social and sexual relationships.

CONCLUSIONS

In summary, we have reviewed the general contents and conclusions of our previous chapter on the same topic published in the first edition of this handbook (Buss, 2005) and extended our reasoning to the evolutionary significance of the GFP, reviewing both its history as a construct and most of recent psychometric tests of its validity. We have proposed an evolutionary theoretical framework for understanding the evolution of the higher-order personality factors as well as the persistence of the lower-order personality factors. We examined and evaluated several empirical tests of risky predictions derived from that framework, found their results to be generally consistent with those theoretical predictions, and followed up with proposals for research designs that should help elucidate the complex and dynamic relationships among the various semi-autonomous components of personality.

Based on this review, we argue that personality is both unitary and manifold, just as the contingencies of survival and reproduction demand; personality is both persistent and stable and, at the same time, subject to fine-tuning. As characterized so long ago by Gordon Allport (1961): "Personality is the dynamic organization within the individual of those psychophysical systems that determine his characteristic behavior and thought (p. 28)." Personality, according to Figueredo, Cox, and Rhine (1995), "(1) exists as a definable construct, (2) represents a fluid property of a constantly changing and adapting organism, and (3) characterizes the individual, rather than being constructed by the observer" (p. 168). It is our future task as differential evolutionary psychologists to discern the ultimate and proximate causes of these organic and protean behavioral phenomena.

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CHAPTER 41

The Evolution of Cognitive Bias

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> Despite widespread claims to the contrary, the human mind is not worse than rational . . . but may often be better than rational.
>
> Cosmides and Tooby, 1994, p. 329

On the surface, cognitive biases appear to be somewhat puzzling when viewed through an evolutionary lens. Because they depart from standards of logic and accuracy, they appear to be design flaws instead of examples of good engineering. Cognitive traits can be evaluated according to any number of performance criteria—logical sufficiency, accuracy, speed of processing, and so on. The value of a criterion depends on the question the scientist is asking. To the evolutionary psychologist, however, the evaluative task is not whether the cognitive feature is accurate or logical, but rather how well it solves a particular problem, and how solving this problem contributed to fitness ancestrally. Viewed in this way, if a cognitive bias positively impacted fitness, it is not a design *flaw*—it is a design *feature*. This chapter discusses the many biases that are probably not the result of mere constraints on the design of the mind or other mysterious irrationalities, but rather are adaptations that can be studied and better understood from an evolutionary perspective.

By cognitive bias, we mean cases in which human cognition reliably produces representations that are systematically distorted compared to some aspect of objective reality. We note that the term *bias* is used in the literature in a number of different ways (see, e.g., Johnson, Blumstein, Fowler, & Haselton, 2013; Marshall, Trimmer, Houston, & McNamara, 2013; Nettle & Bateson, 2012). We do not seek to make commitments about these definitions here; rather, we use bias throughout this chapter in the relatively noncommittal sense defined above.

FOUNDATIONS OF COGNITIVE BIAS

An evolutionary psychological perspective predicts that the mind is equipped with function-specific mechanisms adapted for special purposes—mechanisms with special design for solving problems such as mating, which are separate, at least in part, from those involved in solving problems of food choice, predator avoidance, and social exchange (e.g., Kenrick, Neuberg, Griskevicius, Becker, & Schaller, 2010). In the evaluation of cognitive biases, demonstrating domain specificity in solving a particular problem is a part of building a case that the trait has been shaped by selection to perform that function. The evolved function of the eye, for instance, is to facilitate sight because it does this well (it exhibits proficiency), the features of the eye have the common and unique effect of facilitating sight (it exhibits specificity), and there are no plausible alternative hypotheses that account for the eye's features.

Some design features that appear to be flaws when viewed in one way are revealed to be adaptations when viewed differently. If one were to only consider the idea that selection favors the maximization of direct reproductive success, for example, the fact that human females lose reproductive capability many years before death would appear a design flaw. However, there is evidence that women in traditional societies can enhance their inclusive fitness by transferring investment to their daughters' daughters as soon as the latter are of reproductive age (Voland & Beise, 2002). Viewed in this light, female menopause might be very well designed (Hawkes, 2003).

In sum, there may be many evolutionary reasons for *apparent* design flaws, and a close examination often provides insight into the evolutionary forces that shaped them and their functions. Analogous logic may be applied to understanding cognitive biases. We argue that cognitive biases can arise for at least three reasons (see Table 41.1).

First, selection may favor useful shortcuts that tend to work in most circumstances, though they fall short of some normative standards (*heuristics*); second, apparent biases can arise if the task at hand is not one for which the mind is designed (*artifacts*); and third, biases can arise if biased response patterns to adaptive problems resulted in lower error costs than unbiased response patterns (*error management biases*). As well as being interesting in their own right, the investigation of biases offers the capacity to reveal the contours of the evolved mind by revealing the problems it appears to have been designed to solve: Whereas "accurate" perceptions do little to constrain hypotheses about cognitive design, discovering bias can often reveal it.

Since the original edition of this *Handbook*, the volume of work investigating error management biases has grown rapidly. Therefore, we discuss heuristics and artifacts only briefly and focus on newer work on error management biases (for a more detailed evolutionary discussion of heuristics and artifacts, see Haselton et al., 2009). We do not

Table 41.1
Evolutionary Taxonomy of Cognitive Biases

Type of Bias	Examples
Artifact: Apparent biases and errors are artifacts of research strategies; they result from the application of inappropriate normative standards or placement of humans in unnatural settings.	Some instances of base-rate neglect in statistical prediction Some instances of confirmation bias
Error Management Bias: Selection favored bias toward the less costly error; although error rates are increased, net costs are reduced.	Auditory looming Xenophobia Sexual overperception by men Commitment underperception by women

intend the three categories of bias to be fully exhaustive or mutually exclusive; we offer them instead as a useful way of organizing research on cognitive bias and gaining insight into why biases exist.

HEURISTICS

Perhaps the most commonly invoked explanation for bias is as a necessary by-product of processing limitations—because information processing time and ability are limited, humans must use shortcuts or rules of thumb that are prone to breakdown in systematic ways. Kahneman and Tversky (1973) demonstrated that human judgments often departed substantially from normative standards based on probability theory or simple logic. In judging the sequences of coin flips, for example, people assessed the sequence HTHTTH to be more likely than the sequence HHHTTT or HHHHTH. As Tversky and Kahneman (1974) pointed out, while in some sense representative, the first type of sequence is improbable—it contains too many alternations and too few runs. The "gambler's fallacy" is the expression of a similar intuition. The more bets lost, the more the gambler feels a win is now due, even though each new turn is independent of the last (Tversky & Kahneman, 1974).

Tversky and Kahneman attributed these and other biases to the operation of mental shortcuts: "People rely on a limited number of heuristic principles which reduce the complex tasks of assessing probabilities and predicting values to simpler judgmental operations" (1974, p. 1124). The gambler's fallacy and the conjunction fallacy are attributed to one of the most commonly invoked heuristics, *representativeness*, or the way in which A resembles or is representative of B. According to this account, alternating heads and tails are more representative of randomness than are series containing runs.

The notion that biases result from the use of simplifying heuristics has logical appeal. As expressed by Arkes (1991), "the extra effort required to use a more sophisticated strategy is a cost that often outweighs the potential benefit of enhanced accuracy" (pp. 486–487). This cost can affect the evolution of cognitive mechanisms at two levels. There may be costs in evolutionary terms, since the development of certain brain circuits will either increase the length of ontogeny or move potential energetic allocation away from the development of other mechanisms. There may also be costs in real time, since decisions using complex algorithms will often take longer or require more attentional resources than decisions using simpler alternatives. Adaptive decisions often need to be made fast, and this may well constrain the type of strategies that are optimal. Evidence from a variety of sources demonstrates that people do indeed solve problems differently when under time pressure or when their motivations to be accurate are reduced.

One example of the effects of motivation is the fact that the social perceptions of individuals occupying positions of higher power in social hierarchies are often less accurate than those lower in the hierarchy (Fiske, 1993). Those higher in power are more likely to endorse stereotypes about others than to attend to individuating information specific to the target being evaluated, which presumably enhances accuracy (Goodwin, Gubin, Fiske, & Yzerbyt, 2000). Individuals assigned more decision-making power in reviewing internship applications attend more to stereotype-consistent information and less to stereotype-inconsistent information (Goodwin et al., 2000). Similarly, in a study of two student groups competing for university funding, individuals reporting more personal power judged their opponents' attitudes less accurately (Ebenbach & Keltner, 1998). A common interpretation of findings such as these is that lower-power individuals occupy a more precarious social position and they must therefore allocate more time and energy to social judgments; more powerful individuals enjoy the luxury of allocating their cognitive efforts elsewhere (Galinsky, Magee, Inesi, & Gruenfeld, 2006; Keltner, Gruenfeld, & Anderson, 2003).

Overall, there is ample evidence of cognitive bias and error in humans. Some of these biases may result from the use of shortcuts, which are often effective. For these effects, however, it is important to note that a "processing limitations" explanation is not complete. Of all possible equally economical cognitive shortcuts, why were these particular ones favored by selection? In the *error management biases* section that follows, we suggest that the direction and content of biases is not arbitrary. Selection has sculpted the ways that limited computational power is deployed so as best to serve the fitness interests of humans over evolutionary time.

BIASES AS ARTIFACTS

One criticism of classic heuristics and biases research (e.g., Tversky & Kahneman, 1974) is that the strategies for identifying bias and evaluating cognitive performance might not be fully appropriate. If problems presented in the laboratory *are not those for which the human mind is designed*, we should not be surprised that people's responses appear to be systematically irrational.

One type of artifact arises from *evolutionarily novel problem formats*. Gigerenzer (1997) proposed that tasks intended to assess human statistical prediction should present information in frequency (rather than probability) format, given that natural frequencies, such as the number of times an event has occurred in a given time period, are more readily observable in nature. In contrast, probabilities (in the sense of a number between 0 and 1) are mathematical abstractions beyond sensory input data, and information about the base rates of occurrence is lost when probabilities are computed (Cosmides & Tooby, 1996). Bayesian calculations involving frequencies are therefore computationally simpler than equivalent calculations involving probabilities, relative frequencies, or percentages. Whereas probability calculations need to reintroduce information about base rates, frequency calculations do not since this part of the computation is already "done" within the frequency representation itself (Hoffrage, Lindsey, Hertwig, & Gigerenzer, 2001).

According to this perspective, humans will possess the ability to estimate the likelihood of events given certain cues. If this skill is a part of human reasoning, however, tasks involving probability input are less likely to reveal it than are tasks involving natural frequencies. Indeed, frequency formats do improve performance in tasks like the famous "Linda problem." Whereas a probability format produces violations of the conjunction rule in between 50 and 90% of respondents, frequency formats decrease the rate of error to between 0 and 25% (Fiedler, 1988; Hertwig & Gigerenzer, 1999; Tversky & Kahneman, 1983; but see Mellers, Hertwig, & Kahneman, 2001). More recent research suggests that probability formats pose serious problems for medical doctors: Three quarters of doctors surveyed misinterpreted the meaning and application of "survival rates," and journals frequently publish papers in which these probability statistics are misused in interpreting results (Gigerenzer & Wegwarth, 2013).

A second artifact can arise from *evolutionarily novel problem content*. The perspective on cognitive design we have described suggests that researchers should not necessarily expect good performance in tasks involving abstract rules of logic. Falsification-based logic is sufficiently difficult for humans that university courses in logic, statistics, and research design attempt to teach it to students (with only mixed success). Wason (1983) empirically confirmed this in the laboratory using a task that required subjects to determine whether a conditional rule (if p then q) had been broken. He demonstrated that subjects recognized that confirmatory evidence (the presence of p) was relevant to the decision, but they often failed to check for falsifications of the rule (the absence of q). Research using the Wason task revealed a variety of apparent content effects (Wason & Shapiro, 1971; Johnson-Laird, Legrenzi, & Legrenzi, 1972), in which performance dramatically changed for the better.

In a series of now-classic experiments, Cosmides (1989) demonstrated that a number of the content effects could be attributed to a cheater-detection algorithm. When the content of the conditional rule involves social exchange (if you take the benefit [p], then you pay the cost [q]), people are spontaneously induced to look not only for benefits taken (p) but also costs not paid (not q), and performance dramatically increases from 25% correct (Wason, 1983) to 75% correct (Cosmides, 1989; also see Cosmides, Barrett, & Tooby, 2010, for a more recent update that replicates these findings and helps to rule out alternative explanations proposed by critics).

The conclusion to be drawn from these studies is not that humans are good at using abstract rules of logic. Rather, it is that humans have evolved problem-solving mechanisms tailored to problems recurrently present over evolutionary history. When problems are framed in ways congruent with these adaptive problems (such as social contract violation), humans can be shown to use appropriate reasoning strategies.

ERROR MANAGEMENT BIASES

Like biases resulting from the application of heuristics, biases in this third set—error management biases—are genuine biases. In this case, however, biases are not the result of shortcuts in the design of the mind. Instead, the biases themselves serve evolved functions.

ERROR MANAGEMENT THEORY

Error management theory (EMT; Haselton & Buss, 2000; Haselton & Nettle, 2006; Johnson et al., 2013) applies the principles of signal detection theory (Green & Swets, 1966) to judgment tasks in order to make predictions about evolved cognitive design. An error management framework views cognitive mechanisms not so much as "truth seekers" (as has been previously thought; e.g., Fodor, 2001), but as adaptation executors (e.g., Tooby & Cosmides, 1990). The central tenet of this framework is that cognitive mechanisms can generally produce two types of errors: false positives (taking an action that would have been better not to take), and false negatives (failing to take an action that would have been better to take).

An optimal mechanism would make no errors of either type. However, most real-world judgment tasks are probabilistic and include an irreducible amount of uncertainty. Auditory judgment, for example, is rendered uncertain by the presence of ambient noise, and some error is likely to occur however good the mechanism.

Crucially, the fitness costs of making each type of error are rarely equal. Fleeing from an area that contains no predator results in a small inconvenience cost, but it is much less costly than the failure to flee from a predator that really is close by. EMT predicts that an optimal decision rule will minimize not the total error rate, but the net effect of error on fitness. Where one error is consistently more damaging to fitness than the other, EMT predicts that a bias toward making the less costly error will evolve—this is because it is better to make *more* errors overall as long as they are relatively cheap. Overall, then, EMT predicts that biases will evolve in human judgments and evaluations that fit all of the following criteria: (a) they involve some degree of noise or uncertainty, (b) they have consequences for fitness and reproductive success, and (c) they are consistently associated with asymmetrical costs (where more asymmetry leads to larger biases). For mathematical formalism of this logic and the expectations of EMT, see Haselton and Nettle (2006) and Johnson et al. (2013). (For a related account, see Higgins, 1997.)

Within this framework, many ostensible faults in human judgment and evaluation may reflect the operation of mechanisms designed to make inexpensive, frequent errors rather than occasional disastrous ones (Haselton & Nettle, 2006; Johnson et al., 2013). In the decade since the publication of the first edition of this volume, the scope of EMT research has expanded, with streams of research documenting functionally biased judgments across a variety of fitness-relevant domains. In this section, we highlight key examples across these domains (for reviews containing additional examples, see Haselton & Galperin, 2013; Haselton et al., 2009; Haselton & Nettle, 2006; Johnson et al., 2013).

Error management biases can be generally sorted into three broad categories: biases pertaining to judgments of threat, biases pertaining to evaluations of interpersonal relationships, and biases pertaining to evaluations of the self (following Haselton & Nettle, 2006). Table 41.2 provides examples within each of these categories, the hypothesized costs of each type of error in a given domain, and the expected outcome for each.

THREAT-RELEVANT BIASES

Several biases might protect people from threats to physical safety or to health. We begin by discussing the former.

Auditory Looming People tend to judge a sound that is rising in intensity to be closer and approaching more rapidly than an equidistant sound that is falling in intensity. In a series of experiments involving speakers moving on cables, people showed biased perceptions of the proximity of moving sound sources, as well as a general tendency to underestimate the distance of sound sources (Neuhoff, 2001). People judged an approaching sound source to be closer by than a receding one, when in fact the sounds were located at distances equally far away. There is a clear error management interpretation of this effect: It is better to be ready for an approaching object too early than too late (Neuhoff, 2001).

Recent work has shown that individuals in poorer physical condition—measured by both heart rate recovery time and physical strength—have larger auditory looming biases than individuals in better physical condition (Neuhoff, Long, & Worthington, 2012). An error management interpretation of this relationship is that individuals with

Table 41.2
A Selection of Adaptive Biases

Category and Domain	False Positive (FP)	Costs of FP	False Negative (FN)	Costs of FN	Result
Protective: Approaching Sounds	Ready too early	Low	Struck by source	High	Bias toward underestimating time to arrival
Protective: Foods	Reject a food type that is in fact safe	Low	Ingest toxin or pathogen	High	Bias toward acquiring permanent aversion on the basis of one piece of evidence of toxicity
Protective: Diseased persons	Avoid noninfectious person	Usually low	Become infected	Often very high	Tendency to avoid persons with physical afflictions, even if noninfectious
Protective: Physically threatening persons	Avoid altercation with safe person	Usually low	Suffer physical injury	Often high	Tendency to overestimate physical formidability of potentially threatening persons
Social: Men's inference of female sexual interest	Inferring sexual interest where there is none	Rejection—relatively low	Inferring no interest when there is interest	Missed reproductive opportunity—high	Sexual overperception by men
Social: Women's inference of commitment	Inferring interest to commit where there is none	Desertion—high	Inferring unwillingness to commit where there is willingness	Delayed start to reproduction—relatively low	Underperception of commitment by women
Social: Social exchange	Attempt to free-ride and get caught	Potential ostracism, especially in collectivist social situations—high	Cooperate when one could free-ride	Give up a unnecessary benefit in exchange—relatively low	Bias toward cooperation
Self and Future: Beliefs about future achievements	Believe you can achieve things when you cannot	Low (if costs of failure are low)	Believe you cannot achieve things when, in fact, you could	High (if benefit of success is high)	Optimistic bias (where benefits of success exceed costs of failure); overconfidence bias

reduced motor capacity require a larger "margin of safety." In another recent study, people exposed to an infant cry showed larger auditory looming biases than people not exposed to the cry. And, conversely, people exposed to an infant *laugh* showed smaller auditory looming biases than people not exposed to the laugh (Neuhoff, Hamilton, Gittleson, & Mejia, 2014). Female participants showed larger shifts in auditory looming biases in response to these infant stimuli—a pattern also found in a follow-up study (Neuhoff et al., 2014). Because throughout evolutionary history infants likely required direct care from mothers more so than from fathers (e.g., due to breastfeeding), these effects suggest that self-protective biases like auditory looming are tuned to threats associated with care for vulnerable offspring. At a more general level, adaptively patterned variation in auditory looming demonstrates that error management biases are not fixed, but are responsive to cues of variation in threat.

Movement of Threatening Objects Might there be analogous phenomena in the perception of visual threats? In one recent study, people judged the speed of an approaching spider, ladybug, or rubber ball (Witt & Sugovic, 2013). Although all objects moved at the same speed, spiders were judged to be moving more quickly than the other objects. Further, when people were given the task of "blocking" the spider, they judged the spider as approaching them faster when they used a smaller paddle relative to a larger paddle, demonstrating that the bias was enhanced when avoiding the spider was more difficult.

Properties of Physical Landscapes There are asymmetric costs of injury from underestimating the height of a cliff, and perhaps erroneously judging it safe to jump, than from overestimating it and finding a different means of navigation. Consistent with this idea, people tend to judge the height of a vertical surface as greater when looking from the top than from the bottom (Jackson & Cormack, 2007; Stefanucci & Proffitt, 2009).

A similar example involves the perceived steepness of hills. In one series of studies, people consistently overestimated the steepness of hills—both real and computer-simulated (Proffitt, Bhalla, Gossweiler, & Midgett, 1995). Failing to properly descend a steep hill is far more costly than failing to properly ascend it. An error management perspective therefore predicts that this bias toward overestimating slopes will be greater when people view from the top than from the bottom, which was exactly what is found (Proffitt et al., 1995). Making the situation even more precarious increases the bias even more—people standing on skateboards at the top of hills perceive greater steepness than those standing on flat earth (Stefanucci, Proffitt, Clore, & Parekh, 2008).

Food Aversions Lasting aversion to a food is reliably acquired, in humans and other species, following a single incidence of sickness after ingestion of the food (Garcia, Hankins, & Rusiniak, 1976; Rozin & Kalat, 1971). Given one data point (sickness following the food type on one occasion), the system treats the food as if it is always illness-inducing. There are again two possible errors here. The false positive may be inconvenient, but the false negative is more likely to be fatal. The system appears biased toward overresponsiveness to avoid illness.

Aversion to Diseased or Injured Persons Similar logic predicts an aversion to individuals who have superficial cues that might connote the threat of infectious disease.

The error management account is similar to that for food aversions: The false negative (failing to avoid someone with a contagious disease) is highly costly, whereas the false positive (avoiding contact with a noncontagious person) may have small social or interpersonal costs, but is unlikely to have significant negative fitness consequences. Given the fact that infectious disease has represented one of the key selective forces throughout human history (e.g., Inhorn & Brown, 1990), disease avoidance mechanisms are often expected to be biased to avoid many individuals or objects that are in fact safe.

The significant bias toward false positives in assessing cues of disease threat has far-reaching social and societal implications, and may lie at the root of many forms of stigmatization and prejudice, including racism, ageism, homophobia, and anti-fat prejudice (e.g., Kurzban & Leary, 2001). Hypersensitivity to disease threat leads to stigmatization or avoidance of individuals who pose no risk of disease transmission whatsoever, yet display cues that were associated with disease threat ancestrally. Individuals with noninfectious morphological anomalies, such as prominent birthmarks, activate avoidant responses (Zebrowitz & Montepare, 2006). Similarly, individuals with clearly noninfectious physical disabilities are also implicitly associated with disease (Park, Faulkner, & Schaller, 2003), as are obese individuals (Park, Schaller, & Crandall, 2007). Individuals displaying symptoms of HIV/AIDS are also implicitly associated with the threat of infectious disease, despite knowledge that this ailment is not infectious through superficial contact. These individuals are frequently regarded as disgusting (e.g., Herek, 1999), and they, along with their families, are often ostracized from their communities (Gerbert, Sumser, & Maguire, 1991). Other patently noninfectious afflictions that result in social distancing include cancer (Greene & Banerjee, 2006) and physical disfigurements (Houston & Bull, 1994).

The strength of these implicit associations is predicted by the extent to which individuals perceive themselves to be vulnerable to infectious disease. Individuals who tend to be more worried about disease threat have stronger implicit associations between infectious disease and both obesity and physical disability, and also have more negative attitudes toward obese and physically disabled people (Lieberman, Tybur, & Latner, 2012; Park et al., 2003; Park et al., 2007). Moreover, making a threat of disease temporarily salient amplifies these prejudicial cognitions (Park et al., 2003; Park et al., 2007). Other evidence suggests that prejudicial cognitions regarding elderly people are greater among people who feel more chronically vulnerable to disease (Duncan & Schaller, 2009). Studies have also documented links between perceived vulnerability to disease and overperceptions of unusual morphological features. For example, individuals higher in disease concerns set a lower threshold for categorizing someone as obese, and situationally priming disease threat leads to over-remembering seeing obese targets (Miller & Maner, 2012).

Members of other cultural groups may also be implicitly associated with disease threat. Human immune systems are attuned to local disease threats. Contact with unfamiliar outgroups might have historically increased the risk of contracting dangerous pathogens unfamiliar to locally adapted immune systems (Diamond, 1999). An error management perspective predicts that the benefits of exaggerated avoidance of outgroup members (e.g., xenophobia) may have historically outweighed its costs (Kurzban & Leary, 2001). Indeed, individuals who tend to be particularly worried about infectious disease tend to hold more negative attitudes toward unfamiliar ethnic groups (Faulkner, Schaller, Park & Duncan, 2004), and making the threat of disease temporarily salient increases opposition toward policies allowing immigration of unfamiliar outgroups (Faulkner et al., 2004). Ethnocentric and xenophobic attitudes are also higher for women during the first trimester of pregnancy, when the immune system is temporarily compromised (Navarrete, Fessler, & Eng, 2007). Cross-culturally, individuals in countries with higher levels of infectious disease are more likely to report that they would not want "people of a different race" as neighbors (Schaller & Murray, 2010).

Perceptions of Potentially Threatening People Infectious disease is not the only threat posed by others, particularly for individuals who are physically vulnerable. A recent series of studies manipulated or measured vulnerability to harm and showed that vulnerable individuals overestimated the formidability of potentially threatening individuals. One study found that when people were told that a man was holding a gun, they perceived that person to be taller and more muscular than when they were told he was holding a drill, handsaw, or caulking gun (Fessler, Holbrook, & Snyder, 2012). Similarly, men who were temporarily physically incapacitated (either by being bound to a chair or by standing on a balance board) estimated an image of an angry man to be significantly taller and more muscular than did men who were not incapacitated (Fessler & Holbrook, 2013a). The presence of weapons also appears to influence dispositional judgments: Men who were pictured holding potentially harmful tools in nonviolent situations (such as gardening shears) were judged to be more anger prone than when pictured holding innocuous tools (such as a watering can; Holbrook et al., 2014). In another study, parents with dependent children perceived a potentially threatening criminal to be more physically formidable than did nonparents (Fessler, Holbrook, Pollack, & Hahn-Holbrook, 2014).

Other situational variables can make potentially threatening individuals appear less physically formidable: Men who were in the presence of companions judged a solitary foe as smaller and less muscular than men who made these judgments alone (Fessler & Holbrook, 2013b).

BIASES IN INTERPERSONAL PERCEPTION

A second cluster of error management biases concern our perceptions of the intentions or dispositions of others.

Sexual Overperception Courtship communications are often ambiguous. Does a smile convey mere friendliness, or does it mean more? For men, error management logic predicts a bias toward overestimating a potential mate's sexual interest. This is because, all else equal, the reproductive costs of underestimating a woman's sexual interest and failing to pursue her—thereby missing out on an opportunity to reproduce—were likely to have been greater than the costs of pursuing a disinterested woman (Haselton & Buss, 2000). Men who were more successful in mating with greater numbers of women would have outreproduced other men, passing along this possible over-perception bias to their descendants.

For women, a different logic applies. Because of women's necessarily heavy investment in each child produced, and the necessarily long interval between births, finding high-quality partners—not more numerous partners—probably had a greater impact on women's reproductive success (Buss, 1994; Symons, 1979; Trivers, 1972). Therefore, error management logic predicts that men, but not women, possess the sexual overperception bias. Many sources of evidence support the sexual overperception hypothesis (see Haselton & Galperin, 2013, Table 11.1, for a review). For instance, in the earliest demonstration of the phenomenon, male and female strangers engaged in a get-to-know-you conversation in the lab and were viewed by a second pair of male and female strangers through one-way glass (Abbey, 1982). Both the male participant in the conversation (target) and the male observer rated the female target as more flirtatious and sexually interested than the female observer and female target. In this study and similar later studies, the difference between male and female ratings of women's sexual interest was present when men's ratings were compared to the target woman's self-ratings and when compared to ratings made by third-party women assessing the interaction (Abbey, 1982; Haselton & Buss, 2000).

Similar results are found in surveys of men's and women's misperception experiences. In one study, for example, undergraduate women from the United States reported more instances within the last year in which men overestimated their sexual interest than in which men underestimated it, suggesting that these men overperceived women's sexual interest in naturalistic situations outside of the lab (Haselton, 2003). Men in the same study reported roughly equal numbers of overperception and underperception errors on the part of women, providing no evidence of a bias in women. These patterns were closely replicated in a study of Norwegian undergraduates—a replication that is particularly noteworthy because Norway has a more gender-equal culture than does the United States (Bendixen, 2014). In related studies of opposite-sex friendships, men estimated their female friends' sexual interest to be greater than those women reported it to be (Bleske-Rechek et al., 2012; Koenig, Kirkpatrick, & Ketelaar, 2007). Similarly, a recent speed-dating study similarly found that men estimated greater sexual interest in their female partners than their female partners reported (Perilloux, Easton, & Buss, 2012). This study also assessed variation in this apparent bias and found that men who were higher in short-term mating orientation and who were higher in self-rated attractiveness had a larger bias. Further, men's apparent bias was greater when they interacted with relatively more attractive women. In some birds, insects, and mammals (Alcock, 1993, Chapter 13; Domjan, Huber-McDonald, & Holloway, 1992), males sometimes attempt to copulate with objects that only vaguely resemble females of their species, such as beer bottles or crude female models, suggesting similar behavioral biases in other species.

Commitment Skepticism The reverse asymmetry might have applied to ancestral women as they estimated men's intentions to commit to long-term relationships (Haselton & Buss, 2000). Inferring long-term commitment interest in a man in whom it was absent could have resulted in abandonment after the woman had already conceived a child, a high-cost error potentially associated with reduced offspring survival (e.g., Hurtado & Hill, 1992). Underestimating a man's commitment could also be costly, including delays in reproduction, but these costs might have been lower on average than costs associated with desertion (Haselton & Buss, 2000). Women might therefore possess a bias toward underestimating men's interest in commitment. Consistent with this idea, several studies have shown that women rate men's commitment given various courtship behaviors, such as giving gifts and verbal affirmations of love, lower than men rate it (Haselton & Buss, 2000). In contrast, women and men tend to agree on the level of commitment indicated by women's enaction of the same behaviors (Haselton & Buss, 2000). A recent study similar to earlier research documented apparent commitment skepticism in women who were prior to the age of menopause, but not women past the age of menopause, possibly because women past the age of reproduction would not have faced the same reproductive costs of overestimating men's commitment (Cyrus, Schwarz, & Hassebrauck, 2011).

Further evidence for commitment underperception in women was found in a study of face-to-face interactions between previously unacquainted male–female dyads (Henningsen & Henningsen, 2010). Dyads engaged in a 5-minute conversation and afterwards filled out questionnaires about their own and their partner's perceived level of interest in a committed long-term relationship. Consistent with the commitment underperception hypothesis, women estimated lower levels of commitment interest than men reported for themselves. In contrast, men's estimates of women's commitment were not significantly different from women's reports of their commitment interest, providing no evidence of bias in men's judgments of women.

Negative Outgroup Stereotypes Humans appear to possess a bias toward inferring that members of competing coalitions (or outgroups) are less generous and kind (Brewer, 1979) and more dangerous and ill-tempered (Quillian & Pager, 2001) than are members of their own group. This bias might have been adaptive for reasons that extend beyond those related to the threat of disease transmission, presented above. For ancestral humans, the costs of falsely assuming peacefulness on the part of an aggressor were likely to outweigh the comparatively low costs of elevated vigilance about aggression, particularly for inferences about outgroup members who are not part of an individual's regular social circle. In one study, when participants were exposed to a cue indicating increased risk of injury—ambient darkness in the laboratory—they endorsed racial and ethnic stereotypes connoting violence more so than people completing the task in a brightly lit room (Schaller, Park, & Mueller, 2003). Darkness had no effect on other negative stereotypes of outgroup others (such as laziness or ignorance) (Schaller et al., 2003; for a related recent study see Stroessner, Scholer, & Marx, 2015).

Social Exchange Bias Behavioral economists have puzzled over the fact that people cooperate in economic games with economic incentive structures favoring defection (Camerer & Thaler, 1995; Caporael, Dawes, Orbell, & van der Kragt, 1989; Henrich et al., 2001; Sally, 1994). In the one-shot Prisoner's Dilemma game, for example, participants are expected to defect rather than to cooperate. If partner A cooperates while B defects, partner A suffers a greater loss than if he or she had defected. The interaction is not repeated, so there is no incentive to signal cooperativeness, nor is there prior information about reputation that might serve to provide clues about the partner's cooperative disposition. Yet cooperation often occurs, as it does in other one-shot economic tasks.

One possibility is that cooperation in one-shot games results from the operation of a *social exchange bias* that manages the costs of errors in social exchange (Yamagishi, Terai, Kiyonari, Mifune, & Kanazawa, 2007). According to this logic, the costs of falsely believing one can defect without negative social consequences are often higher than cooperating when one could safely defect. This asymmetry holds when the costs of "unneeded" cooperation are relatively low (e.g., a low dollar amount is lost) or when the social costs of failing to cooperate (potential ostracism) are high. The costs of ostracism may be particularly high in interdependent social contexts, in which cooperation is either highly valued or especially necessary (Yamagishi, Jin, &

Kiyonari, 1999). In Japanese collectivist samples where exchanges are relatively closed to outsiders, cooperation in one-shot experiments is higher than in the more individualist United States samples (Yamagishi et al., 1999). Also consistent with the social exchange bias hypothesis, when people are led to think of the game as an exchange relationship (by making forecasts about their exchange partner's behavior) they cooperate more than when they are not led to think this (Yamagishi et al., 2007; see also Savitsky, Epley, & Gilovich, 2001, and Williams, Case, & Govan, 2003, for related predictions). Similar predictions were tested using evolutionary modeling and showed that one-shot cooperation can evolve due to the asymmetric costs of sometimes mistaking a repeated interaction for one-shot relative to mistaking one-shot for repeated interaction (Delton, Krasnow, Cosmides, & Tooby, 2011).

Note that this bias can be conceptualized as some combination of error management, as in the social exchange bias account, and an artifact of modern living, since in an ancestral environment the probability of re-encountering individuals would have been high and social reputation effects very potent. Thus, people may be predisposed to expect negative consequences of non-prosocial behavior even when, objectively, such consequences are unlikely to follow. The bias toward prosociality has been the subject of competing explanations that take quite different explanatory stances (Bowles & Gintis, 2002; Gintis, Bowles, Boyd, & Fehr, 2003; Henrich & Boyd, 2001; Price, Cosmides, & Tooby, 2002), although these explanations might not be mutually exclusive.

BIASES IN SELF-JUDGMENT

The third cluster of biases concerns judgment about the self and personal efficacy. Here we briefly discuss the representative example of the "positive illusions" (for a more complete review, see Haselton & Nettle, 2006).

Positive Illusions and Unrealistic Optimism These are a well-known cluster of findings in judgment tasks concerning the self (Taylor & Brown, 1988). Individuals display unrealistically positive perceptions of their own qualities (Alicke, 1985), their likelihood of achieving positive outcomes in the future (Weinstein, 1980), and their degree of control over processes in the environment (Alloy & Abramson, 1979; Rudski, 2000). Two classes of evolutionary explanation have been proposed for such tendencies. One explanation is that individuals may have been selected to optimize the impression of their qualities that they display to observers. Given that observers will not be able to accurately assess such qualities directly, individuals may display behaviors that strategically enhance the qualities conveyed (Sedikides, Gaertner, & Toguchi, 2003).

An alternative explanation involves error management. Nettle (2004) outlines such an explanation, building upon the interpretation of the positive illusions given by Taylor and Brown (1988). In evaluating a prospective course of action, there are two possible errors. One may judge that the action is worthwhile when in fact it achieves nothing to promote fitness (or would not have ancestrally), or judge that a behavior is not worthwhile when in fact it enhances fitness to do it (or would have ancestrally). The former error (a false positive) leads to behaviors that are actually useless, whereas the latter (a false negative) leads to passivity. The costs of the false positive and false negative errors may not be symmetrical—that is, trying and failing may not matter very much, whereas failing to try could be very costly, especially in competitive contexts. Thus, evolution can be expected to produce mechanisms biased toward positive illusion in domains where there is uncertainty about outcomes, and the cost of trying and failing is reliably less than that of not trying where success was possible (Nettle, 2004). Recent neuroscientific research suggests that these biases have deep cognitive roots: Individuals tend to encode undesirable information in a distorted manner, which leads to the relative enhancement of desirable information (Sharot, Korn, & Dolan, 2011; Sharot, Riccardi, Raio, & Phelps, 2007). Note that the error management account does not predict blanket optimism, but optimism where fitness gains were potentially high relative to the cost of passivity.

A similar argument can be made for a different type of positive illusion: overconfidence. Although overconfidence can sometimes lead to costly decisions and behaviors, its motivational benefits—in the form of increased ambition and persistence—might outweigh these costs. Evolutionary models are consistent with the notion that biased representations of personal success probabilities can be favored under certain circumstances (Johnson & Fowler, 2011; but see Johnson & Fowler, 2013, and Marshall et al., 2013).

Other evolutionary models suggest that nation states that are overconfident in warlike behaviors are more likely to be successful than accurate or underconfident states (Johnson, Weidmann, & Cederman, 2011).

CONCLUSIONS

Research on cognitive and social bias has been dominated by the failure and bleak implications of heuristics (see Krueger & Funder, 2004). A *Newsweek* magazine account of the heuristics and biases literature summarized it as showing that "most people . . . are woefully muddled information processors who often stumble on ill-chosen short-cuts to reach bad conclusions" (cited in Gigerenzer, Todd, & the ABC Research Group, 1999, p. 27). In reflecting back on the history of social psychology, Aronson (1999) noted that "odious behavior ('sin') is at the heart of [the] most powerful research in social psychology" (p. 104). Browsing journals in social psychology, behavioral economics, and social cognition reveals a proliferation of seemingly foolish bias effects (see Haselton et al., 2009; Krueger & Funder, 2004).

Adopting an evolutionary perspective turns this focus on its head. Natural selection is the force responsible for creating the intricate designs with an improbably perfect match to their environments. Complex visual systems with specialized features tailored to species' differing ecologies have evolved several times, independently (Goldsmith, 1990). Reproductive adaptations allow animals to reproduce small copies of themselves, developmentally intact, complete with miniature versions of the adaptations that will enable their own reproduction. Natural selection is similarly responsible for the intricacy of the human mind. How could natural selection produce systems that equip the brain that are prone to fail as a rule and succeed only in exceptional cases?

The conceptual tide has now turned. There has been a shift toward explanations for bias invoking adaptive function, as well as a demonstration that simple mechanisms (heuristics) can function well in their proper domains. This reconceptualization has stimulated new developments in psychological theory and empirical research. Documenting content effects in biases—where bias effects emerge, recede, or reverse depending on the content of the judgment at hand—suggests that the mind does in fact contain computationally distinct mechanisms governing reasoning in functionally distinct domains. Results demonstrating the presence of adaptive biases where they might logically be expected in one sex but not in the other, and protective biases in response to stimuli that were ancestrally dangerous (but their conspicuous absence in response to modern threats), are key pieces of evidence in the debate about domain specificity. On the empirical side, these newer breeds of explanation cannot reasonably be dismissed as *just-so* stories. Although controversy about their interpretation remains, researchers from many different perspectives have tested competing predictions about classic effects and contributed their findings to the body of knowledge in psychology. The adaptive bias explanation we have featured in this chapter, error management theory, has also stimulated investigation on particular biases that were predicted a priori (e.g., women's commitment skepticism, auditory looming and navigation biases, and overestimation of physical formidability of threatening targets).

Recent investigations have also begun to document conditions that moderate certain error management biases. Further investigations of the sexual overperception bias, for example, have shown that, along with the sex of the perceiver predicting overperception (the classic EMT finding), the perceiver's levels of interest predicted even greater apparent sexual overperception (e.g., Koenig et al., 2007). Similarly, in studies of overperception and commitment skepticism in face-to-face interactions, whereas sexual overperception emerged only among men who were sexually interested in the women they were interacting with, commitment skepticism was reduced or eliminated among women who were sexually interested in the men they were interacting with (Henningsen & Henningsen, 2010). Investigations such as these provide an increasingly nuanced understanding of biases predicted by error management theory.

Many questions remain. Some scholars have noted that a *cognitive bias* is not actually necessary to manage error costs—a wholly accurate *cognitive evaluation* coupled with *behavioral bias* could be equally effective or superior to a cognitive bias (McKay & Dennett, 2009; McKay & Efferson, 2010). Consider sexual overperception. A man does not need to have a *biased belief* that a woman is sexually interested in order to approach her. He might think to himself, "My chances are low, but why not try?"

This is a plausible alternative design for managing error costs. Although EMT was originally advanced to explain cognitive biases, the core logic of the theory is neutral in predicting whether a bias must be built into belief or occur further along in the decision chain, leading more directly to biased actions. The question of whether solutions to error management problems are sometimes rooted in biased *belief* is an open question that can be answered only on a case-by-case basis with empirical research (Haselton & Buss, 2009). However, as sexual misperception biases, perceptual auditory looming biases, navigation biases, and many others demonstrate, there is abundant evidence that people's beliefs are indeed biased. Therefore, the argument that, *in theory*, error management adaptations need not involve biased beliefs does not render true cognitive biases nonexistent or impossible. The state of the evidence clearly indicates otherwise. The fascinating puzzle that remains is an explanation for why humans often seem to have biased beliefs when a behavioral bias might suffice. One possibility is that the functional thinking that has guided error management theory will need to be more fully integrated with an understanding of the proximate mechanisms that give rise to biases (Marshall et al., 2013). Such an integration could reveal that the easiest or most effective way for an evolved brain to deliver behavioral biases is via cognitive biases (Haselton & Buss, 2009).

In sum, the notion that human judgment is fundamentally flawed appears to have been flawed itself. When we observe humans in adaptively relevant environments, we can observe impressive design of human judgment that is free of irrational biases. Because of trade-offs in error costs, true biases might also prove to be more functional than one would think at first. Some genuine cognitive biases might be functional features designed by the wisdom of natural selection.

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CHAPTER 42

Biological Function and Dysfunction: Conceptual Foundations of Evolutionary Psychopathology

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EVER SINCE ARISTOTLE attempted to explain the design-like nature of organismic traits in terms of "final causes" that somehow regulated development, the concept of function and related "teleological" concepts (from the Greek *telos*, "end" or "purpose"), such as "design," "purpose," "adaptation," and "end," have been central to biological theory. As the preeminent evolutionary theorist George Williams explained, "the use of such concepts as biological means and ends . . . is the essence of the science of biology" (1966, p. 11).

Yet, what meaning can such terms have in a universe of mechanical causation? Must teleological attributions to biological mechanisms implicitly rely on illegitimate assumptions of intelligent design?

Darwin's theory of natural selection is the culmination of two millennia of grappling with how to understand biological teleological notions within a nonmystical scientific perspective. Contrary to the common claim that Darwin's theory of natural selection provides a way to eliminate teleology from biology in favor of mechanical causation, Darwin himself suggested that his theory had *explained* teleology rather than eliminated it (Gotthelf, 1999; Lennox, 1993), noting in a letter that it is "difficult for any one who tries to make out the use of a structure to avoid the word purpose" (Buller, 1999, p. 6). In fact, Darwin's conception of function places "the material principle of natural selection in place of the Aristotelian final cause" (Williams, 1966, p. 258).

Natural selection is only one force shaping organisms. There are many other influences on the nature and form of organisms, including developmental and structural constraints, genetic drift, various kinds of linkages between traits, and chance historical contingencies (Williams, 1992). The relative overall influence of such constraints versus natural selection remains a debated question (Orzack & Sober, 1994). Those who believe that such nonselective influences have a major impact sometime inflate this belief into an "anti-adaptationist" argument (Lewontin, 1979).

However, the teleological tradition is exclusively concerned with explaining those striking aspects of organisms that are adaptive and apparently design-like, and no set of developmental constraints, historical conditions, or other nonselective processes can adequately account for this overall domain. Disputes about the specific type of explanation appropriate to a given feature can be addressed empirically (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1999), but the necessity for invoking teleological explanation in a vast number of cases remains.

Anti-adaptationism did, however, fuel methodological concerns about the ease with which one can construct selectionist hypotheses lacking empirical warrant. Such hypotheses were famously demeaned by Stephen J. Gould as “just-so stories” (1991; Gould & Lewontin, 1979). These criticisms were ultimately useful in pointing to the need for greater methodological rigor (Griffiths, 1996), and evolutionary psychological science has dramatically improved its empirical grounding in recent years. But even if objections to specific teleological hypotheses are correct, teleological explanation in some form remains essential for understanding most adaptive traits.

Darwin’s contribution to the teleological tradition can only be appreciated in the context of the challenging conceptual puzzles that perennially afflict discussions of biological function, also known in the philosophical literature as “natural” or “proper” function. To take a simple example: The spider’s web enables the spider to catch insects, and we believe that this benefit is not just a happy accident but the *function* of the spider’s web. We also believe that the spider’s ability to create webs is not a happy accident but the function of a variety of mechanisms, some known and some unknown, within the spider’s body and brain. But what exactly do such function statements add to the descriptive facts that certain internal mechanisms have the effect of enabling the spider to create webs, and webs have the effect of catching insects? They must add something, because the overhang of a house’s roof may provide a particularly fruitful location to place the web and to catch insects, but nevertheless we don’t think that the function of the overhang is to enable the spider to catch insects.

One thing we seem to be adding in citing the function of a trait is a partial explanation of the trait; we are saying that catching insects is part of the explanation for *why* spiders have webs. Thus, function statements imply what has been called *functional explanations*. For example, the heart’s effect of pumping the blood is part of the heart’s explanation because, in virtue of natural selection, one can legitimately partially answer a question like “Why do we have hearts?” or “Why do hearts exist?” with “Because hearts pump the blood.” Thus, pumping the blood is a function of the heart.

It has sometimes been argued that the explanatory dimension of function claims is not essential and that the function of a trait is simply whatever causal role the trait has in conferring various capacities on the larger organismic system (Cummins, 1975). No doubt scientists sometimes talk this way. However, such a “causal role” view allows accidental effects to count as functions. Even pathologies have “functions” according to this account, because they confer distinctive effects and capacities on the organism. Thus, such views by themselves cannot provide an adequate conceptualization either of biological function in the evolutionary nonaccidental sense or pathological dysfunction that is without any biological function. Something needs to be added to causal role to account for function and dysfunction.

However, the requirement that a function must be explanatory raises a classic problem of seeming backward causation. Given that catching insects is an effect of spiders’ webs, and thus comes after the webs, how can the effect of catching insects explain its own cause, the web-building, while still observing the scientific prohibition on backward causation and rejecting Aristotelian notions of final causes? An adequate account of biological functions must dispel the notion that backward causation is being invoked. Moreover, even those who do not believe in a divine creator sometimes say colloquially that catching insects is the *purpose* of the spider's web, but how can a natural object have a purpose in a mechanical universe? Thus, a common concern is that biological function statements are somehow reading human intentionality into physical processes (Cummins, 1975), and an adequate account must make clear that this is not so.

Evolutionary psychologists have a particular need to address such issues and to be as clear as possible about the concept of biological function. Claims about how people's minds are designed and about the functions of known or hypothesized mental modules constitute evolutionary psychology's most distinctive contribution to psychology. These functional claims are often highly controversial and undergo unusually intense critical scrutiny. It is therefore important for evolutionary psychologists to have a nuanced understanding of what function claims mean, what kinds of evidence might count for or against them, and what ambiguities or misunderstandings might arise in making such claims. Fortunately, the growing importance of these issues is paralleled by a developing philosophical literature on the concept of function, which is already so large and diverse that only a few strands can be considered here.

One area in which evolutionary psychology is having a major impact is clinical psychology. An account of "function" implies a corresponding account of "dysfunction" or "malfunction," the concept on which theories of psychopathology are based. Thus, one major test for a theory of function is whether it provides an account of dysfunction that offers an adequate evolutionary-psychological foundation for theories of psychopathology. The ways in which the analysis of function presented here illuminates the foundations of clinical psychology will be considered later in this chapter.

In this chapter, I first examine recent developments in the philosophical analysis of the concept of biological function and propose what I believe is the most adequate approach. I focus on "etiological" or "historical" accounts that interpret functions primarily as naturally selected effects. Then, in the second part, drawing on my "harmful dysfunction" analysis of disorder (Wakefield, 1992a, 1999a, 1999b), I illustrate how the etiological analysis of function offers a conception of dysfunction that can illuminate the concept of mental disorder and the nature of psychopathology.

BIOLOGICAL FUNCTIONS

In the 1960s and 1970s, at about the same time within the literatures of evolutionary theory and philosophy of biology, there were critical turning points in the analysis of the concept of function. In biology, George Williams (1966) complained that "biologists have no logically sound and generally accepted set of principles and procedures for answering the question: 'What is its function?'" (p. 252). He corrected this situation by publishing his powerful analysis of the field's foundations, including his definition of natural function as naturally selected effect. In philosophy, Larry Wright (1973, 1976) established the etiological account of "function," which, after it was revised to deal with counterexamples, converged to a natural-selection-based account as well.

Both Wright's and Williams's analyses were aimed at distinguishing functions in their explanatory sense from accidental benefits and other extraneous factors that often are confused with functions. The philosopher Carl Hempel (1965) had posed the challenge of drawing such a distinction in his classic account of functional explanation.

The heart has many effects, observed Hempel, included among which is pumping the blood and making a sound in the chest. Indeed, both of these are beneficial effects, due to the medical uses of heart sounds. Yet among these effects, only some are biological functions of the heart. The challenge for a theory of function is to explain how to distinguish those effects of a trait that are its functions from those that are not. And the primary constraint on the account is that it must explain how attribution of a function offers a functional explanation. That is, the analysis must show, in a naturalistic and scientifically acceptable way, without invoking backward causation or divine design, how the effect that is a function can explain the presence of the very trait of which it is an effect. Thus, for example, the analysis must show how it is that, when asked "why do kangaroos have pouches," one can correctly answer, "to protect their developing young." This challenge of distinguishing functions from other effects has been the standard framework for recent inquiries into function.

Traditionally, this explanatory sense of function is known as the "strong" sense of function, versus some "weak" senses to be discussed shortly. To describe the function of a trait in the strong sense has been considered a way of outlining a partial explanation of the trait's existence and/or structure and/or maintenance in the species. It has always seemed apparent that the degree of design-likeness of organisms' traits cannot be accidental and that, for example, the eyes must somehow be the way they are *because* they enable us to see. The challenge has been to provide a scientifically adequate understanding of this fact. Replacing "final cause" and theistic accounts, Darwin's theory of natural selection offers the only scientifically adequate explanation we have of how such nonaccidental effects can exist and can explain the traits that cause them; literally, the effects must be cited in an explanation of the cause. Thus, those analyses of function, known as "etiological" or "historical" analyses, that analyze the strong sense of function by appealing in one way or another to natural selection, best address the traditional conundrum of effects explaining their causes.

The analysis of the concept of biological function is made considerably more difficult by the fact that the term "function" is used in a great variety of ways, most of which have nothing to do with biological functions in the strong sense but which are often confused with this concept. We often metaphorically extend function talk to just about any cause that contributes to any salient or valued outcome, as if it were designed to do so, as in "heart sounds function to alert doctors to medical problems," or "gravity functions to hold the solar system together." Moreover, there are a variety of colloquial uses that are essentially value judgments, such as when one says that one has a functional or dysfunctional marriage or work situation. None of these uses are explanatory. Some writers on function mistake these metaphorical extensions for the real thing, hopelessly confusing the account of biological functions. Rather than taking the time to disentangle all these variant uses, I simply confine myself to the "strong" use noted above. Note that one way the strong sense is often marked is by the locution "the function of X is to Y," as opposed to locutions such as "X functioned to Y," which are often used in the weak sense. So, for example, the fact that "the pocket Bible functioned to stop a bullet" does not imply that "the function of the pocket Bibles is to stop bullets."

WRIGHT'S ETIOLOGICAL ANALYSIS

A watershed in the philosophical analysis of function occurred with Larry Wright's (1973, 1976) "etiological" analysis, from which a variety of competing descendants have sprung. Wright's analysis relies on the insights noted above regarding the effect-explanatory nature of artifact functions. Wright asserted, as a general account of "function," the following:

> The function of X is Z means
> X is there because it does Z,
> Z is a consequence (or result) of X's being there. (1976, p. 81)

The basic idea is that functions refer to explanatory effects, that is, effects of an entity that explain why that entity exists or is present. As an approach to biological function, Wright's analysis suffered from some technical flaws. One cannot say that a specific instance of a mechanism X is there because it does Z, because that implies backward causation; rather, X is an instance of a *type* of mechanism and is there because *past instances* of that type did Z. Similarly, one cannot say that the function Z is a consequence of X's being there, because X could be defective, damaged, or diseased and thus malfunctioning; rather, Z was the consequence of past instances of Xs.

A more fundamental problem was that Wright's claim that sheer effect-explanation is sufficient for the existence of a function cannot be correct. Such effect-explanations are everywhere; for example, a rock resting against another rock is in a state of pressure equilibrium in which its position is explained by its effect in pressing against the other rock in a way that causes the other rock to press back with equal force. Another common example is that, in certain meteorological phenomena, there arise feedback-loop systems that sustain themselves by their own effects; for example, whirlpools and storm systems often move water or air in a circular path that forms a set of pressures that cause continued stable movement in the same way. Yet it is not the function of the whirlpool's water movement or the storm's air movement to maintain the whirlpool or storm.

More problematically for the analysis of "biological function," these examples can have analogs within the organism. For example, near the heart valves, the turbulent blood flow may regularly form small whirlpools of blood with effect-explanatory structures that cause stable continuation of the whirlpool pattern. Yet the existence of such a stable vortex might be merely a mechanical oddity with no fitness implications, thus no functions.

BIOLOGICAL FUNCTIONS AS NATURALLY SELECTED EFFECTS

The reaction to the failures of Wright's analysis was to conclude that the analysis simply was not specific enough, and that biological functions, at least, must involve *selected* effects, not merely any explanatory effects; the *reason* the effects are explanatory must be that they were *selected*. Ruth Millikan (1984) attempted to address this problem by building into the analysis of "function" abstract analogs of the critical features of natural selection.

It is generally held that natural selection in the general sense occurs if and only if four conditions are met: (1) reproduction, in which a family of entities is such that one generation gives rise to another of their kind ("offspring"); (2) variation among the traits of the members of the population; (3) inheritable traits, so that offspring tend to be like their "parents"; and (4) differential reproductive success, in which different variants leave different numbers of offspring. Or, as Hull (1990) has characterized natural selective processes, they consist of the activities of *replicators*, "an entity that passes on its structure largely intact in successive replications," and *interactors*, "an entity that interacts as a cohesive whole with its environment in such a way that this interaction causes replication to be differential" (p. 96). Millikan (1984) builds all these standard conditions into her analysis. She requires a "reproductively established family" in which new members are produced by some kind of copying procedure, and a selection process that explains changed proportions of family members bearing given traits over time by greater reproductive success in the copying process due to the possession of the trait.

However, Bedau (1993), borrowing an example from Dawkins (1986), describes a process occurring in inorganic clay silicates in which chemical processes mimic all the elements of natural selection captured in Millikan's analysis, yet no function attributions seem warranted. Moreover, there are many structures within organisms that are "selected" in Millikan's sense but appear not to have functions. For example, parasitic DNA builds linkages to other genes such that it replicates when the others do, yet its linkage-building, though an effect that via selection explains the parasitic DNA's presence, has no organismic biological function. A further persuasive example is that of the segregation distorter gene, which has special mechanisms that manipulate the cell division (meiosis) which produces eggs and sperm (gametes) in a way that gets the gene into more than its usual share of half of the gametes. But, as Godfrey-Smith (1999b) explains, "disrupting meiosis is something that segregation distorter genes do, that explains their survival. . . . Further, this explanation appeals to natural selection, at the gametic level. . . . Disrupting meiosis is not generally claimed to be the genes' *function* though" (p. 204).

Segregation distorter genes manage to increase their representation in future generations and are thus "selected," but via a causal pathway that does not increase the individual's fitness. Consequently, these genes are not considered to have biological functions for the individual. Functions need not be at the organismic level, and some traits of parasitic DNA and segregation distorter genes possess specifiable biological functions relative to these genes (e.g., certain segregation distorter gene features have the function of causing sperm carrying the rival chromosome to self-destruct, thus increasing the frequency of the segregation distorter gene). But the segregation distorter genes themselves, although selected in Millikan's abstract sense, possess no biological function within the organism because they do not contribute to the organism's greater selective advantage. Consequently, if something goes wrong with a segregation distorter gene's mechanisms, that is not in itself a dysfunction in the sense that yields disorder attributions.

Thus, sheer selection of a feature in Millikan's abstract sense is insufficient for function. The selection must occur because the feature contributes to the organism's fitness (Brandon, 1990; Godfrey-Smith, 1999b). Neander (1991) puts the point this way:

> It is the/a proper function of an item (X) of an organism (O) to do that which items of X's type did to contribute to the inclusive fitness of O's ancestors, and which caused the genotype, of which X is the phenotypic expression, to be selected by natural selection. (p. 174)

Note that Neander's and other etiological analyses of "function" cite not simply the trait's fitness value but the *causal contribution* that the trait makes to fitness. For example, co-occurring traits, such as the weight and warmth of a polar bear's coat, have the same fitness values, but of course it is the warmth of the coat and not its weight that contributes to fitness. Crucial here is Sober's (1984) now-classic distinction between "selection for" versus "selection of" a trait. For example, imagine a machine that separates balls by sifting them for size through various-sized holes and selects for retention only one size that does not fit through any of the holes. The machine may also happen to separate the balls by color and retain only one color, if size and color correlate. In such a case, the machine's selection process results in the "selection of" one color, but the machine's process "selects for" size because the latter property is the one that has the causal impact on the selection process. Similarly, it is the warmth of the polar bear's coat that is selected for, even though there is selection of weight. It is only those features that are selected for, and thus have a causal impact, that are considered relevant to the etiological account of function.

THE IMPORTANCE OF MAINTENANCE: WILLIAMS VERSUS GOULD ON FUNCTION

Neander's phrase that a trait's function caused it "to be selected by natural selection" seems to refer to the *original* selection of the trait, during which the trait initially spread through and became stabilized in the population. However, natural selection also works to maintain traits once they are selected. Without continued selective force acting to preserve a trait and eliminate alternatives, there generally would be eventual erosion of the trait in the population. It is tempting to assume that selective forces stay roughly constant so original selective forces are more or less identical to maintaining forces. However, recent developments in evolutionary theory, especially Gould's influential criticisms of functional reasoning, have underscored the potential complexity of the history of natural selection of a trait and focused attention on divergences between original and maintaining selection.

Problems in addressing maintenance in accounts of function date back at least to Williams's (1966) seminal analysis, in which he distinguished the function of a mechanism from its other effects using an etiological analysis: "The designation of something as the *means* or *mechanism* for a certain *goal* or *function* or *purpose* will imply that the machinery involved was fashioned by selection for the goal attributed to it. When I do not believe that such a relationship exists I will avoid such terms and use words appropriate to fortuitous relationships such as *cause* and *effect*" (p. 9). Williams intended to exclude from the "function" category any benefits not specifically the product of design for that benefit: "One should never imply that an effect is a function unless he can show that it is produced by design and not by happenstance" (Williams, 1966, p. 261). Williams's language (e.g., "fashioned by selection for the goal attributed to it," "produced by design") is most plausibly interpreted as referring to the original selection of a trait. Williams was quite aware that in the search for functions what one initially sees in a population is the ongoing maintenance of design-like selected traits, and the "next task would be to explain why the mechanism in question is maintained as a normal characteristic of the species and not allowed to degenerate" (1966, p. 259). Nonetheless, his definition of function appears to presuppose that original and maintaining selective forces must be the same for a function attribution, because only then can one infer from current maintenance why a trait was originally fashioned.

Gould (1991; Gould & Vrba, 1982) coined the term "exaptation" for novel effects of a trait that increase fitness and thus maintain the trait but were not involved in the trait's original selection. Exploiting the flaw in Williams's analysis, Gould argued that exaptations are neither functions nor explained by natural selection because the feature in question was not originally fashioned for its current purpose. He thus constructed a critique of explanation by natural selection squarely on Williams's definition. Indeed, Williams's definition continues to be cited as justification for Gould's claims about exaptation and function: "By convention (see Williams [1966] for a brief history), the term 'function' applies to the beneficial effect that explains *the alteration of a trait through positive selection*, a usage that Gould and Vrba (1982) merely adopted" (Andrews, Gangestad, & Matthews, 2002, p. 539; emphasis in original).

Thus, in trying to clarify the definition of "function," Williams inadvertently provided ammunition for an attack on evolutionary functional explanation. The snowballing confusion offers a cautionary tale about the importance of getting clear about conceptual issues. Williams (personal communication, 1995) agreed that changing his definition to include maintenance was necessary, and in later years emphasized in talks the necessity of including maintenance in the definition of function (Randolph Nesse, personal communication, 2002).

Gould is correct that the benefits of a trait can change over time; thus, one cannot blithely equate the current benefit with the original benefit for which the trait was naturally selected. For example, although penguins' wings were selected in non-aquatic ancestors for the function of enabling flight, in penguins' more recent evolutionary history the wings have been maintained exclusively as swimming appendages for enabling penguins to propel and steer themselves in the water, and not for flight, so the fitness-enhancing effects of wings have changed. However, contrary to both Williams's definition and Gould's views, "function" attributions do not require original selection for the claimed function but only selective pressure, whether original or maintaining. Natural selection and functions exist whenever there is maintaining selection because maintaining selection offers genuine causal explanation by selected effects of the (continued) existence of the trait. Consequently, it is considered that the function of penguins' wings is swimming, not flight. Maintaining selection is just as much "natural selection" as original selection; thus, so-called exaptations are simply one type of naturally selected function.

Consider, for example, a species of moth in which white coloration has been originally selected for its effect of camouflage against white bark. Imagine further that due to habitat destruction the species migrates to a new forest in which the bark is dark, yet over generations it maintains its white coloration due to a novel selective advantage in the new environment, namely, mimicry of a toxic white species of moth that inhabits the same forest and is avoided by predators. In the first generation in which the moths arrive in their new habitat, it is a lucky accident that their whiteness has the novel benefit of mimicry; however, after generations of maintaining selection for mimicry and no maintaining selection for camouflage, would anyone resist labeling mimicry as the naturally selected function of the moths' coloration? Original selection with alteration of a trait is not a necessary condition for natural selection or function. Consequently, the entire notion of exaptation as Gould deployed it is of questionable usefulness, other than as a marker for changes in selective pressures and thus in function (Wakefield, 1999b).

TIMELINE PROBLEMS

A further challenge for natural selection accounts of function concerns exactly when natural selection must have taken place to warrant a current attribution of function.

Not any selection, no matter how transient or remote in time, qualifies. Obviously, in prototypical cases in which a trait is originally designed and continuously maintained through to the present for the same effect, timeline issues do not arise. However, especially in light of Gould's arguments, evolutionary thinkers have become sensitive to the ways in which selective pressures for the same trait can vary over time. Questions about the evolutionary timeline can enter into disputes about what is normal versus pathological and so are not purely theoretical issues.

It must be kept in mind that to be a function, an effect has to explain the *current presence* of the trait via its effect on fitness. To explain the current presence of a trait, one must cite forces operating earlier than the present that led to the present trait. Neither initial shaping per se nor current selective pressure per se provide such an explanation. Current pressures do not suffice because, for example, there can be sudden changes in selective pressures due to alterations in social circumstances (e.g., oppression of a minority) that do not imply functions because they are too brief to influence the presence of distinguishing features. In attributing a function, we must be assuming that there has been some recent period of explanatory selective pressures that may or may not be the same as original or current pressures and that explain the current trait.

How, then, do changing selective pressures over the history of the trait influence current function? The answer, according to recent proposals, is that what is relevant is relatively recent evolutionary periods of time leading up to the present in which significant selection did take place or might have taken place. This analysis has come to be known as the "modern history" etiological view (Godfrey-Smith, 1999a; Griffiths, 1999): The function of X is Y only if selection for Y has been responsible for maintaining X in the recent past (see Kitcher, 1999, for a discussion of this and other timeline options).

Obviously, this leaves unresolved exactly what is "recent." Griffiths (1999) attempts to explicitly define "recent" in terms of periods during which regressive evolution might be expected to take place:

> An evolutionarily significant time period for trait T is a period such that, given the mutation rate at the loci controlling T, and the population size, we would expect sufficient variants for T to have occurred to allow significant regressive evolution if the trait was making no contribution to fitness. A trait is a vestige relative to some past function F if it has not contributed to fitness by performing F for an evolutionarily significant period. (p. 155)

An interesting feature of this definition is that it recognizes that for a variety of reasons actual variation in a trait, and thus actual selective processes, may not occur during an evolutionarily relevant period. The analysis allows for judgments of function based on what we believe would have happened ("we would expect") if a trait had sufficiently varied during such a period. The assumption that in principle all traits could vary, and they could do so independently even of other traits to which they may be currently linked, is an idealization that seems to be assumed in some function judgments we make in certain kinds of cases in which actual selection has not occurred. For example, a gene that has two vital effects will be judged to have both as its functions. Yet one role might occur during early development, so that actual variations in the gene may always be selected out due to the loss of this developmentally early and critical role, and never because of the developmentally later but equally vital role, simply because variations never allow the opportunity for the organism to develop to the point where there can be selection against the gene based on the later phenotypic variation. In such cases, based on the idealizing assumption that the roles could be independently controlled in principle and that such variations would occur over adequate time spans, we judge that the second role is a function, despite lack of any actual process of natural selection.

Function as a Black Box Essentialist Concept

Williams (1966) notes that many function attributions can be confidently made independently of any particular theory and without reference to the history of the organism, on the basis of careful observation of design-like adaptive qualities. These judgments would be the same whether the observer is Darwinian, Lamarckian, creationist, or Aristotelian, and thus are entirely independent of evolutionary theory.

Thus, Williams really presents two concepts of function: the intuitive widely shared concept defined by direct observation of design-likeness, and the concept defined by the theory of natural selection. The first concept has existed since antiquity. For example, without knowing anything about evolution but just working within the intuitive concept of function, Harvey discovered that the function of the heart is to pump the blood. Presumably the concept of biological function transfers some basic understanding from the sphere of human-designed artifacts to the biological realm, but this does not explain what the basic common feature is that allows such a transfer of conceptual structure because many theorists from earliest times assumed no actual intelligent designer of biological features and their functions. Presumably this basic notion common to artifact and biological explanation is that the effect of a feature must be invoked in explaining why the feature that has the effect is present. Both artifact and biological function explanations have this unique explanatory structure.

The second concept represents the modern scientific account of the essential nature of functions. Analogously, "water" has a traditional intuitive meaning of "the stuff in the rivers and lakes," but we now have a scientific theory of the essential nature of that stuff, namely, molecular structure H_2O. Indeed, for clarity, it might be better not to call the Darwinian account a *concept* of function at all, but rather a *theory* of what biological functions (in the intuitive sense) essentially are and how they came to exist. If the *meaning* of "function" were "effect responsible for the natural selection of a trait," then it would be an empty tautology that the functions of biological traits are naturally selected effects. However, the reality is that Darwin's discovery that natural selection explains why traits have their traditionally understood functions is a momentous scientific discovery, not a tautology.

What, then, is the intuitive concept of biological function that is shared by Darwinians and non-Darwinians and provides the target of Darwin's analysis? The formation of the concept starts from obvious facts. Organisms are unique in the way their features are complexly related, hierarchically organized, strikingly beneficial for survival and reproduction, and produce a viable overall pattern of life. There is no other natural context where causal processes are so seemingly miraculously interwoven. It is not difficult to imagine how a storm or whirlpool might accidentally occur and, via causal feedback processes, remain stable; it is much more difficult to imagine how organisms' design-like traits might have come about, and this cries out for explanation. However, the specific nature of the process long remained unknown. The concept "biological function," I suggest, was a placeholder to refer to the hypothesized unique kind of biological process, whatever they are, that explained apparent functions.

Based on philosophers' insights into natural kind concepts (Putnam, 1975; Searle, 1983) as well as psychologists' insights into essence placeholders (Medin & Ortony, 1989), I call this kind of concept a *black box essentialist concept* (Wakefield, 1999a, 2000a, 2004). Such concepts postulate and allow one to talk about a hidden unknown "essence"—that is, an underlying theoretical process or structure—that explains some initial prototypical set of phenomena. The concept remains agnostic on the specific identity of the underlying essence until scientific research provides an answer. In the case of "function," the prototypical instances would consist of such clear explanatory-effect functions as eyes seeing, hands grasping, feet walking, teeth chewing, fearing danger, thirsting for needed water, and so on.

According to the black-box-essentialist approach, having observed that prototypical biological functions clearly involve effects that must themselves explain the presence of the mechanisms that give rise to them, but not understanding how such a thing was possible, early biologists defined *function* as encompassing any effect of a trait that explains the trait's presence by the same underlying process, whatever it is, by which the prototypical instances of function explain the traits of which they are effects. Of course, theorists have differed greatly over the nature of the hypothesized underlying process that explains the observed clear cases of design-likeness. It was Darwin's explanation in terms of natural selection that succeeded in providing the needed explanation and thus provided a scientific theory of function.

CONCEPTUAL FOUNDATIONS OF EVOLUTIONARY PSYCHOPATHOLOGY: DISORDER AS FAILURE OF DESIGNED FUNCTION

Evolutionary psychopathology is a growing subdiscipline with many diverse strands. First, evolutionary psychopathologists put forward specific evolutionary hypotheses about naturally selected mental modules and their normal functions, and offer theories of the dysfunctions of those mental modules that may underlie specific mental disorders; for example, evolutionary hypotheses suggest the ways in which normal emotional reactions may malfunction to yield panic attacks (Klein, 1993; McNally, 1994) or pathological depression (Nesse, 1991). Second, evolutionary psychopathologists attempt to explain how specific debilitating mental disorders have continued to exist in the population despite presumed selective pressures against them, by showing how they might be the direct or indirect results of selective pressures. For example, certain personality disorders may be due to unselected extremes on dimensional traits. Third, evolutionary theorists use an evolutionary framework to distinguish psychopathology from other problematic conditions that might be subject to treatment by mental health professionals (Cosmides & Tooby, 1999), including excessive designed defensive reactions (as in high fever or sadness) and mismatches between naturally selected mechanisms and the current environment (e.g., the appetite for sugar and fat in our food-rich environment).

I focus here on a further and more fundamental issue for clinical psychology, namely, clarifying the concept of mental disorder itself. A mental disorder may be considered a disorder of mental mechanisms and thus is conceptually analogous to disorders of other kinds of mechanisms. Thus, the problem is to define "disorder" in the general sense used in medicine and then apply it to the domain of mental mechanisms. It is here, at the foundation of clinical psychology, that evolutionary psychopathology is crucial and determines an agenda that heavily involves evolutionary considerations in psychopathology research.

Disorder as Harmful Dysfunction

The view to be considered here is the harmful dysfunction (HD) analysis of the concept of mental disorder (Wakefield, 1992a, 1992b, 1993, 1996, 1997, 1999b, 2000b, 2006; Wakefield & First, 2003), which asserts that a mental or physical disorder must be (a) harmful, that is, negative as judged by social values, and (b) caused by a dysfunction, that is, by failure of a psychological mechanism to perform its function, in the sense of "biological function" as analyzed earlier in this chapter. This concept is arguably at the root of both psychiatric and lay judgments of disorder versus nondisorder. Dysfunction and function in the relevant sense are theoretically best understood in evolutionary terms, and thus in principle are factual scientific concepts. Thus, disorder in the medical sense is a hybrid value and factual concept. Because dysfunction is a necessary requirement for disorder according to the HD analysis, this offers a way to critique standard diagnostic criteria in the *DSM-5* (American Psychiatric Association [APA], 2013) when they are applied to problems of living that are not true disorders, while still accepting the reality of mental disorders as genuine medical disorders and thus rejecting the anti-psychiatric claim that mental disorder does not exist (Szasz, 1974). I focus here on exploring the evolutionary dysfunction component.

The view that the concept of disorder somehow involves dysfunction emerges with remarkable consistency in the remarks of many authors who otherwise differ in their views (e.g., Ausubel, 1971; Boorse, 1975; Kendell, 1975, 1986; Klein, 1978). Spitzer and Endicott (1978) note the seeming necessity and virtual universality of using "dysfunction" to make sense of "disorder": "Our approach makes explicit an underlying assumption that is present in all discussions of disease or disorder, i.e., the concept of organismic dysfunction" (p. 37). The *DSM-5* (2013) also specifies that a disorder exists only when symptoms are due to an underlying dysfunction: "A mental disorder is a syndrome characterized by clinically significant disturbance in an individual's cognition, emotion regulation, or behavior that reflects a dysfunction in the psychological, biological, or developmental processes underlying mental functioning" (p. 20). To understand "disorder," one requires an adequate analysis of "function" and "dysfunction."

Supposing that a disorder is a dysfunction, what, then, is a dysfunction? Dysfunction implies unfulfilled function, thus failure of some mechanism in the organism to be able to perform its function. However, not all uses of "function" and "dysfunction" are relevant to disorder judgments. The medically relevant sense of "dysfunction" is clearly *not* the colloquial sense in which the term refers to failure of an individual to perform well in a social role or in a given environment, as in assertions like "I'm in a dysfunctional relationship" or "discomfort with hierarchical power structures is dysfunctional in today's corporate environment." These kinds of problems need not be individual disorders. Moreover, the kinds of functions that are relevant are *not* those that result from social or personal decisions to use a part of the mind or body in a certain way. For example, the nose functions to hold up the glasses, and the sound of the heart performs a useful function in medical diagnosis. Nonetheless, a person whose nose is shaped in such a way that it does not properly support glasses does not thereby have a nasal disorder, and a person whose heart does not make the usual sounds clearly enough to be useful for diagnosis is not thereby suffering from a cardiac disorder. A disorder is different from a failure to function in a socially or personally preferred manner precisely because a dysfunction exists only when a feature cannot perform its naturally (i.e., independently of human intentions) designed function. The functions that are relevant to disorder attributions are precisely the "natural" or "biological" functions analyzed above.

Thus, disorders involve dysfunctions, and dysfunctions are failures of organismic mechanisms to perform their biologically designed functions. More strictly, to eliminate possible counterexamples in which normal organisms cannot perform their functions because the environment does not allow them to (in which case they are not generally considered disordered), dysfunctions are failures of mechanisms to be capable of performing their functions under environmental circumstances for which the mechanisms were designed to perform such functions. The disruption of the biologically designed "order" is why there is a "disorder," according to this view.

One might object that sometimes, for example in reading disorders, what goes wrong is a social function that has nothing to do with naturally selected categories. However, even though we are not biologically designed to read, inability to read is only considered indicative of disorder when evidence suggests the cause is a failure of some brain mechanism to perform its natural function.

If one looks down the list of *DSM-5* (APA, 2013) disorders, it is apparent that it is a list of the various ways that something can go wrong with the seemingly designed features of the mind. Roughly, psychotic disorders involve failures of thought processes to work as designed, anxiety disorders involve failures of anxiety- and fear-generating mechanisms, depressive disorders involve failures of sadness and loss-response regulating mechanisms, disruptive behavior disorders of children involve failures of socialization processes and processes underlying conscience and social cooperation, sleep disorders involve failure of sleep regulation, sexual dysfunctions involve failures of various mechanism involved in sexual motivation and response, eating disorders involve failures of appetitive mechanisms, and so on. There is also a certain amount of nonsense in the *DSM-5*. However, in the vast majority of categories, a good case can be made that the category is inspired by conditions that even a layperson would correctly recognize as a failure of designed functioning.

When we distinguish normal grief from pathological depression, or normal delinquent behavior from conduct disorder, or normal criminality from antisocial personality disorder, or illiteracy from reading disorder, or normal lack of empathy for enemies of one's group from sociopathic lack of empathy for anyone, or normal childhood rambunctiousness from attention-deficit/hyperactivity disorder, we are implicitly using the "failure-of-designed-function" criterion. That criterion explains why some of these conditions are considered disorders and others that are quite similar and also negatively evaluated are not.

DISORDER AS EVOLUTIONARY DYSFUNCTION

The HD analysis holds that the intuitive concept of "disorder" requires dysfunction, and dysfunction occurs when an internal mechanism is incapable of (or impaired in) performing one of its natural functions. Until this point in the analysis, *natural function* is used in the intuitive black-box essentialist sense that has existed for millennia, not in a technical evolutionary sense. The further evolutionary theoretical argument applied in the case of "function" applies to "dysfunction" as well. Given that evolutionary theory explains natural functions, disorders are harmful failures of mechanisms to perform functions for which they were naturally selected.

Thus, evolutionary psychology and the field of psychopathology converge. Indeed, evolutionary psychopathology *becomes* the discipline of psychopathology. The *DSM-5* can be seen as an attempt to list categories that prima facie involve failures of naturally selected mental mechanisms to perform their functions, whether they concern thought, emotion, sexual functions, sleep functions, socialization and moral development functions, and so on.

The HD analysis implies that a society's categories of mental disorder offer two pieces of information. First, they indicate a value judgment that the society considers the condition negative or harmful. Second, they make the factual claim that the harm is due to the mind's failure to work as designed. This claim may be correct or incorrect. The value component cannot be reduced to the evolutionary component because natural selection works ultimately on genes, not people, and sometimes what serves the gene's replication is not what a given culture considers good for the individual, or failure of some function does not matter enough to be labeled a disorder. Natural human functioning and human visions of a good life do not necessarily coincide. Moreover, normal human defensive responses are often biologically designed to over-respond to potential signals of threat and thus confer needless but normal distress for the same reason that smoke detectors often respond to harmless conditions such as the smoke coming from cooking fish, namely, because the cost of missing a true danger is so much greater than the cost of some needless responses to false signals.

The HD analysis is often the framework for arguments that conditions that are considered disorders are in fact naturally selected variants and thus not disorders, contrary to *DSM-5* (Nesse & Stein, 2012). For example, intense normal sadness can easily be mistaken for depressive disorder (Horwitz & Wakefield, 2007; Wakefield, 2013); intense anxiety over evolutionarily shaped fears can be mistaken for anxiety disorders (Horwitz & Wakefield, 2012; Stein & Nesse, 2011); adolescent rambunctious behavior can be mistaken for conduct disorder (Wakefield, Pottick, & Kirk, 2002); and so on. The HD analysis has been applied to a great range of diagnostic categories in debates over their diagnostic status as disorders or nondisorders, including hebephilia (the proposed disorder of sexual desire for young teenagers; Rind & Yuill, 2012), psychopathy (which has been argued to be a normal variant; Krupp, Sewall, Lalumiere, Sheriff, & Harris, 2012), and substance dependence (Martin, Chung, & Langenbucher, 2008; Vergés, Steinley, Trull, & Sher, 2010; Wakefield & Schmitz, 2014).

Pitfalls in Arguments That Mental Disorders Are Naturally Selected Conditions

The HD analysis is in tension with arguments in evolutionary psychopathology that attempt to explain apparent disorders (e.g., schizophrenia, major depression) as naturally selected. The HD analysis implies that such claims that disorders are naturally selected are not merely false but incoherent. A disorder is a failure of a natural function and thus cannot itself be the function of a naturally selected trait, according to the HD analysis. A major source of confusion in attempts to explain how disorders were naturally selected is that current disorder categories are not adequately founded on an evolutionary understanding of normality (Nesse & Stein, 2012) and thus tend to run together normal distress and true pathology.

Proponents of natural-selection explanations of disorders generally attempt to explain away the apparent paradox of a seemingly debilitating disorder being naturally selected in one of two ways: either the disorder has hidden fitness benefits that offset its seeming disadvantages, or the disorder increased fitness in past environments but has become problematic in the current environment. However, if the apparent negative effects of a condition are just the evolutionary price paid for the condition's positive effects, then the condition should not be labeled a disorder. For example, the immense pain associated with childbirth is not judged a disorder because birth is obviously a designed process. Similarly, mismatches between human nature and our changing social environment are not necessarily disorders. For example, sexual desire for individuals other than one's spouse and desire for sugar and fat are aspects of human nature that are mismatched to our monogamous and food-rich environment and are thus often harmful, but neither is a disorder.

In advancing explanations of why seeming disorders are in fact naturally selected, evolutionary psychologists often ignore the more plausible hypothesis that the mechanisms underlying the condition are malfunctioning, yielding a condition that was never selected for. There are many pitfalls that can lead a theoretician astray when making claims that disorders have been naturally selected.

First, an evolutionary psychologist might rely on standard *DSM-5* (APA, 2013) diagnostic categories and criteria as the targets of the analysis, without independently assessing the conceptual validity of the criteria. Thus, what are claimed to be natural-selection explanations of disorders in fact may be explanations of nondisorders. Ample evidence suggests that *DSM-5* criteria often mistakenly diagnose nondisorders as disorders. For example, *DSM-5* symptom-based criteria likely erroneously classify many normal states of sadness and anxiety as disorders (Horwitz & Wakefield, 2007, 2012). Nondisordered states of sadness might indeed be subject to evolutionary explanation in terms of, say, retreat during periods of threat, that erroneously is thought to explain depressive disorder. However, true depressive disorders that chronically debilitate cannot be explained as fitness enhancing in this way and are better explained as malfunctions in sadness-generating mechanisms. Because of the invalidity of *DSM-5* diagnostic criteria, the theorist may not adequately distinguish cases within a category that are disorders from other relatively mild and possibly adaptive versions of the same condition.

Second, *DSM-5* criteria aside, an evolutionary psychologist might unreflectively assume that any harmful condition that is treated or treatable can be considered a disorder. Again, this can lead to the theoretician evolutionarily explaining conditions that he or she labels disorders but are not true disorders. Obviously, there are many life problems that are treated but are not disorders. For example, normal shortness is sometimes treated with growth hormones, and normal grief with antidepressants, and birth control pills and abortion treat normal reproductive conditions.

Third, an evolutionary psychologist might embrace a natural-selection explanation of a condition that is an apparent disorder, and overlook a more plausible indirect evolutionary explanation of why the condition has been retained in the population (e.g., retention of a homozygous condition such as sickle cell anemia due to selective advantage of heterozygous condition). However, the indirect explanation may imply that the condition has no function at the organismic level.

Finally, evolutionary analysis may succeed in explaining a condition currently labeled a disorder, and the theorist may erroneously assume that the explanation itself has no implications for the condition's classification. That is, the theorist may fail to appreciate that demonstrating that a condition is part of human design inevitably casts doubt on the condition's disorder classification and triggers its reclassification as normal. This is exactly what happened, for example, with fever, which was once considered a pathology involving a breakdown in temperature regulation, but was reclassified as normal when it turned out that fever is a highly regulated process designed to aid recovery from illness. Treatment of fever is still undertaken because this problematic defense often is not needed for recovery, although it remains possible that reduction of fever may have some negative consequences (Earn, Andrews, & Bolker, 2014). Such defensive reactions are not considered disorders once they are recognized for what they are.

CONCLUSION

Conceptual analysis leads to the conclusion that at the roots of "function," "dysfunction," and "disorder" are notions of design and failure of designed functioning. These notions in turn are built on the idea of effects that explain why the mechanisms that produce them are there, and, in the case of "dysfunction," on the failure of such mechanisms to be capable of producing such explanatory effects. Darwin's scientific discoveries revealed that the only plausible way to understand such explanatory effects in biology is in terms of natural selection. Consequently, judgments of psychological normality and disorder are in fact judgments about evolutionary design. Whether the *DSM-5* diagnostic criteria used by clinicians and researchers every day are valid, and how to make them more valid, hangs on our understanding of human mental design and on progress in evolutionary psychology.

Fortunately, plausible judgments about design and failure of design often can be made without knowledge of evolutionary history, based on immediate evidence regarding design-like properties. Current *DSM-5* categories, which pick out some categories of disorder reasonably well, testify to this fact. So, clinical psychology need not come to a halt while awaiting evolutionary psychology's progress. But in the long run, the *DSM-5* must attend to evidence of dysfunction and work towards a functional understanding of mental mechanisms (First & Wakefield, 2013; Nesse & Stein, 2012). The scientific progress of the mental health professions in understanding the etiology, diagnosis, and treatment of mental disorder may well depend partly on progress in evolutionary psychology.

However, there is the potential for intense controversy about function judgments, as issues of what is human nature become politicized. Moreover, judgments of dysfunction and disorder are often highly controversial due to the stakes of different constituencies in pathological versus normal classification of certain conditions. The intersection of these two intensely controversial areas promises that those in the field of evolutionary psychopathology will continue to find themselves living in interesting times.

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CHAPTER 43

Evolutionary Psychology and Mental Health

RANDOLPH M. NESSE

MENTAL HEALTH RESEARCH is in a crisis (Brüne et al., 2012). The predominant framework has assumed that mental disorders have specific brain causes of the sort that explain multiple sclerosis. However, thousands of reductionist researchers supported by billions of dollars have not found a specific cause, or even a reliable biomarker, for any of the major mental disorders. The evolutionary perspective that revolutionized understanding of animal behavior over a generation ago (Alcock, 2001) can help explain why the search has not succeeded, and it can suggest new approaches.

At the core of that revolution is recognition that a full explanation of any biological trait requires a description of its evolutionary history as well as its mechanism (Nesse, 2013; Tinbergen, 1963). For a disease, a full understanding requires knowing not only why some individuals get sick, but also why all members of the species have traits that are vulnerable to failure (Nesse, 2005b; Nesse & Williams, 1994; Williams & Nesse, 1991). Seeking such explanations has led to rapid developments in evolutionary medicine (Nesse et al., 2010; Stearns, 2012). They are now ready for application in psychiatry.

The core insight is that evolution can explain not only why most traits work so well, but also why many are vulnerable to failure. Attempts to explain why the mind is vulnerable have a long history. What is new is taking such questions seriously and posing and testing alternative evolutionary hypotheses. This chapter summarizes recent progress and the substantial challenges associated with seeking evolutionary explanations for mental disorders.

WHAT EVOLUTION OFFERS

Early applications of ethology to mental disorders (McGuire & Fairbanks, 1977) gave rise to more specific and comprehensive evolutionary approaches (McGuire & Troisi, 1998; Nesse, 1984; Wenegrat, 1990). Several books cover specific conditions (Baron-Cohen,

Table 43.1
Eight Contributions of an Evolutionary Perspective on Mental Disorders

1. Explains why humans are vulnerable to mental disorders
2. Offers a functional understanding of behavior
3. Fosters a deeper and more empathic understanding of individuals
4. Explains how relationships work
5. Provides a way to think clearly about developmental influences
6. Provides a functional approach to emotions and their regulation
7. Provides a foundation for a scientific diagnostic system
8. Provides a framework for considering how multiple causal factors can explain why some people get mental disorders while others do not

1997; Gilbert, 1992; Horwitz & Wakefield, 2007, 2012; Wenegrat, 1995). The field finally has a textbook (Brüne, 2008) to augment the previous major treatment (McGuire & Troisi, 1998). Many articles address specific mental disorders, and some provide a new foundation for defining the categories that describe disorders (Cosmides & Tooby, 1999; Nesse & Stein, 2012; Wakefield, 1992). Several chapters in this *Handbook* and many general books about evolutionary psychology tackle specific disorders.

The diverse ideas in these sources can be summarized in eight fundamental contributions that an evolutionary perspective offers to psychiatry and clinical psychology (see Table 43.1). A brief summary of each sets the stage for considering specific disorders.

EXPLAINING VULNERABILITY TO MENTAL DISORDERS

The task of explaining why all humans are vulnerable to mental disorders is no different from that of explaining why we are vulnerable to other diseases. The tendency in both cases has been to attribute vulnerability to the limited powers of natural selection. These limits are important explanations for some diseases, but there are five other possible reasons why the body and mind are not better designed (Nesse, 2005b; Nesse & Williams, 1994; Williams & Nesse, 1991) (see Table 43.2). Brief summaries of each kind of explanation are an important prelude to their application to mental disorders.

Constraints Mutations happen, and deleterious ones can persist despite natural selection. Also, there is no starting fresh with bodily designs, so substandard aspects abound. But this is not the main explanation for vulnerability to disease.

Table 43.2
Six Evolutionary Explanations for Vulnerability

1. Natural selection constrained
2. Mismatch with modern environments
3. Coevolution with fast-evolving organisms
4. Trade-offs
5. Advantages for alleles at the expense of health
6. Defenses that are useful

Mismatch Most common chronic diseases are caused by novel environmental factors (Gluckman & Hanson, 2006). For instance, atherosclerosis and breast cancer are prevalent now because our bodies are not well-suited for life in a modern environment. Whether rates of mental disorders are increasing remains uncertain. An international effort to gather prevalence data on mental disorders from 72,000 interviews in 14 countries (Kessler & Ustun, 2000) uses urban or rural agricultural sites. No comparable effort has estimated disorder rates in hunter-gatherer populations. Technical difficulties make this understandable, but it is nonetheless unfortunate, because such studies may not be possible in the next generation.

Mental disorders are often blamed on the modern environment (Stevens & Price, 1996), and that is certainly correct to some extent, but it is hard to tell which disorders are really more common. Retrospective data suggested that depression rates were increasing rapidly with each generation (Cross-National Collaborative Group, 1992). However, data gathered using consistent questions in the same population over recent decades showed no such increase (J. M. Murphy, Laird, Monson, Sobol, & Leighton, 2000).

Infection and Coevolution Natural selection cannot remove vulnerability to infection because pathogens evolve faster than we can (Ewald, 1994). Furthermore, the defenses that protect us, especially immune responses, tend to cause problems themselves. Some mental disorders may result from arms races with pathogens and their autoimmune sequelae. For instance, some cases of obsessive compulsive disorder may result from streptococcal-induced autoimmune damage to the caudate nucleus (Swedo, Leonard, & Kiessling, 1994). Prenatal exposure to infection may predispose to schizophrenia (Ledgerwood, Ewald, & Cochran, 2003). Infectious causes have been proposed for a wide range of mental disorders, especially affective disorders (Ewald, 2000), and the role of inflammation in depression is increasingly recognized (Raison & Miller, 2013).

Trade-Offs Design trade-offs make perfection impossible for any trait, natural or human-made. We could have less anxiety, but only at the cost of being more likely to be injured or killed. We could be more trusting, but at the cost of being exploited.

Selection Is for Reproductive Success, Not Health A gene that decreases health, longevity, or happiness will nonetheless be selected for if it increases reproductive success (RS). Such genes are likely responsible for many of our least valued characteristics, such as bitter competition, envy, greed, and unquenchable sexual desire and jealousy (Buss, 2000). The differences between the sexes arise largely because different reproductive strategies shape different physical and mental traits, even at the expense of longevity and individual well-being (Cronin, 1991; Daly & Wilson, 1983; Geary, 1998; Kruger & Nesse, 2004).

Defenses As noted above, pain, cough, fever, and other protective responses are unpleasant but useful responses that protect us from danger and loss. The prevalent tendency to confuse these defenses with diseases and defects has been called "The Clinician's Illusion" (Nesse & Williams, 1994). Most physicians know that cough and inflammation are adaptations, but the utility of fever, diarrhea, and anxiety is less widely recognized. A naïve view sees our vulnerability to negative emotions as examples of poor design. But natural selection does not care a fig for our happiness; it just mindlessly shapes whatever emotional tendencies increase RS (Nesse, 1991a; Tooby & Cosmides, 1990). The smoke detector principle (discussed later) explains why many instances of negative emotions are excessive or unnecessary (Nesse, 2005c).

The Challenges of Evolutionary Medicine Some evolutionary approaches to mental disorders emphasize one of these six possible explanations, to the exclusion of others. For instance, some authors emphasize the effects of living in a modern environment (Glantz & Pearce, 1989; Stevens & Price, 1996); others emphasize infection (Raison & Miller, 2013) or constraints, tradeoffs, or path dependencies (Crow, 1997; Horrobin, 1998). Others propose that mental disorders persist because of fitness benefits, even for conditions such as schizophrenia (J. S. Allen & Sarich, 1988; Shaner, Miller, & Mintz, 2004), bipolar disorder (Wilson, 1998), and suicide (deCatanzaro, 1980). Emphasizing one cause to the exclusion of others causes substantial confusion.

This is only one of 10 mistakes that are common in attempts to find evolutionary explanations for diseases. See the text box for a list of others. They can be prevented by addressing 10 questions systematically when pursuing projects in evolutionary medicine (Nesse, 2011).

Ten Common Mistakes When Attempting to Find Evolutionary Explanations

1. Attempting to explain a disease instead of vulnerability to a disease
2. Proposing an explanation based on group selection
3. Proposing adaptive functions for rare genetic conditions
4. Confusing proximate and evolutionary explanations
5. Framing learning as an alternative to an evolutionary explanation
6. Viewing environmental or cultural differences in a trait as evidence against evolutionary influences
7. Offering a genetic explanation as an alternative to an evolutionary explanation
8. Failing to consider all alternative hypotheses
9. Assuming that evidence for one hypothesis is evidence against another
10. Presenting the evidence in favor of a pet hypothesis and the evidence against other hypotheses, instead of considering all evidence for and against all hypotheses

AN EVOLUTIONARY FRAMEWORK FOR UNDERSTANDING HUMAN BEHAVIOR AND EMOTIONS

When a patient comes to the general medical clinic with a cough or kidney failure, the physician knows that a cough is a protective response and that the kidney regulates salt and water balance. By contrast, when a patient comes to a mental health clinic with a phobia, the utility of anxiety may never be considered. When someone comes with jealousy, consideration of its normal functions is unlikely. Mental health professionals lack knowledge about normal emotional functions comparable to the understanding physiology offers to general medicine. Evolutionary psychology is beginning to provide this missing body of knowledge, as shown by the chapters in this *Handbook*, and by evolutionary perspectives on motivation (French, Kamil, & Leger, 2000), emotion (Nesse, 1990a; Plutchik, 2003), and specific topics such as grief (Archer, 1999; Nesse, 2005a).

UNDERSTANDING INDIVIDUAL LIVES

EP can bring information about an individual's idiosyncratic values, goals, and life situations into a scientific framework. Consider John, a depressed 20-year-old man who works two jobs in local stores to support his disabled mother. When he was 14, his dying father made him promise to take care of his mother always. He has been doing that ever since, but with increasing resentment and depression. These three sentences give more insight into his depression than a dozen demographic variables and a brain scan. An evolutionary understanding of motivation can bring such information into a nomothetic framework based on the behavioral ecology categories of life history effort: somatic, reproductive, and social.

RELATIONSHIPS

EP's greatest contribution may be a deeper understanding of relationships. For instance, Bowlby's insights about the evolutionary functions of attachment (Bowlby, 1969) have been extended by suggestions that apparently "abnormal" kinds of attachment may represent alternative strategies for infants to get resources from their mothers in difficult circumstances (Belsky, 1999; Chisholm, 1996) and a deeper understanding of women's reproductive strategies in general (Hrdy, 1999). Analysis of mutually beneficial reciprocal exchanges has led to extensive studies of economic games (Fehr & Fischbacher, 2003) that illuminates the origins of the social emotions (Fessler & Haley, 2003; Fiske, 1992). However, interpreting all human relationships as calculated exchanges ignores aspects of human life that are essential to understanding mental disorders, such as our capacities for moral action, and the emotions of pride and guilt (Katz, 2000). Selection has shaped capacities for commitment that are sometimes superior to rational calculation (Frank, 1988; Gintis, 2000; Nesse, 2001a). People choose the best partners available. These selfish choices create powerful selection forces that shape prosocial capacities, including altruism and moral sensitivities (Nesse, 2010; Noë & Hammerstein, 1995).

Psychodynamics Freud's theories are ridiculed because some are wrong and psychoanalytic treatment is not reliably effective. However, the reality of repression is a profound fact of human nature that needs an evolutionary explanation (Badcock, 1988; Nesse, 1990b; Sulloway, 1985). Trivers and Alexander separately suggested that self-deception is a strategy for deceiving others (Alexander, 1975; Trivers, 1976, 2011), but people also may repress the sins of others to preserve valuable relationships (Nesse, 1990b).

Closely related is Trivers's insight that regression may be a strategy used by offspring to manipulate their parents into providing resources that would be appropriate only if they were younger or sick (Trivers, 1974). His more general theory of parent-offspring conflict is the neglected foundation for understanding many childhood disorders (Trivers, 1974). Attempts to provide an evolutionary foundation for psychodynamics are developing (Badcock, 1988; Nesse & Lloyd, 1992; Slavin & Kriegman, 1992; Sulloway, 1985), but remain relatively unappreciated by psychoanalysts. This may be because an evolutionary view fosters skepticism that undermining repression will be helpful routinely (Slavin & Kriegman, 1990).

DEVELOPMENT

Developmental psychology now offers sophisticated assessments of extensive data about what children do at different stages of life, and how these phenomena vary across cultures. It increasingly considers evolution (P. P. G. Bateson & Martin, 2000; Geary & Bjorklund, 2000; Rutter & Rutter, 1993). In the midst of a burst of interest in facultative developmental mechanisms and their role in evolution (Hall, 1998; West-Eberhard, 2003), evolutionary psychologists have begun looking for mechanisms that use environment inputs to adjust developmental pathways (Del Giudice, Ellis, & Cicchetti, in press).

A possible adaptation with particular relevance for mental disorders is the adjustment of the gain in the hypothalamic pituitary axis system in response to early stress, and the transmission of this sensitivity across the generations by maternal influences on fetal brain development (Ellis & Del Giudice, 2014; Essex, Klein, Eunsuk, & Kalin, 2002; Teicher et al., 2003).

Advances have been rapid in applying evolutionary thinking to aspects of child development that contribute to psychopathology (Bjorklund & Pellegrini, 2002; Del Giudice et al., in press; Frankenhuis & Del Giudice, 2012; Narvaez, Panksepp, Schore, & Gleason, 2012). In particular, intensive work focuses on early effects, even in utero, that influence stress reactivity via genomic imprinting (Bateson et al., 2004; B. J. Ellis, Jackson, & Boyce, 2006; Gluckman et al., 2009; Meaney, 2010). An important debate is underway about how to distinguish epiphenomena from facultative adaptations that detect and transmit information that increases fitness for future generations.

EMOTIONS AND THE EMOTIONAL DISORDERS

Most mental disorders are emotional disorders. People come for treatment because they experience anxiety, depression, anger, or jealousy. Many assume that such negative emotions are abnormal, but they are useful, at least for our genes. People with depression and anxiety are so obviously impaired that it is hard to see how such emotions could be useful. However, the principles of signal detection theory explain why selection shapes emotion regulation mechanisms that often give rise to normal but useless suffering—the smoke detector principle (Nesse, 2005c). Emotions are now routinely recognized as special states shaped by selection to give advantages in fitness-significant situations that have recurred over evolutionary time (Ekman, 1992; Nesse, 1990a; Nesse & Ellsworth, 2009; Plutchik, 2003; Tooby & Cosmides, 1990), but this fundamental principle has yet to be incorporated into research on emotional disorders.

DIAGNOSIS

When is an emotion abnormal? The criteria for psychiatric diagnoses are based on symptom intensity, duration, and associated disability, with no consideration of context (American Psychiatric Association, 2013). The extremes are reliably abnormal, but without knowing the functions of emotions, the line between normal and abnormal remains subjective (D. Murphy & Stich, 2000; Nesse, 2001b; Nesse & Stein, 2012; Troisi & McGuire, 2002; Wakefield, 1992). The lack of an evolutionary foundation fosters serious errors, including describing continuous emotions as categories and neglecting abnormal conditions characterized by excess positive or deficient negative emotions. If general medicine ignored context the way psychiatric diagnosis does, it would diagnose "abnormal cough disorder" based on cough frequency and severity without considering possible causes. Far from genuinely atheoretical, the *DSM* system fosters a crude view of mental disorders that considers only mechanisms, while neglecting the other half of biology (Horwitz, 2002).

Wakefield (1992) offers a strong critique of the *DSM*, using the concept of "harmful dysfunction" to clarify what is and is not a disorder. This sophisticated evolutionary analysis of psychiatric diagnosis argues that it is essential for mental as well as physical disorders to separate normal from abnormal phenomena based whether they are harmful and whether they arise from a dysfunction (Wakefield, Chapter 42, this volume).

INDIVIDUAL DIFFERENCES

Most psychiatric research attempts to explain individual differences—why some people get sick while others do not. Despite growing agreement on the importance of gene-environment interactions (Kendler, Kuhn, & Prescott, 2004; Ridley, 2003; Rutter & Rutter, 1993), different authorities emphasize different causal factors (genetic, developmental, situational, etc.). Far from emphasizing genetic differences, an evolutionary view provides a framework that highlights the relationships among all factors and levels. It also contributes strategies for avoiding some simple mistakes.

Much misunderstanding arises from confusing attempts to explain the existence of a trait with attempts to explain variations in a trait. As Richard Lewontin has emphasized, it is senseless to ask whether the area of a rectangle is caused more by its length or its width. However, *variation* among rectangles can only arise from differences in width or length. Likewise, all traits result from genes interacting with environments, but variations among individuals can result only from differences in genes, differences in environments, and GxE interactions. The proportion of variance attributable to each component is, of course, not fixed, but varies depending on the particular environment and the range of genotypes. Preoccupation with nature versus nurture has distracted attention from the many different routes to a disorder. An evolutionary approach fosters simultaneous consideration of the many factors that may explain individual variation in a trait (see also Arslan & Penke, Chapter 45, this volume).

The task of accounting for individual differences should not be reduced to arguing about the relative importance of one factor compared to another. It is, instead, the challenge of explicating how each contributes to individual differences in a particular trait, and how their contributions to a particular trait may be different not only among families, populations, or cultures, but *even among individuals*. The responsible factors may be mainly genetic in one individual and mainly environmental in another. An individual can have one depression episode triggered by relationship failure and another triggered by inflammation. This has practical implications for mental health research. For instance, research that looks for "the cause" of depression is unlikely to succeed.

SPECIFIC DISORDERS

The fundamental principles of evolutionary biology prove their utility when applied to specific mental disorders. Following traditional categories, these principles apply to emotional, behavioral, and cognitive disorders.

EMOTIONAL DISORDERS

Most mental disorders are emotional disorders, but diagnosis and treatment are not yet based on knowledge about the evolutionary origins and functions of emotions. Instead, intense or prolonged negative emotions are viewed as abnormal, irrespective of the situation, while deficits in negative emotions and excesses of positive emotions are rarely recognized as disorders. Progress will require correcting this fundamental error.

Anxiety Disorders Although anxiety can be useful, a dry mouth and tremor when standing before a large group is worse than useless. Likewise, the symptoms of panic may help escape from a lion, but they are unhelpful in a grocery store. We now have vast knowledge about the responsible brain mechanisms, but no comparable body of knowledge about the evolutionary origins and utility of social anxiety or panic (Nesse, 1987). Similarly, hundreds of studies document every aspect of excessive anxiety states, but only a handful look for states of deficient anxiety, the hypophobias (Marks & Nesse, 1994). One study tried to confirm that fear of heights often results from severe falls early in life. It found adult fear of heights in 18% of the control group, but only 3% of the group that had experienced a fall early in life. Those with hypophobia early in life still had deficient anxiety decades later (Poulton, Davies, Menzies, Langley, & Silva, 1998).

Anxiety illustrates the diversity of the body's regulation mechanisms. For instance, rigid defensive responses to fixed cues, such as chicks hiding from hawk-shaped shadows, are useful when a correct response to the first encounter is essential, but they result in many false alarms and do not protect against novel dangers. Flexible learning mechanisms protect against novel dangers but may fail during a crucial initial exposure, and they are prone to result in phobias. Social learning is another solution. Infant rhesus monkeys show no innate fear of snakes; however, a single observation of another monkey displaying fear of snakes induces long-lasting avoidance. Watching another monkey display fear of a flower induces no such fear (Mineka, Keir, & Price, 1980).

Exposure treatment is effective for phobias, but it does not undo the learned fear response. Instead, new cortical processes suppress the fear response (Quirk, 2002). Exposure to danger disrupts this suppression. Thus, the great flood in Moscow caused the reemergence of previously extinguished fears in Pavlov's dogs. This may reflect a constraint in a path-dependent mechanism; simple unlearning may not be possible.

Other fears cannot be extinguished. For instance, post-traumatic stress disorder (PTSD) illustrates one-time learning of the strongest sort. Proximate science is steadily homing in on the mechanisms that account for this syndrome, but evolutionary hypotheses about the potential utility of PTSD are just being considered (Cantor, 2005). Nearly dying is so important to fitness that a learning mechanism that responds to a single experience to cause severe symptoms could nonetheless give an advantage.

Fear has distinct subtypes that seem to have been partially differentiated from generic anxiety to cope with domain-specific challenges (Marks & Nesse, 1994). For instance, panic flight is just the ticket to escape from a predator, but frozen immobility is superior when teetering on a cliff. Social anxiety is present in most people (Gilbert, 2001; Leary & Kowalski, 1995), and people who lack it are often insufferable, even if they do not qualify for a psychiatric diagnosis. One wonders how they would have fared in small hunter-gatherer groups.

The smoke detector principle helps to explain some apparent peculiarities of the mechanisms that regulate anxiety and other defenses (Nesse, 2005c). Because most anxiety responses are inexpensive and protect against huge potential harms, an optimal system will express many alarms that are unnecessary in the particular instance, but nonetheless perfectly normal. This suggests that using drugs to block defenses may be safe in most instances, but that in some situations blocking a defense may be fatal. A sophisticated formal mathematical treatment should help to advance research in this area (M. Bateson, Brilot, & Nettle, 2011). A major book takes an evolutionary view of when anxiety is a harmful dysfunction (Horwitz & Wakefield, 2012), and why it is so difficult for psychiatric researchers to recognize the utility of anxiety.

Mood Disorders The utility of sadness and depression is less obvious than for anxiety, but Bibring long ago suggested that depression signaled the need to detach when libido persists in a connection to an unrewarding object (Bibring, 1953). Hamburg (Hamburg, Hamburg, & Barchas, 1975) and Klinger (Klinger, 1975) described how emotions regulate goal pursuit more generally, with inability to reach a goal first arousing aggressive attempts to overcome a frustrating obstacle, then low mood motivating disengagement. If the person does not give up, the ordinary low mood escalates into depression. This principle, now confirmed by much research (Brickman, 1987; Carver & Scheier, 1990; Carver & Scheier, 1998; Emmons & King, 1988; Janoff-Bulman & Brickman, 1982; Little, 1999; Wrosch, Scheier, & Miller, 2003), provides the foundation for a more general approach to mood as a mechanism that allocates effort proportional to propitiousness (Nesse, 1991b, 2000, 2009). When payoffs are high, positive mood increases initiative and risk-taking. When risks are substantial or effort is likely to be wasted, low mood blocks investments. In this perspective, ordinary episodes of sadness and low mood motivate changing behavioral strategies (Watson & Andrews, 2002). If no alternative is found and the goal is essential, persistence may result in depression (Klinger, 1975; Wrosch, Scheier, & Carver, 2003).

Observations of chickens and monkeys who lost their positions in the hierarchy has suggested a view of depression as "involuntary yielding" that protects against continuing attack (Gilbert, 1992; Sloman, Price, Gilbert, & Gardner, 1994). This is consistent with data showing that stressful events cause depression mainly if they are characterized by humiliation and/or being trapped in an impossible quest (Brown, Harris, & Hepworth, 1995; Kendler, Hettema, Butera, Gardner, & Prescott, 2003). Also related is the suggestion that sex differences in depression may arise from the male tendency to strive for position and resources, leaving many women vulnerable to depression because they have fewer options (Gilbert, 1992; Wenegrat, 1995). The role of defeat and entrapment observed in animal studies (Blanchard, Litvin, Pentkowski, & Blanchard, 2009), in human studies by Brown (Brown et al., 1995), inspired by Price (Price, Sloman, Gardner, Gilbert, & Rohde, 1994), has been extended by Gilbert (2006), and now is the focus of an extensive literature confirming that generic stress is not nearly as potently depressogenic as defeat and entrapment (Taylor, Gooding, Wood, & Tarrier, 2011).

Depression has also been viewed as a social manipulation (Hagen, 2002; Watson & Andrews, 2002). Hagen sees postpartum depression as a "blackmail threat" to abandon the infant, but other theories could also explain the association of postpartum depression with poor resources and relationships. In a related but more general view, Watson and Andrews suggest that depression facilitates "social navigation" by signaling that current strategies are failing and new directions are needed (Watson & Andrews, 2002). This approach echoes psychoanalyst Emmy Gut's work on productive and unproductive depression (Gut, 1989). Nettle (2004) notes inadequacies of the social navigation hypothesis, and emphasizes the possible adaptive value of neuroticism.

The role of rumination in solving social dilemmas is highlighted in a recent article that gained wide attention (Andrews & Thomson, 2009), but also criticism from those who view rumination as an unhelpful symptom with little evidence for utility and some evidence that tendencies to rumination increase the risk of depression (Nolen-Hoeksema & Morrow, 1993). Earlier work by Gut considers the possibility that such rumination can be productive or unproductive, depending on the circumstances (Gut, 1989).

DeCatanzarro proposed that suicide can be adaptive if an individual has no chance for reproduction but can increase future reproduction of kin by ceasing to use resources that they could use instead (deCatanzaro, 1980). Data showing that suicides are more common in old and sick people are consistent; however, alternative explanations are available, separation from kin does not protect against suicide, and there are no animal examples. The role of the group is also central to Allen and Badcock's model, in which people carefully monitor what they can contribute to a group (N. Allen & Badcock, 2003). People who realize they can contribute little retreat into depression that is hypothesized to prevent active expulsion from the group.

These approaches are quite different from the prevalent view that depression is a brain disorder. The brain mechanisms that mediate mood certainly can go awry, but two questions need consideration. First, is low mood a useful response, like a cough, or an abnormality unrelated to defenses, like epileptic seizures? Second, do individual differences in vulnerability to depression arise mainly from primary brain differences, or from brain changes mediated by social experience? These are not mutually exclusive alternatives, and most depression is best understood as the outcome of gene × environment interactions (Caspi et al., 2003). Also, there are different routes to depression, some of which progress irrespective of environment, others of which arise mainly from life circumstances, perhaps especially those involving pursuit of unreachable goals. Then, of course, there is the reality that depression can have different causes in different individuals, or even in the same individual at different times.

Other Emotional Disorders Anxiety and depression get the attention, but every emotion is subject to at least two kinds of disorder: excesses or deficits. For instance, pathological jealousy is common, but few clinicians know why jealousy exists (Buss, Larsen, Westen, & Semmelroth, 1992). Jealousy may arise for good reasons (Buss et al., 1999) or from delusions. Feelings of inadequacy make some men think that their partners might prefer someone else, and then that they do prefer someone else. Depression treatment often relieves pathological jealousy (Stein, Hollander, & Josephson, 1994). The syndrome of pathological lack of jealousy has yet to be described.

BEHAVIORAL DISORDERS

Other disorders involve inability to control behavior. Most obvious are the addictions and other habits, but other problems of behavioral control range from eating disorders to violence.

Addiction The human toll taken by addictions is magnified because their effects harm others as well as the addict. A special issue of *Addiction* was devoted to evolutionary approaches (Hill & Newlin, 2002), with suggestions about the adaptive significance of addiction (Sullivan & Hagen, 2002), life history theory (Hill & Chow, 2002), and the significance of fermentation (Dudley, 2002), among others. One evolutionary insight is simple; learning is chemically mediated, so exogenous substances that directly stimulate reward mechanisms can cause addiction (Nesse, 1994; Nesse & Berridge, 1997). The subjective sensations are pleasurable and the associated reinforcement increases the frequency of drug taking. Withdrawal symptoms stimulate further drug taking. Over time, subjective "liking" wanes, withdrawal effects become more severe, and the habit strength of "wanting" increases, trapping the addict in a vicious cycle that may offer little pleasure, even as it consumes most of what is valuable in life.

Vulnerability to substance abuse results from our novel environment. The reliable availability of pure chemicals and clever new routes of administration increase the rate of drug taking. Tobacco administered via the technological advance of cigarettes is the most widespread and harmful addiction, with alcohol a close second. The so-called hard drugs of abuse, such as amphetamines and cocaine, act even more directly on ascending dopamine tracts to establish addiction. Substance abuse is a universal human vulnerability to drugs that hijack reward mechanisms. Several recent papers challenge this model, arguing that long coevolution with drug-producing plants has shaped humans to pursue and use drugs that give advantages, via medical benefits or by augmenting energy and abilities (Hagen et al., 2009; Sullivan, Hagen, & Hammerstein, 2008). This interesting possibility seems to complement the possibility that drug abuse has become common because novel environments make pure drugs readily available via novel routes.

Eating Disorders Half of Americans are now overweight and a third are clinically obese. They spend billions on books and treatment, but nothing works very well. Vast amounts of research have tried to understand what is wrong with the heavy half. An evolutionary approach suggests a different question: Why are we all vulnerable to obesity? A simple answer is that our behavior-regulation mechanisms were shaped in the very different environment of the African savannah, where the penalty for eating too little was swift and fatal. Even when food was plentiful, obesity remained rare because choices were limited and getting food involved burning as many calories per day as a modern aerobics instructor (Eaton, Shostak, & Konner, 1988).

Attempts to control weight by willpower leads to the other eating disorders, anorexia nervosa and bulimia. Explanations for anorexia as an adaptive variant mating strategy have been suggested (Surbey, 1987; Voland & Voland, 1989). However, a simpler starting place is the observation that these disorders usually begin with strenuous diets motivated by attempts to be attractive and thus preferred as a mate, a strategy that has been more important for women than men. Such diets cause episodes of gorging, a hallmark of bulimia, but life-saving during famine. Gorging precipitates shame, feelings of lack of control, more intense fear of obesity, and new resolutions in a vicious cycle of escalating anorexia and bulimia. Eating disorders are also fostered by the intense mating competition in large social groups, augmented by media images that make real bodies seem inadequate. In light of the pervasiveness of mating competing, this makes perfect sense (Buss, 1988, 1994).

Sexual Disorders Given its importance, you might think selection would have made sex foolproof. Instead, it exemplifies the vulnerabilities of a trait shaped by multiple strong forces of selection (Troisi, 2003). For instance, men complain about premature orgasm while women complain about lack of orgasm. Why? Sex differences in brain mechanisms and differences in anatomic proximity to stimulation, yes, but these are proximate explanations. Why is the system so poorly designed for mutual satisfaction? Because selection does not shape mechanisms for mutual satisfaction. Women who had orgasms very quickly might well have had fewer children, as might men who dallied too long when interruption is likely (Nesse & Williams, 1994). This is consistent with the observation that premature ejaculation is a problem mainly for men who are young or fearful.

COGNITIVE AND OTHER DISORDERS

Not every disorder fits neatly into a traditional category, especially some of the more serious disorders such as schizophrenia and autism. For these disorders the focus is less on any possible adaptive significance and more on evolutionary reasons why systems are vulnerable to failure.

Schizophrenia Schizophrenia is the most serious common mental disorder of adults, with a prevalence rate consistent at about 1% across cultures (Jablensky, Satorius, & Ernberg, 1992). This undermines the idea that novel environment explains psychosis, although new reports suggest some variations of rates between cultures (van Dongen & Boomsma, 2013). There is also strong evidence that schizophrenics have lower than average RS: 0.3 of average for males and 0.5 for females (Pulver et al., 2004). The same data show no increased fitness of their close relatives, arguing against any selective benefits via kin selection. As mentioned already, infection has also been implicated. Low fitness should pose strong selection against alleles that increase vulnerability to schizophrenia, but they persist, posing the paradox of genes for schizophrenia. A comprehensive review of possible explanations was published recently (van Dongen & Boomsma, 2013).

Selection might not be powerful enough to purge deleterious mutations if they occur often enough to balance selection. This seems increasingly likely, as we have been unable to find any common alleles that account for even 1% of the vulnerability to schizophrenia and increasing evidence of the influence of rare alleles and copy number variations. Further support for the role of new mutations comes from recent confirmation that the rates of schizophrenia increase dramatically for children who were conceived when their fathers were over 40 (Malaspina et al., 2002). Genes transmitted by the mother have divided only 24 times per generation, compared to 800 cell divisions for the DNA in sperm of older fathers, suggesting that many cases of schizophrenia arise from new mutations.

Another possibility is that so many genes are involved that selection can act on them only weakly, so normalizing selection can never shape a design parameter to an extremely narrow zone, and some individuals will have parameters beyond the range of good functioning (Keller & Miller, 2006). This general idea is an important antidote to theories positing benefits from schizophrenia, even though an enormous number of genes contributing to a trait may make it less vulnerable, not more.

Schizophrenia genes might also spread if they are linked to strongly beneficial genes (Burns, 2005), but pleiotropic effects are more important. Cliff-edge effects offer a related possibility. For instance, racehorse breeding has resulted in longer and thinner leg bones that increase speed but are prone to fracture. If some mental characteristic gives increasing fitness up to a point where some mental trait suffers catastrophic failure, such cliff-edge effects could account for the genetic patterns seen in schizophrenia and manic-depressive illness (Burns, 2007; Nesse, 2004).

AUTISM

The same lines of reasoning also apply to other severe mental diseases that also have an incidence of about one in 100, autism in particular. Baron-Cohen has suggested that the manifestations of autism are examples of a pathological extreme of cognitive styles that are typically male (Baron-Cohen, 2002). This would help to explain the 4 to 1 predominance of males for autism with higher IQ scores.

One of the more significant lines of research in evolutionary psychiatry, by Crespi and colleagues, investigates the possibility that schizophrenia and autism are flip sides of a coin that is influenced by genetic imprinting that benefits paternal versus maternal genomes (Badcock & Crespi, 2006; Crespi, Summers, & Dorus, 2007). The idea is derived from Trivers's recognition that alleles derived from paternal and maternal genomes can have conflicting interests (Burt & Trivers, 1998) and Haig's work showing differential imprinting of genes that regulate the resources a fetus extracts from a mother in patterns consistent with the hypothesis that paternal alleles gain an advantage by extracting more and maternal alleles gain an advantage by controlling this manipulation (Haig, 2010). Emerging evidence supporting Crespi's theory includes an axis from schizophrenia to autism in a principle components analysis of symptoms (Dinsdale, Hurd, Wakabayashi, Elliot, & Crespi, 2013), and genetic evidence that autism and schizophrenia are best described as diametric disorders (Crespi, Stead, & Elliot, 2010).

ATTENTION DISORDERS

The evolutionary origins of attention-deficit/hyperactivity disorder (ADHD) have been the focus for several articles suggesting possible functions (Baird, Stevenson, & Williams, 2000; Brody, 2001; Jensen et al., 1997; Shelley-Tremblay & Rosen, 1996), or that it is a facultative adaptation to certain environments (Jensen et al., 1997). The striking male bias of the sex ratio, over 5 to 1, gives hints that ADHD may simply be the extreme end of a continuum on which males tend to be higher than females, much akin to a recent suggestion about autism (Baron-Cohen, 2002). In the ancestral environment, a tendency to move quickly to a new activity when current efforts are unproductive is a foraging strategy that may pay off more for hunting males than gathering females. As for the capacity to sit in one place indoors for hours under enforced contact with a boring book, that is so far from anything the natural environment ever required, it is astounding that any of us can do it!

Child Abuse Child abuse has been a major focus for mental health prevention and treatment. Understanding the evolutionary origins and functions of attachment has helped to explain why most parents do not abuse their children despite provocations (Bowlby, 1984). An evolutionary perspective motivated two behavioral ecologists to ask the now-obvious question: Is child abuse more common in families with a stepparent? Their astounding result, not recognized by decades of previous work, is that death at the hands of parents is 80 times more common if there is a stepparent in the house (Daly & Wilson, 1988). This finding is commonly presented in a context framed by the tendency of males in many species to kill all unweaned infants shortly after they take over a female mating group (Hrdy, 1977). However, the mating pattern of humans does not routinely involve males fighting to take over a harem with multiple females who are nursing infants, so the analogy is incorrect. Instead, the mechanisms that protect babies from violence in families with two related parents seem more prone to fail in reconstituted families (Gelles & Lancaster, 1987).

IMPLICATIONS

The question one usually gets about evolutionary psychiatry is, "So, what can you cure that others cannot?" This is a fair question if evolutionary psychiatry is just another approach to therapy along with a hundred others. However, what evolution offers psychiatry is two steps back from proposing new cures, but far more fundamental. Instead of new treatments, it seeks explanations for mental disorders. Instead of explanations for why some individuals get sick and others do not, it seeks to explain why we all have minds that leave us vulnerable to mental disorders, and why natural selection has not eliminated genetic variations that result in disease for some.

Its most profound contribution is a solid framework for understanding how behaviors are regulated to accomplish the many conflicting tasks of life, from getting food and surviving, to competing for status, to finding mates and protecting children. Instead of viewing one kind of life as normal and others as deviations, it sees the inherent conflicts in relationships, the struggles that go on in groups, and the dilemmas every person faces to allocate efforts among a host of competing needs. Far from providing a rigid and cold perspective, an evolutionary view fosters deeper empathy for the challenges we all face, and deeper amazement that so many people are able to find loving relationships, meaningful work, and a way to juggle a bevy of responsibilities with good humor, and even joy.

Does this presage a new kind of psychotherapy? There certainly are major implications for how to do psychotherapy (Gilbert & Bailey, 2000) and psychoanalysis (Slavin & Kriegman, 1992), and some have called for applications now (Gilbert & Bailey, 2000; McGuire & Troisi, 2006; Troisi, 2012), but it is essential not to reduce evolutionary approaches to just another theory in the crowded clinical marketplace. It is broader and deeper. Every clinician should understand how selection shaped behavior, and all kinds of therapy should make use of evolutionary principles.

Finally, an evolutionary view of mental disorders in no way suggests accepting the pains and difficulties of the human condition; it instead suggests that much suffering is useless, even when it is normal. It supports using medications or other methods when they can relieve suffering safely, and it provides knowledge about the functions of negative emotions and the smoke detector principle that are crucial for making wise, individualized decisions. Most of all, it fosters a deeper sympathy for the human plight.

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PART VIII

INTERFACES ACROSS TRADITIONAL ACADEMIC DISCIPLINES

DAVID M. BUSS

This section of the handbook considers evolutionary psychology as it infuses different disciplines that may at first seem far removed from the evolutionary sciences. Four of the five chapters are entirely new, reflecting how far and how deeply evolutionary psychology has influenced adjacent disciplines.

The first focuses on *evolutionary anthropology*, written by Dan Fessler, Jason Clark, and Edward Clint. The authors highlight the ways in which evolutionary psychology can be informed and enriched by evolutionary anthropology, and reciprocally, the ways in which evolutionary anthropology can be informed and enriched by evolutionary psychology. They stress the importance of tools such as phylogenetic analysis, exploitation of primatological comparisons, the study of small traditional societies, the use of anthropological data banks of ethnographies that can be analyzed quantitatively, the use of modern techniques emerging from genetics, and the "kludge-like" nonoptimal nature of adaptations. It's an exciting chapter that should foster increased cross-disciplinary collaborations between evolutionary psychologists and evolutionary anthropologists who, although often operating within the paradigms of their respective guild-like coalitions, truly have much to offer each other.

The second new chapter, written by Reuben Arslan and Lars Penke, deals with *evolutionary genetics*—a field that was virtually absent a decade ago. Evolutionary genetics focuses on the *mechanisms* that explain the existence and maintenance of genetic variation in traits. In decades past, it was widely believed that natural selection exhausted genetic variation. Biologists and geneticists have been increasingly astonished to discover large reservoirs of genetic variation—differences that lead to manifest individual differences—that must be explained. These authors review the candidate evolutionary forces that create and maintain genetic variation within a species. The evolutionary genetics toolkit offers evolutionary psychologists an array of methods for the rigorous testing of some evolutionary psychological hypotheses. Evolutionary genetics enriches evolutionary psychology. It provides a theoretical framework for integrating individual differences and recent evolution, bringing us closer to understanding why we are the way we are and the causal processes by which we became that way.

Evolutionary endocrinology offers yet another scientific toolkit for evolutionary psychology, as represented by a superb new chapter by James Roney. He notes that a complete understanding of evolved psychological adaptations requires deep understanding of "Tinbergen's Four," which include phylogeny, ontogeny, adaptive function, and neurobiological implementation. Evolutionary endocrinology offers a set of tools for illuminating all four explanatory levels. Roney makes his case by outlining what is known about the evolutionary endocrinology of mating—an especially apt target of selection, given that it is so close to the "engine" of evolution by selection, differential reproduction. He concludes aptly: "No model of human nature will be complete without a clear understanding of the functional roles of these chemical messengers."

Evolutionary psychology is beginning to infuse *political science*, and Michael Bang Petersen provides the road map for a deeper and richer integration. Humans have been called "the political animal" for a good reason—politics is all about "games" in which players have conflicting interests and lobby to determine "who is entitled to what, when, and how." Peterson outlines the fundamental premises of evolutionary political psychology, starting with "*Evolved political psychology is designed to operate adaptively within and between small-scale groups.*" He proceeds to discuss the coevolution of information manipulation strategies and counter-strategies. Petersen shows how adaptations for politics in small-group living get played out in the modern settings of massive populations. Along the way, he unearths an important collection of psychological adaptations for politics, including those of negotiating status, reputation, power, coalitional allegiance, political leadership and followership, persuasion, moralization, and information manipulation. Peterson's chapter is likely to serve as a beacon for political scientists, providing not the final word, but the first key outlines of a road map for the field ahead.

The final contribution is a chapter by Joseph Carroll on *evolutionary psychology and literature*. Traditionally, science and the humanities (and particularly the arts) have been regarded as separate endeavors. Carroll, in a conceptually synthetic essay, argues for consilience—a unified causal understanding that integrates the sciences and humanities. He reviews the various approaches to the evolutionary analysis of literature, including the key themes of human nature reflected in literature and the possibility of adaptations for producing literature and its oral antecedents. The evolutionary analysis of literature and the arts is beginning to flourish, and Carroll's excellent chapter takes stock of where this exciting enterprise has been and where it promises to go.

Evolutionary psychology has penetrated many disciplines, and space limitations unfortunately precluded inclusion of all of them. As these words are written, there are rapidly emerging new hybrid disciplines, such as evolutionary economics, evolutionary organizational behavior, evolutionary sociology, and evolutionary analyses of history. In the final analysis, all human behavior—including economic behavior, legal behavior, artistic behavior, and organizational behavior—is a product of evolved psychological mechanisms and the environments within which those mechanisms operate. I predict that in the distant future, all of these diverse and seemingly unrelated fields will be based on a new evolutionary foundation.

CHAPTER 44

Evolutionary Psychology and Evolutionary Anthropology

DANIEL M. T. FESSLER, JASON A. CLARK, and EDWARD K. CLINT

INTRODUCTION

Evolutionary psychology (EP) is a paradigm, not a discipline, and from its inception, it has both drawn on and influenced practitioners in a variety of academic fields. Many chapters in this volume testify to the contributions evolutionary anthropology (EA) has made to EP. Here, rather than catalog past interplays, we underscore the positive affordances of EA for the practice of EP and vice versa.

The student of EP interested in learning what EA has to offer encounters an assortment of approaches and findings, including:

- The biology and behavior of extinct hominids and their relationship to the origins of H. sapiens
- The study of extinct primates and their relationships to contemporary species
- The evolution of technology, both in prior hominids and in humans
- Human biology and the biology of extant primates
- The study of behavior, cognition, and affect in other species as a window onto the evolution of analogous or homologous human capabilities
- Human evolution and population history through the lens of genetics
- Behavior, mind, reproduction, and health in extant societies, importantly including small-scale societies

Given the range of topics addressed by EA, we cannot provide a full accounting of the interface, or potential for interface, with EP within a single chapter. We ourselves work on but a small subset of these topics, limiting our ability to comment on the full scope of EA. We instead focus on what we consider some of the most exciting and promising areas in this regard, an accounting that overtly reflects our own interests. Seeking to outline opportunities to advance the study of human behavior, we present examples of how some existing approaches are challenged by the intersection of the EP perspective and the knowledge base and methods of EA.

SOME LESSONS FROM PALEOANTHROPOLOGY

We begin with the study of hominid evolution through fossil remains and archeological materials. While specific paleoanthropological discoveries will often be relevant to particular EP enterprises, for the purposes of advancing EP in general, several overarching implications transcend such specifics.

Skeletal features are well preserved in the fossil record, and skeletal adaptations present ideal case studies of the transformation of traits that is the hallmark of natural selection. For example, paleoanthropologists have documented in detail the modifications of the hip, pelvis, knee, and spine that occurred in the course of the evolution of bipedality (e.g., Lovejoy, 2005). Our species' particular form of locomotion may raise discrete questions for the evolutionary psychologist, such as, for example, the correspondence between the frequency of oscillation that infants find soothing (Vrugt & Pederson, 1973) and the cadence of human walking (MacDougall & Moore, 2005); the absence of motion sickness in young infants (Gordon & Shupak, 1999), who must be carried; and the nature of locomotory experience required for the development of visual cliff responses in infants (Witherington, Campos, Anderson, Lejeune, & Seah, 2005). However, as interesting as such topics may be for the specialist, they hinge only on the fact that humans are bipedal, and do not depend on the specifics of how bipedality evolved. In contrast, the latter is relevant for all evolutionary psychologists, be they interested in locomotion or not, because it reveals the importance of path dependence in natural selection, the kludgy nature of the adaptations that natural selection constructs, and the conflicts that can arise between multiple adaptations, along with the higher-order adaptations that can evolve as a consequence. For example, the S-curve in the human spine reflects the determinative influence of the original function of the spine as a suspensory beam in a quadrupedal mammal, in contrast to its current function as a load-bearing pillar: Whereas the original design functioned efficiently in a horizontal position, the transition to bipedality required the introduction of bends in the spine to position weight over the pelvis (Lovejoy, 2005). The resulting configuration makes humans prone to lower-back injury, illustrating how path dependence can both set the stage for kludgy designs and constrain their optimality. Moreover, the combination of bipedality and pressures favoring large brain size in humans exacerbates a conflict between the biomechanics of locomotion (favoring a narrow pelvis) and the need to accommodate a large infant skull during parturition. This increases the importance of higher-order adaptations such as relaxin, a hormone that loosens ligaments during pregnancy, allowing the pelvic bones to separate.

The take-home lesson is not that understanding the human mind starts with understanding our mode of locomotion, but rather that the evolution of bipedality, a well-documented progression, reveals (a) the importance of phylogenetic history in understanding extant traits; (b) the jury-rigged nature of many adaptations; (c) the degree to which optimality can be constrained; (d) the fact that most adaptations are not isolated responses to discrete challenges, but rather the confluence of numerous evolutionary trends (opposing and synergistic), many of which are independent of ultimate function; (e) the importance of phylogenetically appropriate comparative studies; and (f) the manner in which adaptations can spawn higher-order adaptations. Though none of these observations are new to EP, in practice they are frequently overlooked, as evolutionary psychologists often adopt optimality assumptions, focusing on selective pressures that pertain to the postulated ultimate function of the trait to the exclusion of constraints and affordances that play a strong role in shaping its final form. Relative to evolutionary anthropologists (see, for example, Nunn, 2011), scholars from other disciplines who employ the EP paradigm are also more prone to either underestimate the importance of comparative studies or employ comparative evidence distant from the human phylogenetic tree that (at best) reflects analogies rather homologies. This is illustrated by the fact that, particularly in the United States, EP and comparative psychology proper remain, in practice but not in principle, distinct in both disciplinary and conceptual senses. Inattention to the points mentioned above unnecessarily limits the scope, richness, and complexity of inquiry into evolved psychology.

Applying Phylogenetic and Comparative Perspectives to Emotions

Emotions provide one opportunity to apply to the study of mind the phylogenetic and comparative perspectives that are central to paleoanthropology in particular and EA in general (Fessler & Gervais, 2010). For example, ethological, cross-cultural, and cross-species analyses suggest that the uniquely human emotions *shame* and *pride* are derived from ancestral pan-primate emotions that regulate dominance and subordinance in hierarchical interactions (Fessler, 1999, 2007; Weisfeld, 1999). Moreover, the coexistence of both the ancestral and the derived forms of these emotions in contemporary humans reveals the importance of serial homology in the study of mind, the process whereby traits are duplicated, with both the duplicate and the original retained in the same organism, and one or both then available for cooptation into a derived trait (Clark, 2010a, 2010b). The need for such biologically informed phylogenetic analyses of psychological adaptations is further illustrated by the case of *disgust*. Disgust has multiple forms, operating in such distinct domains as pathogen avoidance, sexuality, and morality (cf. Fessler & Navarrete, 2003; Haidt, McCauley, & Rozin, 1994; Tybur, Lieberman, Kurzban, & DeScioli, 2013). Although progress has been made in understanding how, over the course of human evolution, a single emotion came to address such diverse adaptive challenges (see, for example, Kelly, 2011), nevertheless, much remains to be done. Also of relevance here, one form of disgust, pathogen disgust, functions in part as a third-order adaptation, as disease-avoidance responses are up-regulated in a manner that compensates for the increases in vulnerability to pathogens that accompany pregnancy and preparation for implantation—changes that are themselves a second-order adaptation addressing the conflict between maternal immune defenses and the parasitic behavior of the half-foreign conceptus (Fessler, Eng, & Navarrete, 2005; Fleischman & Fessler, 2011; Jones et al., 2005). In sum, the model provided by paleoanthropologists' studies of morphological evolution provides a rich source of insights regarding analogous aspects of psychological evolution.

UNDERSTANDING THE ENVIRONMENT OF EVOLUTIONARY ADAPTEDNESS

By its nature, paleoanthropology is concerned with the relationship between particular traits evident in a given species and particular features of the environment. Although paleoanthropologists (and evolutionary biologists more broadly) productively explore such relationships without employing the concept of the environment of evolutionary adaptedness (EEA), this notion is not inherently inconsistent with said enterprise. Evolutionary psychologists who have advanced the concept of the EEA have been careful to stress that it is not a particular time or place, but rather a set of selective pressures relevant to explaining a given trait (Symons, 1995; Tooby & Cosmides, 1990). This articulates well with paleoanthropology given the role the latter can play in reconstructing the EEA for a given human trait. Notably, despite the aforementioned efforts by promoters of the EEA concept, there is a strong temptation for evolutionary psychologists to conceptualize it as a unified set of circumstances. Consider, for example, how Kanazawa introduces the concept: "This environment—African savanna where humans lived in small bands of fifty or so related individuals as hunter-gatherers—is called the environment of evolutionary adaptedness (EEA)," (2004, p. 42). Such reification is a critical error, as, far from being unified, there are actually many EEAs, depending upon which trait is at issue (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). For example, periovulatory reductions in caloric intake, arguably the product of an adaptive mechanism that solves the time-allocation conflict between foraging and mate-seeking in favor of the latter, are found across a wide range of mammals, including humans (Fessler, 2003). The key features of the EEA for this adaptation are the combination of food resources that require time and attention to procure and a social/spatial distribution of prospective mates wherein finding and attracting a valuable partner requires time and attention. These features occur in the environments of many mammals, likely including a long succession of hominid species. Hence, while humans' hunting and gathering on the African savanna during the Middle Paleolithic era maintained the EEA for this trait, it by no means uniquely defined it.

RECONSTRUCTING THE EEA FOR DISGUST—THE QUESTION OF TIME DEPTH

A careful reading of the EA literature is often fundamental to the proper reconstruction of the EEA for a given trait, a goal that, in turn, influences assessments of both function and phylogeny. Consider again the case of disgust. Disgust was clearly originally focused on the mouth, as oral incorporation of contaminated matter is a primary disgust elicitor, and both oral rejection and nausea/emesis remain characteristic responses to a broad range of elicitors, whether ingestible or not (Rozin & Fallon, 1987). Seeking to explain how an emotion so centered on oral incorporation has as one of its principal domains of operation the avoidance of contact—oral or otherwise—with cues of the presence of pathogens, Kelly (2011) posits that meat-eating played a central role in the evolution of disgust. Building on prior work on the ultimate functions of dietary preferences and avoidances, Kelly reasons that, while a rich source of nourishment, meat is also a primary source of pathogens. He argues that two separate mechanisms, one regulating oral incorporation, the other focused on cues of the presence of other pathogens (e.g., ectoparasites, etc.), became "entangled," meaning that they fused into a single adaptation in humans. This occurred, Kelly asserts, because our ancestors adopted meat-eating too quickly for more conventional physiological defenses to evolve in time. While the centrality of meat-eating in Kelly's explanation is both cogent and consonant with other evidence regarding the unique salience that meat holds for humans as both a resource and a threat, nevertheless, his account runs afoul of a realistic reconstruction of the EEA for the postulated adaptation. Paleoanthropology provides abundant evidence that meat-eating evolved over a period of at least 3 million years (McPherron et al., 2010), hence Kelly's need-for-speed explanation cannot be correct—the EEA for this trait was not merely human meat consumption, but rather meat consumption practiced by a succession of hominid species (Clark & Fessler, n.d.). This matters because if we abandon this aspect of Kelly's account, we must direct our attention to other facets of the EEA for this trait, prominent among which are the longstanding sociality of hominids and the corresponding progressive increases in encephalization, a feature that reduces the costs of brain-based (i.e., psychological) adaptations relative to physiological adaptations (Clark & Fessler, n.d.)—a pattern of likely importance in explaining many aspects of human evolved psychology.

THE IMPORTANCE OF CONTEMPORARY SMALL-SCALE SOCIETIES IN EEA RECONSTRUCTION

As the above case illustrates, paleoanthropology provides vital time depth in the reconstruction of EEAs. Nevertheless, the richness of the portraits of the past that paleoanthropology can provide is necessarily limited given that past behavior cannot be observed, but rather must be inferred. Paleoanthropology thus provides one of two pillars needed to operationalize the concept of the EEA for many features of mind, the second being anthropologists' observations of contemporary small-scale societies that provide points of reference with which to approximate ancestral humans' ecological and social conditions. Traditionally, the study of small-scale societies was the heart and soul of anthropology, with cultural anthropologists playing the central role. Over the course of the past four decades, cultural anthropologists have increasingly focused on large societies, while sometimes also eschewing the objective methods—and scientific objectives—most likely to produce findings of relevance to EP. However, even as cultural anthropology has retreated some from the investigation of small-scale societies, evolutionary anthropologists have increasingly taken such groups as their central objects of study. Anthropologists—evolutionary or otherwise—thus generate a rich corpus of material offering many positive affordances for EP. When exploring a particular EP hypothesis, operationalizing the concept of the EEA can be greatly enhanced through the use of observations of life in small-scale societies in general, and extant hunter-gatherer groups in particular. The importance of this is illustrated by two topics of extensive debate in the current literature: (1) the evolution of cooperation, and (2) the relationship between disease avoidance and social attitudes.

CASE STUDY: THE EVOLUTION OF COOPERATION

First, viewed in comparison with the vast majority of other species, humans are remarkable for the degree to which they cooperate in large groups of unrelated individuals, a feature that must play a central role in explaining human history (Chudek, Muthukrishna, & Henrich, Chapter 30, this volume; Norenzyan, Chapter 35, this volume). Considerable disagreement surrounds the processes whereby the capacity for such cooperation arose, with postulated positions ranging from various forms of biological group selection (e.g., Sober & Wilson, 1999; Wilson, 2012), to combinations of biological and cultural group selection (e.g., Bowles, 2006), to gene-culture coevolution (e.g., Boyd & Richerson, 2009; Chudek, Zhao, & Henrich, 2013), to the scaling up of mechanisms and processes operating in dyadic interactions due to evolutionarily novel increases in the scope of social life in contemporary societies (e.g., Burnham & Johnson, 2005; Hagen & Hammerstein, 2006). Recent work synthesizing diverse studies of extant hunter-gatherers indicates that such societies characteristically involve co-residence among many unrelated individuals (Hill et al., 2011) combined with high rates of contact with members of other bands (Hill, Wood, Baggio, Hurtado, & Boyd, 2014)—including ephemeral interactions (Chudek et al., 2013). Taken together, the resulting portrait of the likely social dimensions of the EEA calls into question the thesis that the evolved psychological mechanisms governing human cooperation at larger scales derive principally from kin selection and reciprocal altruism, as such a position is more consistent with an EEA characterized by high degrees of relatedness within groups, more restrictive social networks, and a paucity of short-term interactions (reviewed in Brown & Richerson, 2014).

CASE STUDY: THE PARASITE-STRESS THEORY

Second, findings from EA underscore the importance of the extensive variation in ecologies and social structures likely characteristic of our species throughout its history and beyond (Foley, 1995). It is vital to understand that, for many traits of interest, the relevant features of the environment have been variable. This is because, depending on the nature of that variation, it is likely that one of two classes of adaptations will have evolved, namely, either (1) adaptations that facultatively adjust their output in light of local environmental cues or (2) adaptations for cultural acquisition. Illustrating this, one rapidly expanding area of research concerns the relationship between pathogen prevalence and social attitudes. In a series of influential papers, Fincher, Thornhill, Schaller, Murray, and colleagues have argued that pathogen prevalence predicts the extent of individualism versus collectivism (Fincher, Thornhill, Murray, & Schaller, 2008) and conformism (Murray, Trudeau, & Schaller, 2011) across cultures; ingroup homophily and outgroup avoidance (Fincher & Thornhill, 2012) and resulting speciation in cultural evolution (Fincher & Thornhill, 2008); cross-national differences in personality (Schaller & Murray, 2008; Thornhill, Fincher, Murray, & Schaller, 2010); and a wide range of related social phenomena (Thornhill & Fincher, 2014). The core thesis, termed the parasite-stress theory (PST), holds that the mind contains adaptations that regulate social behavior to optimize disease avoidance (see Schaller, Chapter 7, this *Handbook*, Volume 1). The PST then argues that, in the relevant EEA, members of outgroups constituted a key source of unfamiliar—and thus dangerous—pathogens. However, the extent of the threat posed by pathogens varied across the ecologies inhabited by ancestral populations. As a consequence, selection produced psychological mechanisms that adjust the degree to which individuals preferentially assort with members of the ingroup, and avoid and are hostile to members of the outgroup, as a function of cues indicative of the density and virulence of socially transmitted pathogens in the local ecology. Aggregated across the members of a society, the outputs of these mechanisms then produce a wide variety of sociocultural concomitants, including phenomena as diverse as political orientation and religiosity.

The PST elegantly deploys the notion of adaptations that, by virtue of having ecological variation as a central feature of the relevant EEA, incorporate facultative adjustment to local circumstances. While the authors are to be applauded for their sophisticated thesis, and while their rapidly growing corpus of findings demonstrates that there are important phenomena to be explained here, when examined in terms of a more complete reconstruction of the EEA for the postulated adaptation, there are many reasons to doubt the theory, at least in its strictest form.

First, the PST assumes an EEA for the proposed mechanism in which (a) interactions between neighboring groups were rare and (b) such groups were sufficiently geographically and ecological disparate as to allow distinct pathogens to evolve independently in each group, such that, upon contact, members of one group would lack a history of prior exposure—and thus immunity—to the given strain. As discussed above, studies of extant hunter-gatherers indicate high rates of contact between bands. The PST concerns relations between groups that possess distinct, bounded cultural identities (termed *ethnies* in anthropology); as such, at first glance, interband interactions might seem irrelevant, as, in most cases, the two bands will belong to the same ethnie. However, from an epidemiological perspective, frequent interband contact unites all members of a given hunter-gatherer ethnie into a single group, as infectious disease contracted by members of one band will rapidly spread to other bands. The archeological record provides extensive evidence of long-distance trade during the Paleolithic (see Blades, 2001; Chalmin et al., 2007; d'Errico et al., 2009), indicating that both intra-ethnie and inter-ethnie contact occurred with some frequency. Viewed with regard to the interests of the various members of a group, the costs and benefits of intergroup contact are unevenly distributed. Individuals who elect to interact with members of another group (be they of the same ethnie or a different one) stand to reap the benefits of trade, as well as expanded access to territorial resources, mating opportunities, knowledge transfer, and so on. Such individuals are also at risk of both disease transfer and aggression or exploitation. Notably, while both the benefits of intergroup interaction and the risks of aggression and exploitation are primarily limited to those individuals who elect to interact with outsiders, the same is not true of the risk of disease transfer. In a world with minimal hygiene, little knowledge of disease transmission, extensive food-sharing, and intimate physical proximity, if one individual in a band contracts a transmissible illness, all members of the band become exposed, and, if bands interact regularly and band composition is fluid, then the same holds true for the entire ethnie. This creates an evolutionarily unsustainable dynamic from the perspective of the PST. For highly transmissible diseases (precisely the type assumed by the PST), if individual A interacts with outgroups and thereby both reaps fitness gains and suffers pathogen-inflicted costs, while individual B avoids outgroups but suffers the same pathogen-inflicted costs due to intragroup disease transmission from A, then A's fitness will be higher than B's fitness. Thus, following the dictum that reconstructions of the EEA for a given trait should leverage the findings of EA regarding present and past behavior, it appears that the portrait of the world of our ancestors that can be compiled using ethnographic and archeological sources is inconsistent with that EEA required for the evolution of an adaptation that would facultatively adjust attitudes toward ingroups and outgroups as a function of pathogen prevalence.

Reconstructions of EEAs should employ all relevant material. Historical and archeological evidence indicates that infectious disease decimated the New World in the initial stages of colonialism. Does this speak to the EEA required by the PST? No. Extensive direct contact between previously widely separated groups only occurred following the evolutionarily recent development of transoceanic sailing technology. Paleolithic pedestrian hunter-gatherer groups, inhabiting similar ecologies to those of their neighbors and linked to them through trade, would have coevolved with endemic pathogens, precluding the devastation recorded during historical times (R. Thornton, personal communication). Indeed, in many areas, the depopulation of Native American tribes due to European diseases is thought to have predated direct contact with Europeans (Thornton, Miller, & Warren, 1991), revealing the population-level networks that preclude both substantial intergroup variation in pathogen types and the utility of ethnocentrism and xenophobia as prophylactic measures.

Many evolutionary psychologists assume that the human mind has changed little since the Paleolithic (e.g., Tooby & Cosmides, 1989). While this is a reasonable heuristic, a heuristic is not an inviolate rule, and EA presents evidence of rapid genetic evolution since the domestication of plants and animals (Hawks, Wang, Cochran, Harpending, & Moyzis, 2007), including genes relevant to pathogen defense (see Laland, Odling-Smee, & Myles, 2010). Might life in the Neolithic therefore fit the PST's requirements for an EEA? On the one hand, agriculture, animal domestication, and increases in population density led to new diseases and large-scale epidemics (R. Barrett, Kuzawa, McDade, & Armelagos, 1998), while network size probably shrank due to lesser reliance on far-flung partners for risk management. However, trade increased dramatically (e.g., Bradley & Edmonds, 2005; Hirth, 1978; Robb & Farr, 2005). Combined with the greater transmissibility and virulence characteristic of pathogens that evolve to exploit high-density hosts (Ewald, 1994), the elevation of trade—and the increase in the profits to be reaped thereby—would have enhanced the fitness advantages of those who interacted with outgroups relative to those who eschewed doing so. Hence, while we encourage investigators to entertain the possibility of relatively recent EEAs for some traits, in this case, neither the Paleolithic nor the Neolithic provide the requisite features of an EEA for the adaptation postulated by the PST.

Earlier, we stressed the importance of comparative and phylogenetic analyses. Commendably, PST advocates have sought to employ these more than is typical in EP, arguing that the requisite social and epidemiological dynamics have precursors in other animals. However, here too, details matter. We noted previously that when evaluating comparative evidence, investigators must take phylogenetic distance into consideration. Many of the species cited by proponents of the PST are phylogenetically removed from humans, making parallels explicable in terms of analogy rather than homology. While analogies can illuminate the possibility space of adaptations, they do not aid in reconstructing the history of a postulated trait. PST advocates do note possible precursors in primates, citing Freeland (e.g., 1976), who provided initial evidence concerning the possible effects of pathogens on primate behavior and group structure. However, Freeland's hypothesis has not been tested, and the evidence is equivocal. The closest primate correlate of xenophobia and ethnocentrism is territoriality, yet territoriality appears to primarily function to protect resources rather than avoid disease, and can actually *increase* pathogen stress (see Nunn & Altizer, 2006).

How, then, can we account for the evidence amassed by proponents of the PST, which almost certainly reflects an important pattern of cultural differences? These correlations may reflect factors unrelated to the postulated adaptation, such as the effectiveness of government institutions (Hruschka & Henrich, 2013a) and the broad impact of differing life history trajectories (Hackman & Hruschka, 2013a). Research and debate continues (see Cashdan & Steele, 2013; Hackman & Hruschka, 2013b; Hruschka & Henrich, 2013b; Pollet, Tybur, Frankenhuis, & Rickard, in press; Thornhill & Fincher, 2014; van Leeuwen, Koenig, Graham, & Park, in press); hence, the jury is still out on these questions. However, one possibility neglected in these debates is that the correlations at issue may reflect the interaction of individual-level evolved disease-avoidance adaptations and group-level cultural evolution.

EVOLVED PSYCHOLOGY AND CULTURAL EVOLUTION

In addition to our remarkable cooperativeness, humans are unique in our reliance on socially transmitted information in addressing adaptive challenges. While a variety of adaptations likely undergird this capacity, one class in particular is relevant here. Whenever a critical challenge is present in all environments historically inhabited by humans, but differs in key attributes across environments, we can expect natural selection to have crafted domain-specific culture-acquisition mechanisms (Fessler, 2006; Fessler & Machery, 2012). Consider, for example, H. C. Barrett's work (Chapter 9, this *Handbook*, Volume 1) concerning dangerous animals. All environments occupied by humans contain dangerous animals. Some features, such as a sinuous legless body, prominent teeth, or large size, reliably predict the hazard posed by an animal in most environments; hence, natural selection can build sensitivity to such cues into mechanisms that address this challenge. However, many dangerous animals lack these features (e.g., scorpions). Cultural evolution involves the cumulative accretion and refinement of locally relevant information (Chudek, Muthukrishna, & Henrich, Chapter 30, this volume). Dangerous animals pose an important threat; hence, all cultures can be relied upon to contain information about avoiding or addressing endemic dangerous species. Natural selection has exploited this reliable feature of culture by crafting mechanisms that motivate and support early, rapid acquisition of cultural information regarding dangerous animals. Importantly, for the same reasons, selection can be expected to have crafted culture-acquisition mechanisms in many other domains as well. Hence, paralleling Barrett's work, similar considerations apply to the question of disease avoidance.

EVOLVED PSYCHOLOGY AND CULTURAL EVOLUTION: THE CASE OF DISEASE AVOIDANCE

Disgust and related disease-avoidance motivators play a prominent role in some PST work. These responses are elicited by two distinct classes of stimuli. First, disgust is evoked by cues that, across all ecologies, have uniformly been associated with the presence of pathogens: feces, vomit, odors of putrefaction, and so on are reliable indices of disease risk, and thus appear to be either hardwired, or privileged with regard to learning (Curtis & Biran, 2001). Second, disgust is also evoked by information the meaning of which is entirely cultural in origin: For example, whether decayed or fermented items are viewed as disgusting or delectable depends in part on cultural framing (Rozin & Fallon, 1987); the same is true of the perceived disease risk of drinking untreated water, having unprotected sex, and so on. This is understandable given the parochial nature of some avenues for disease transmission, and the inventive countermeasures that cultures devise using locally available technologies. Evolved human disease-avoidance mechanisms thus contain an important culture-acquisition component. Though functional in many instances, this feature also creates an opportunity for cultural evolution to highjack this system for other purposes.

While paralleling biological evolution in a number of respects, cultural evolution importantly differs in that it does not necessarily maximize individual fitness, instead operating to maximize the spread of a given set of ideas, often by increasing the size of a corresponding culture-bearing group; this process is sometimes parallel to, and sometimes orthogonal to (or even opposed to), individual fitness maximization (see Chudek, Muthukrishna, & Henrich, Chapter 30, this volume). Relations with other groups are often a central determinant of the size of a cultural group: Ceteris paribus, belief systems that motivate their holders to direct their cooperative efforts toward ingroup members, and their exploitative efforts toward outgroup members, will outcompete belief systems that are less ethnocentric in this regard (Bowles & Gintis, 2011; Neuberg & DeScioli, Chapter 28, this volume). Behavioral avoidance and a desire to expel targeted individuals are adaptive responses to persons posing a risk of disease transmission. Cultural evolution can therefore achieve group-functional (but possibly individually costly) ingroup favoritism and outgroup hostility by depicting outgroup members as posing a disease risk (witness outgroup derogations such as "cockroaches," "rats," "scum," or "vermin").

Earlier, we stressed the importance of attending to trade-offs. Disease avoidance is not free. It entails time, energy, and attention costs, and comes at the expense of dietary efficiency and social exchange. We have already seen that mechanisms governing this behavior are sensitive to changes in individual vulnerability, and the same considerations of efficiency make it likely that, as is presumed by the PST, these mechanisms are calibrated in light of the incidence of disease (see Schaller, Chapter 7, this *Handbook*, Volume 1). If so, and if the upregulation of these mechanisms involves increased attention to, and importance placed on, socially transmitted information regarding disease, then individuals occupying environments with high pathogen prevalence will be particularly vulnerable to those factually inaccurate messages concerning disease threats posed by outgroup members that promote xenophobia and ethnocentrism. In turn, this will produce the patterns of correlations documented by PST proponents. Although the correlations alone do not adjudicate between the original PST and our alternative formulation, experimental avenues for doing so exist. To exploit the power of cultural information in navigating adaptive challenges, individuals must be credulous, as the rationale for cultural practices is often unknown or opaque (Legare & Watson-Jones, Chapter 34, this volume), while the costs of individual trial-and-error learning will sometimes be high, especially when the information concerns hazards (Boyd & Richerson, 2006; Boyd & Richerson, 2009). However, credulity entails the risk of falling victim to both manipulative actors and, as our proposal presumes, inaccurate information (Kurzban, 2007). Accordingly, we can expect selection to have crafted mechanisms that adjust credulity in light of expected benefits and costs (Fessler, Pisor, & Navarrete, 2014). Cues of the prevalence of a given class of hazards should therefore shift the balance toward greater credulity in that domain. Specifically, our proposal predicts that individuals living in (or, perhaps, who were raised in) high-pathogen environments should evince elevated credulity toward cultural information relevant to disease avoidance. This is a testable prediction.

Whether our proposal is correct or not, this discussion serves to illustrate a number of important points central to the intersection of EP and EA. The first of these concerns the distinction between evoked culture and transmitted culture. Although classically defined in anthropology as information acquired through learning from one's group, the term "culture" is often used simply to refer to behavioral and psychological features that are shared within a group but differ across groups—whether or not there is evidence that such patterns stem from socially transmitted information. Tooby and Cosmides (1992) noted that such commonalities need not be the product of such information, but can instead result from the output of shared adaptations responding to the same environmental input, a pattern that they termed *evoked culture*, in contrast to *transmitted culture*. Hence, the PST argues that patterned differences across groups that correlate with differences in pathogen prevalence constitute evoked culture, being the aggregate of the output of each individual's biologically evolved disease-avoidance mechanisms. In contrast, the alternative explanation that we have proposed assumes that such patterned differences constitute transmitted culture, as individuals acquire the given beliefs and attitudes by learning them from other members of their group. Note, however, that, in both models, both biologically evolved psychological adaptations and processes of cultural evolution must be adduced.

In the PST, psychological adaptations generate attitudes toward ingroup versus outgroup members, traditional versus novel practices, and so on, but such adaptations do not create specific beliefs or practices; rather, these must be the product of cultural evolution. Religious fundamentalism, for example, may exhibit common features the world over, and may hold particular appeal for individuals in high-pathogen environments, but the identities of the deities, the rituals performed for them, and so on must all necessarily be the product of transmitted culture; the PST seeks to explain why some beliefs are more attractive than others in a given environment, but it in no way promotes the (untenable) notion that evolved mechanisms specify the details of beliefs. Our proposal that cultural evolution promotes within-group solidarity by exploiting psychological disease-avoidance mechanisms similarly does not presume a tabula rasa mind, instead arguing that an adaptation that exists specifically for the purpose of acquiring cultural information in a particular domain can be hijacked such that it operates in ways that do not serve its ultimate function.

Viewed more broadly, in both proposals, psychological adaptations create attractors (Sperber, 1996) such that some ideas are more likely to be attended to, acquired, retained, and transmitted than other ideas, thereby influencing which possibilities succeed and which fail in the marketplace of ideas (see Chudek, Muthukrishna, & Henrich, Chapter 30, this volume). Thus, as this case illustrates, as tempting as it is to interpret the dichotomy between evoked and transmitted culture in terms of nature versus nurture, doing so is a grave misstep—there are likely few cases in which evoked culture alone can explain humans' rich beliefs and practices, while even what seem the purest cases of transmitted culture will necessarily involve an underlying set of evolved adaptations. Moreover, while we have argued in the above case that the relevant adaptations focus on information acquisition, the set of likely possibilities is far larger than this, as cultural evolution often exploits or bootstraps evoked preferences and ideas produced by a variety of adaptations. For example, military history reveals increasing refinement of procedures for recruitment, training, and deployment of troops, techniques that harness the evolved mechanisms that generate small-group affiliation in the service of fielding effective armies of millions (Richerson & Boyd, 1999); likewise, incest taboos and, more broadly, marriage rules (key components of the social structures of small-scale societies) extrapolate sentiments generated by evolved inbreeding-avoidance mechanisms; and so on.

INTERPRETING CROSS-CULTURAL VARIATION AND CROSS-CULTURAL UNIFORMITY

Consonant with the complexity described above, neither cross-cultural variation nor cross-cultural uniformity is uniquely indicative of the processes generating observed patterns. Variation can reflect divergent pathways of cultural evolution acting in different societies, or it can reflect diverse evoked cultures produced by divergent physical or social ecologies. Uniformity can reflect uniform functioning of panhuman adaptations across different ecologies, or it can reflect convergent cultural evolution. In exploring these possibilities, the question of the relevant EEA again becomes central. Is it likely that variation in the relevant features of the environment characterized the EEA required for a postulated adaptation? If so, then selection may well have crafted mechanisms for facultative adjustment, in which case evoked culture may play a central role in cross-cultural variation. For example, due to differing ecologies and degrees of intergroup competition, the environments occupied by ancestral populations will have varied in rates of extrinsic mortality and the reliability of resources. Such variation is directly linked to fitness, and therefore likely favored adaptations that calibrate future orientation, risk-taking, mating strategy, parental investment, cooperativeness, and aggression in light of local circumstances. This topic has been productively explored in EP, often by evolutionary anthropologists (see Del Giudice, Gangestad, & Kaplan, Chapter 2, this *Handbook*, Volume 1; Mace, Chapter 22, this *Handbook*, Volume 1). When viewed at the level of societies, the resulting evoked cultures may drive much observed variation along these and related dimensions. In contrast, the Neolithic Revolution brought about forms of social organization and related adaptive challenges that were largely unprecedented. These radical departures make it likely that corresponding axes of cultural variation reflect a greater proportion of transmitted relative to evoked culture. For example, although hunter-gatherer groups vary in the degree to which individuals must defend resources against theft, or the degree to which present labor yields returns far in the future, these considerations loom vastly larger in pastoralist versus agriculturalist societies. The correspondence between these modes of subsistence and locally functional values and social orientations (Edgerton & Goldschmidt, 1971) is therefore best explained principally in terms of cultural evolution (albeit plausibly bootstrapping evolved mechanisms). Likewise, cultural evolution likely applies in the case of adjacent regions in which people pursue either rice or wheat agriculture: These crops entail different levels of interdependence, and reliance upon each is matched by corresponding differences in social orientation (Talhelm et al., 2014). Lastly, phylogeny is again important, albeit here in terms of the histories of the cultures at issue, as cultural phylogenetic inertia (driven by the self-reinforcing nature of institutions and values) can create differences between groups that persist after the respective selective pressures have vanished (e.g., differences between formerly pastoralist and formerly agriculturalist U.S. subcultures—Nisbett & Cohen, 1996).

As the above examples illustrate, while the complexity of the relationships between biological and cultural evolution makes the investigator's task more challenging, the range of possibilities means that there is much to explore in any area of behavior. We view all of these as within the purview of EP. At a minimum, questions of cultural variation, uniformity, and the causes thereof must always be considered given the risk that reliance on parochial samples may lead to erroneous assumptions of universality (Henrich, Heine, & Norenzayan, 2010); indeed, some of the most compelling EP research has long contained a substantial cross-cultural component (e.g., Buss, 1989). More broadly, given that we are a highly social species that is fundamentally reliant on socially transmitted information, many processes operating outside the skull fall squarely within the mandate of EP. We are thus encouraged by ventures, such as the PST, in which nonanthropologists increasingly explore such dynamics.

THE APPLICATION OF EP IN EA

Given the principal audience for this book, the above discussion focuses on how EA can enhance EP. The chapter would be incomplete, however, without considering how EP can enhance EA.

Central to EA research exploring gene-culture coevolution (see Chudek, Muthukrishna, & Henrich, Chapter 30, this volume) is a focus on the question of when it pays to imitate successful individuals versus imitate the majority, as the consequences of these choices ramify across diverse social phenomena. Though defined in behavioral terms, these are psychological processes, hence EP can illuminate them. Although investigators have begun to explore cues operating in such imitation (e.g., Chudek, Heller, Birch, & Henrich, 2012; Chudek, Muthukrishna, & Henrich, Chapter 30, this volume), the underlying psychological mechanisms remain largely unexplored. Earlier, we stressed the importance of emotions as evolved drivers of behavior, yet the psychology of cultural imitation remains largely divorced from the psychology of affect. Likewise, we emphasized the importance of understanding adaptations as kludgy mechanisms colored by their phylogeny, yet, beyond laudable efforts to compare learning biases across humans and apes (Haun, Rekers, & Tomasello, 2012), no research addresses how the structure of learning mechanisms reflects their evolution. Lastly, the nature and ramifications of domain-specific culture-acquisition mechanisms remain largely overlooked. There are thus many ways in which EP can further gene-culture coevolutionary EA.

The late introduction of EP into work on gene-culture coevolution reflects the centrality of population-level models in the latter field. In contrast, EP shares with human behavioral ecology (HBE) a focus on individual behavior. However, HBE differs from EP in that it generally eschews exploration of mechanisms (psychological or otherwise) in favor of outcome measurements used to test optimality predictions. Far from engendering harmony, the shared focus on individual behavior instead witnessed acrimonious debates between proponents of HBE and advocates of EP (Smith, Borgerhoff Mulder, & Hill, 2001). Central to these was the criticism by the latter that HBE's assumption that behavior maximizes fitness—termed the behavioral gambit—is unreasonable in highly variable contemporary environments. The behavioral gambit is problematic, advocates of EP argued, given the combination of the domain-specific nature of adaptations and the slow rate of their evolution relative to the rapidity of recent socio-ecological change (i.e., the problem of evolutionary disequilibrium, or adaptive lag). Proponents of HBE, in return, criticized practitioners of EP for underestimating both the range of environmental variation characteristic of our species' history and the attendant adaptive plasticity to be expected of behavior. Advocates of EP pointed to the apparently maladaptive nature of much contemporary behavior; supporters of HBE countered that fitness outcomes cannot be merely presumed. And so on.

While outcome measurement remains the central pillar of HBE, behavioral ecologists increasingly recognize the importance of attending to mechanisms, as (a) doing so illuminates trade-offs and other constraints on optimality ignored by the behavioral gambit (Monaghan, 2014), and (b) cultural evolution can account for the particular form of a local configuration (via cultural phylogeny), account for behavior that may be maladaptive at the individual level but adaptive at the group level (Brown, 2013), and, given the possibility of adaptive lag in cultural evolution itself, account for behaviors that may be maladaptive at both the individual and group levels (Mace, 2014).

Against the above backdrop, Nettle, Gibson, Lawson, and Sear (2013) recently advocated employing the behavioral gambit in HBE until it fails in a given case, and only then resorting to the examination of mechanisms. While their prescription for HBE is defensible, it unnecessarily limits the range of phenomena that HBE addresses. HBE presents polished methods and strategies for assessing real-world behavior and its somatic correlates, tools that can be productively deployed in exploring many of the challenges facing societies today. Contemporary epidemics of addictions to alcohol, tobacco, and drugs of abuse, or the spread of obesity, osteoarthritis, or cardiovascular disease—to name but a few—are fitness-reducing behaviors that cry out for the careful methods of HBE. Happily, some of these same investigators are beginning to explore such problems from a decidedly EP angle (cf. Pepper & Nettle, 2014), investigating, for example, how evolutionarily novel environments present cues to evolved mechanisms that calibrate future discounting in light of mortality risk (Nettle, Coyne, & Colléony, 2012). Whether explicitly acknowledged or not, HBE is thus starting to expand its scope, and its impact, by incorporating EP—a promising trend.

A ROAD MAP FOR THE USE OF EA IN EP

Having examined ways in which EP can benefit EA, we return to the central thrust of this chapter, our effort to encourage nonanthropologists who practice EP to take advantage of EA to enhance their research. Exhortations are most effective when accompanied by road maps, hence we close by discussing tangible steps toward this end.

First, consonant with our emphasis on the importance of plausible reconstructions of EEAs, regardless of discipline, evolutionary psychologists should take full advantage of the rich literatures in paleoanthropology and comparative psychology (especially primatology), as well as the ethnographic and behavioral-ecological depictions of contemporary small-scale societies in general, and of hunter-gatherer societies in particular. Granted, some reliable assumptions about life in the worlds of our ancestors can indeed be made on the basis of casual observation alone (e.g., babies were helpless and required care; paternity could not be determined with certainty; etc.). However, in many cases, the relevant facts cannot be so readily inferred. When this applies, scientific due diligence in EP should include conscientious efforts to utilize available literatures to reconstruct the relevant EEAs and plausible phylogenies, a principle that editors and reviewers—regardless of discipline—should enforce.

Second, of relevance to the above, an important scholarly resource that is arguably both the most accessible to, and the most underutilized by, evolutionary psychologists is the Electronic Human Relations Area Files (eHRAF), a collection of digitized ethnographies spanning the full range of human societies. This remarkable archive allows for comparisons relevant not only to attempts to reconstruct EEAs (e.g., Wrangham & Glowacki, 2012), but, in addition, efforts to test for cultural patterns predicted to arise from postulated psychological adaptations (e.g., Fessler et al., 2014), examine hypotheses concerning large-scale phenomena (e.g., Kline & Boyd, 2010), and pursue similar goals that go far beyond questions of EEAs.

Third, while the eHRAF provides a valuable avenue for testing a broad range of hypotheses, because the information contained therein was collected for a wide variety of reasons, investigators will often find that there is no substitute for direct measurement of behavior. Importantly, as we hope to have conveyed, rapid, evolutionarily recent culture-based changes in lifestyle constitute both a challenge and an opportunity for the evolutionary psychologist. Small-scale societies in which state regulation of behavior is minimal, kinship and longstanding social ties are central pillars of the social structure, economic activities are intimately linked to subsistence, access to health care—including contraception—is limited, and life is less awash in the sea of global electronic media provide important points of contrast for studies conducted in large-scale technologically sophisticated societies. Increasingly, evolutionary anthropologists working in small-scale societies are incorporating the EP paradigm into their work, seeking to test hypotheses—such as the facultative calibration of sexual and emotional jealousy in light of paternal investment (Buss, Larsen, Westen, & Semmelroth, 1992)—that predict patterned differences or similarities across divergent cultures (e.g., Scelza, 2014). Often, such work is collaborative, incorporating the complementary expertise of scholars from multiple disciplines (e.g., Bryant & Barrett, 2007). Indeed, as is evident in the composition of this edition of the *Handbook of Evolutionary Psychology*, cross-disciplinary collaborations and exchanges are increasingly generating a fertile syncretic paradigm in the evolutionary behavioral sciences. The future of the relationship between evolutionary psychology and evolutionary anthropology is thus a bright one indeed.

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CHAPTER 45

Evolutionary Genetics

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INTRODUCTION

When Charles Darwin developed the theory of evolution, he knew nothing about genetics. Hence, one of its biggest weaknesses was that Darwin had to base it on crude ideas of inheritance. Around the same time, Gregor Mendel discovered the laws of inheritance, but the scientific community initially failed to appreciate his work's importance. It was only in the 1930s that Dobzhansky, Fisher, Haldane, Wright, Mayr and others unified genetics and the theory of evolution in the "modern synthesis." Still, the modern synthesis was built on a basic understanding of genetics, with genes merely being particulate inherited information. The basics of molecular genetics, like the structure of DNA, were not discovered until the 1950s. When modern evolutionary psychology emerged from ethology and sociobiology in the late 1980s, it had a strong emphasis on human universals, borne from both the assumption that complex adaptations are monomorphic (or sexually dimorphic) and have to go back to at least the last common ancestor of all humans, and the methodological proximity to experimental cognitive psychology, which tends to treat individual differences as statistical noise. As a consequence, genetic differences between people were marginalized in evolutionary psychology (Tooby & Cosmides, 1990). Evolutionary psychology and behavior genetics developed nearly orthogonally for over a decade. Behavior geneticists discovered that virtually every psychological or behavioral difference shows genetic variation (Turkheimer, 2000) and that the molecular genetic underpinnings of most heritable traits are far more complex than assumed in the modern synthesis. Meanwhile, evolutionary psychologists increasingly realized the importance of genetic variation, for example, in models of sexual selection for attractiveness, intelligence, and other assumed honest signals of genetic quality (Gangestad & Simpson, 2000) or heritable variation in life history traits (see Miller & Penke, 2007). During the past decade, evolutionary genetics gradually gained acceptance among evolutionary psychologists (Buss & Hawley, 2011; Gangestad & Yeo, 1997; Buss & Penke, 2014; Penke, Denissen, & Miller, 2007), though most still defer fully incorporating the genetic perspective (Miller, 2011).

Evolutionary genetics is concerned with the *mechanisms* that explain the existence and maintenance of genetic variation in traits. All else equal, one would expect selection to deplete genetic variation in heritable traits related to fitness eventually (Penke et al., 2007). However, such genetic variation is ubiquitous and underlies stable individual differences that play prominent roles in psychological theories, be it as traits under intersexual (e.g., attractiveness, agreeableness, intelligence; Buss, 1989) and intrasexual selection (masculinity, aggressiveness; Puts, Bailey, & Reno, Chapter 13, this *Handbook*, Volume 1), life history traits, formidability in recalibration theory (Sell, Tooby, & Cosmides, 2009), sociometer sensitivity (Denissen & Penke, 2008), perceived vulnerability to infection in the behavioral immune system (Schaller & Park, 2011), attachment security (Rholes & Simpson, 2006), or the tendency to show strong reciprocity in cooperation (Fehr, Fischbacher, & Gächter, 2002). Though these theories ascribe adaptive roles to individual differences, more or less explicitly linking them to fitness, their genetic variation is often taken for granted.

Evolutionary genetics can help evolutionary psychologists unearth clues to the ultimate reasons behind, for example, humans' cognitive faculties that go beyond what can gleaned through paleontology and archaeology (Enard, Messer, & Petrov, 2014). This information can have very practical implications, such as helping to understand how natural and sexual selection, when altered through changing mores or policy, will affect certain traits.

One aim of this chapter is thus to introduce some of the tools available to researchers in evolutionary genetics. Prior to that, we provide an overview of the forces of evolution and how their interactions can maintain genetic variation. To illustrate the various ways in which evolution can maintain individual differences, we will often invoke specific traits that seem to serve as good, didactically useful examples. The general approach, however, would be applicable to all sorts of traits, including those with relevance to evolutionary psychological theories. Rarely have all possible explanations been weighed explicitly in the literature; we thus tried to refrain from definite statements. With this caveat in mind, we believe that our examples will help evolutionary psychologists make use of the rich theoretical framework that evolutionary genetics provides.

GENETIC ARCHITECTURE

Some research in molecular genetics has been carried out with the aim of characterizing the *genetic architecture* of traits, sometimes also called the genotype-phenotype map (Mackay, 2001). The genetic architecture of a trait can provide important clues to the evolutionary history and the mechanisms that govern the maintenance of genetic variation in the trait (Penke et al., 2007). Characterizing the genetic architecture of a quantitative trait would ideally involve its robustness to mutations (*canalization*) as well as its *evolvability*. It would also imply gauging its degree of *pleiotropy* (whether the genes involved also have simultaneous other effects) and the importance of *nonadditive genetic variation* (i.e., epistasis and dominance, variation that does not breed true to the next generation). Unfortunately, many examinations of the genetic architecture are limited to estimates of the number and effect size of involved genetic variants. Often the goal in such examinations is predicting which molecular genetic studies will succeed in the gene hunt and lead to biological pathways and drug targets, not to discover the ultimate, evolutionary explanations for heritable variation in a trait. In this chapter, we hope to suggest conceptual approaches to the latter goal.

It may feel like a step back from identifying causative genetic variants, but we feel it is prudent to set aside the exciting prospects of what a successful gene hunt might entail (Chabris et al., 2013) and the different ideas about how we might succeed at that (Graur et al., 2013; Mitchell, 2012), focusing instead on finding common theoretical ground.

Researchers disagree how, if ever, we might explain a substantial portion of the "missing heritability" (Mitchell, 2012), the observable genetic variation left unexplained by molecularly identified genetic variants. The limits of currently available tools can sometimes act as blinders, so that some theoretically plausible genetic architectures are hidden in our blind spots. Fortunately, as rapid technological and statistical development in molecular genetics adds to our toolkit, fewer blind spots should impede us. Humility is still very appropriate, though, considering fairly principal problems such as the sheer parameter explosion that is encountered when relating genomic sequences to traits (but see Ma, Clark, & Keinan, 2013).

Neither should we be too eager to jump to the conclusion that our purported core traits will be reflected at the genetic level. For example, Mitchell (2012) argued against the continuous liability-threshold model of psychiatric disease, saying that there truly are discrete disorders, we just tend to group them broadly and arbitrarily. Similar arguments can be construed for the structure of psychological traits like personality and intelligence.

In addition, there are often unresolved questions about the genetic architecture implied by the available evidence. For example, researchers used to believe that selection would reduce genetic variation in fitness traits, driving associated variants to fixation. This seemed to be borne out by low heritability coefficients. However, when researchers realized that fitness traits present a large target for mutation (Merilä & Sheldon, 1999), they reexamined the same heritability data expressed as the mean-standardized coefficient of variation (an absolute measure) and obtained large estimates of genetic variation. Heritability expressed as a proportion of total variation (a relative measure) had only appeared small in comparison, dwarfed by the large environmental variation (Miller & Penke, 2007). The conceptualization of fitness traits effectively reversed through a more appropriate statistic for variation.

Our understanding of how the forces of evolution shape traits' genetic architectures will continue to evolve. Thus, we begin with mechanisms potentially maintaining genetic variation before we discuss methods to identify causative genetic variants.

FORCES OF EVOLUTION

We begin by introducing four basic forces that affect genetic variation in populations.

Mutation

All existing genetic variants once arose by mutation. Relative to the 6.4 billion base pairs of the human genomic sequence, mutations are rare events. Beneficial mutations are the rarest of all, the majority likely being neutral to fitness, with deleterious mutations making up the rest. Because the idea of a neutral mutation can be reduced to chance (or *drift*) being more important for its fate than selection, calling a mutation neutral also depends on its commonness, not just its effect size. A mutation with a small beneficial effect will have its fate determined mostly by chance while it is rare, because chance events can eliminate all copies. Once its frequency rises and in larger populations drift becomes relatively less important, so the mutation will be governed more by selection (Lanfear, Kokko, & Eyre-Walker, 2014).

The most common mutational event in humans is the change of a single base pair (the letters of the DNA), but there are also deletions, duplications, and insertions of base pairs or even longer parts of DNA (copy number variants). Aneuploidies (chromosomal aberrations), such as the duplication of chromosome 21, which causes Down syndrome, are rare but massive, accounting for most altered base pairs per birth. Except for aneuploidies, which are well known to exponentially increase in frequency with advancing maternal age, all types of mutations occur more often on the paternal side, and increasingly so with advancing paternal age at conception (Campbell & Eichler, 2013). Proximately, this is often attributed to the continuous division of cells in the paternal but not maternal germline (Kong et al., 2012), but ultimate explanations such as Bateman's principle (male investment in each offspring is lower) should be kept in mind (Stearns, 2005).

SELECTION

Selection occurs when there is heritable variation in fitness. Natural selection is frequently broken down into different subcategories. One grouping distinguishes positive, directional selection (favoring increases), disruptive selection, (favoring extremes), and stabilizing selection, (favoring decreased variation in a trait). Another grouping considers survival and sexual selection separately. Sometimes this is differentiated further into "episodes of selection." Survival selection could, for example, be divided into the chances of an ovum to be released in ovulation, sperm fertilizing an ovum, a zygote implanting, the pregnancy being carried to term (Stearns, 2005), surviving birth, living to reproductive age, and further. Sexual selection might be divided into the odds of finding and attracting a mate, outcompeting same-sex rivals, the number of mates, the number of offspring per mate, and the fitness and number of offspring in the next few generations. Often the mistaken impression that selection has diminished in humans is, on closer inspection, limited to factors affecting perinatal and postnatal survival selection, with little heed paid to components of sexual selection.

Correlated Selection, Genetic Hitchhiking, and Pleiotropy Genetic variants are not independently selected for. As the term "genetic hitchhiking" vividly implies, alleles can hitch a ride on the coattails, or *haplotype*, of a neighboring allele that is being selected for or against. The chances of inheriting a specific gene from a parent are not independent from those of its neighbors because we inherit genes in chunks. Over generations, recombination breaks haplotypes apart. Long, unbroken haplotypes signal strong recent selection for a new mutation, because the neighboring alleles of a beneficial mutation are "swept" along on the coattails before recombination can break them apart (known as a "hard sweep"). Shorter unbroken haplotypes can signal selection on standing (preexisting) genetic variation ("soft sweeps"; Pritchard, Pickrell, & Coop, 2010). Two or more alleles that usually co-occur (are in "linkage disequilibrium") and thus form a haplotype can have different, even opposing effects on fitness. Until recombination breaks them apart, they cannot be selected for independently.

Alleles experience correlated selection not only through proximity. Even a variant at a single locus can have multiple, *pleiotropic* effects on fitness via different phenotypic consequences. It can also make sense to distinguish fitness effects of an allele in different episodes of selection. For example, a mutation may be selected for premeiotically in the testes, but lead to Apert syndrome later on (Choi, Yoon, Calabrese, & Arnheim, 2008).

Genetic Drift

Luck plays a lead role when numbers are small. If there are few carriers of even a highly beneficial genetic variant, random events can eliminate all of them. Similarly, a deleterious variant can be fixated by chance, or a beneficial rare variant can randomly get lost in recombination. Either way, a gene variant may drift to fixation or extinction just by chance. If all variants at a locus are common (because no single variant is infrequent and the population is large), the law of large numbers implies that it will take long before either drifts to fixation. In humans, a comparatively extremely low genetic diversity points to genetic *bottlenecks* having been an important instance of drift (Gazave, Chang, Clark, & Keinan, 2013). Bottlenecks may occur through migration, such as when founder populations emigrated to North America, or when population sizes decreased dramatically through harsh conditions such as droughts, epidemics, or ice ages. If the resulting population is small and not diverse (e.g., a clan), even beneficial alleles from the parent population may be lost through drift.

Gene Flow (or Migration)

When individuals carrying certain alleles move from one group to another, the frequency of alleles in each group also changes. This process is distinguished from unsystematic genetic drift, because relevant genetic variants may differentially influence the propensity to migrate and the success in each group and environment.

MAINTENANCE MECHANISMS

Prolonged directional or stabilizing selection on a trait will deplete its genetic variance. The mechanisms that maintain heritable variation in a trait can be understood as equilibria or trade-offs between the forces of evolution that change allele frequencies: selection, mutation, genetic drift, and gene flow. In some cases, it may seem as if evolution should lead to alternative genetic architectures with fewer trade-offs. Note that evolution is not over and that optimal solutions may not always be sufficiently better to be selected over merely adequate ones, which is, for example, why we still have blind spots in our eyes.

Mutation-Selection Balance (MSB)

Mutations continuously emerge. If they are entirely neutral, they are invisible to selection and may drift or hitchhike to extinction or fixation. But if they are deleterious, purifying selection will act against them. We rarely hear of dominant lethal mutations because they tend to be eliminated within one generation. Huntington's disease, which develops after the age of reproduction, is one example to the contrary.

If a trait is genetically complex, as most traits of interests to evolutionary psychologists likely are, many genes will be involved, not all of which play a crucial role. Hence, some deleterious mutations will be selected against less intensely and might linger for a few generations. If the mutational target size of a trait (the number of associated genetic loci) is large, mutations affecting the trait will accumulate, so that individuals carry a certain mutational load. Thus, variation in a trait such as physical attractiveness can be maintained even though it is likely under directional selection. In research on the genetics of autism spectrum disorders, new mutations appear to explain about 15% of cases (Devlin & Scherer, 2012), though this should not be equated with the part that MSB plays for autism, which may well be larger owing to older, inherited mutation load. Debate revolves around the number of genes likely to be involved in a trait and on the question whether rare, recent or common, older mutations mostly disrupt such genes (Gazave et al., 2013).

Mutations in Balance With Stabilizing Versus Directional Selection Traits under mutation-selection balance can be meaningfully differentiated further. If increases in a trait are linked to increased fitness (directional selection), new mutations should usually cause a decline in the trait. This assumption is implicit in most studies of MSB.

If fitness is instead linked to a certain optimum in a trait, it is said to be under stabilizing selection. Stabilizing selection acts to increase robustness to deleterious mutations, for example, by increasing genetic redundancy. For sexually recombining species, such as ours, it has also been suggested that increased mutational robustness need not imply a decrease in the evolvability of a trait (its potential to react to selection): Redundancy reduces the selective pressure on individual variants and thus allows variation to build up in the backup copy, creating a playground for genetic innovation. In this case, new mutations should cause comparatively smaller deviations from the optimum and might lead us to miss genetic associations if we focus on directional declines. The optimum would be expected to be the mean of a trait, at least in traits that were not subject to recent environmental changes. The shape of the eye might be an example of this exception: Myopia (shortsightedness; elongated eyes) is more common than hyperopia (early-onset farsightedness; shortened eyes), but the preponderance of myopia sufferers might be attributed to changes in our environment, in which near work became common and time outdoors decreased (Mingroni, 2004). To determine the not immediately visible optima of psychological traits, researchers could draw on associations of trait levels with survival and mate preferences as proxies of fitness consequences.

BALANCING SELECTION

We now introduce a class of balancing mechanisms. In all of them, one selective pressure is counteracted by another in a different location, time, developmental stage, social environment, or intraindividual genetic context.

By Spatial Environmental Heterogeneity (Migration-Selection Balance) Humans can experience different selective pressures in different environments. Selection by location need not be limited to selective pressures such as varying solar intensity (Norton et al., 2007) or altitude (Simonson et al., 2010), though these examples are best characterized.

Because personality may affect one's penchant for travel, migration can support spatial balancing selection: If those who want to see the world keep leaving their home island for the mainland, the remaining islanders may end up less open to experience on average (Ciani & Capiluppi, 2011). Selection would also reduce variance in openness if sedentary islanders did not occasionally interbreed with visitors from the mainland. This sort of recurring gene flow can maintain variation in openness. Similarly, sociability supports migration tendencies from rural to urban areas (Jokela, Elovainio, Kivimäki, & Keltikangas-Järvinen, 2008). In scenarios such as these, genetic variation is maintained because people within a population select themselves into the environments for which they are best adapted. Such niche picking (also known as active gene-environment correlation) is potentially a strong force in the maintenance of genetic variation in humans (Penke, 2010). In the population as a whole, no trait or underlying genetic variant would effectively be favored; thus, the selective pressures would balance.

Because cultural and other environmental explanations are hard to disentangle from genetically based psychological differences between populations, we advocate a cautious approach to this controversial topic. Some jump to premature conclusions about major genetic differences and even superiority based on flimsy evidence such as fairly high within-group heritability coefficients, but a balanced view of the evidence shows how difficult explaining group differences genetically is (Berg & Coop, 2014).

Because of humans' ecological dominance and concomitant capacity to shape the environment to their needs (niche construction), Penke and colleagues (2007; Penke, 2010) argued that the most important fluctuating aspect that humans need to adapt to is their social environment.

By Social Environment (Negative Frequency-Dependent Selection) There are three *morphs* (types) of male common side-blotched lizards (*Uta stansburiana*), and three alleles at one Mendelian locus govern their throat color and concomitant behavior. Blue-throated males guard one mate and territory. Their mates can be stolen by larger, aggressive, orange-throated males, who keep large territories and multiple mates. Because they do not guard their mates well, they are vulnerable to having their mates stolen by yellow-throated males, who pretend to be female to sneakily gain access. This nontransitive mating game has been compared to rock-paper-scissors (Sinervo & Lively, 1996) and leads to oscillations in which the least common morph becomes more common in the next generation.

Biological sex is probably the most familiar morph under such negative frequency-dependent selection (NFDS) in humans, as the rarer sex becomes more desirable and thus has reproductive advantages due to mating market forces (Del Giudice, 2012). NFDS has also been invoked to explain primary psychopathy (Mealey, 1995), personality traits (Penke et al., 2007), and, perhaps most fruitfully, immunity to parasites (Sutton, Nakagawa, Robertson, & Jamieson, 2011).

If psychopathy were under frequency-dependent selection, we might, through altered policy, lower the equilibrium frequency of psychopaths within few generations (Mealey, 1995).

Over Time (Generations) If selection fluctuates over time more quickly than is needed for trait alleles to be driven to either fixation or extinction, variation can be maintained in oscillations. For example, if sex ratios in populations naturally fluctuate over time, genetic variation in personality traits that lead to better mating outcomes in one sex can be maintained by balancing selection (Del Giudice, 2012). If the fluctuations are predictable, selection should act to create genetically fixed conditional (facultative) strategies instead, a rich topic for life history theory (Nettle, Frankenhuis, & Rickard, 2013; Penke, 2009, 2010).

Over Time (Ontogenetic Development) Earlier, we mentioned an allele that proliferates in the testes but leads to disease (Choi et al., 2008). Negatively correlated selection across developmental stages is also plausible for quantitative traits. For instance, large heads may support cognitive ability in later life, but they complicate birth (Miller & Penke, 2007). Selection should favor traits that are not subject to such trade-offs, but especially in conjunction with fluctuations of the fitness effects at different developmental stages, variation could be maintained.

By Genetic Variant at Other Loci (Epistasis) An allele may have a beneficial or deleterious effect only in the presence or absence of other genetic variants. The sheer complexity of considering all the interactions in conjunction with the already large number of variants in the human genome has led some to propose that evolution would lead to mainly additive and even modularized variation in certain traits (W. G. Hill, Goddard, & Visscher, 2008), but epistasis might also be missed owing to insufficient statistical power.

By Genetic Variant at the Same Locus (Overdominance, Heterozygote Advantage, Selection-Drift Balance) Consider a polymorphism, such as the one involved in sickle-cell anemia. Two copies of the polymorphism make blood cells sickle-shaped under low-oxygen conditions and typically lead to premature death. But having only one copy (heterozygosity) confers greater resistance to malaria. Individuals from areas in which malaria was a strong selective pressure are more often carriers of the sickle-cell polymorphism. Heterozygotes have a selective advantage over homozygotes with either allele and so the sickle-cell allele can persist in the population at equilibrium frequency.

These equilibria are not stable: An allele that has the benefits but not the disadvantages will easily displace its competitor. We expect to see overdominance especially under strong, recent selection, such as that incurred by epidemics.

MUTATION-DRIFT BALANCE (SELECTIVE/ANCESTRAL NEUTRALITY)

If mutations affecting a neutral trait arise so frequently that some linger before they drift out of existence, we expect genetic variation in this trait to linger as well. Because of the nature of genetic drift, existing, entirely neutral polymorphisms would linger longer in large populations. Because most human DNA is nonfunctional junk, which is not conserved through purifying selection, most mutations are neutral (Graur et al., 2013). One's first intuition might then be that most human individual differences are selectively neutral or "evolutionary noise" (Tooby & Cosmides, 1990). However, a commonly variable trait that is phenotypically visible to selection is less likely to be entirely neutral. This is especially the case since we tend to be interested in traits *because* they have predictive value for consequential life outcomes such as reproductive success, and thus evolutionary fitness. Additionally, because populations are larger nowadays, selection is more efficient, and will more often be stronger than drift (Penke et al., 2007).

In humans, with their rapidly changing culture and environment and with their rapidly increasing population size (Gazave et al., 2013), we might want to pay special heed to traits that used to be selectively neutral or nearly so, but no longer are. These are traits where we might expect natural selection to rapidly deplete genetic variation. Because traits under mutation-drift balance have a repository of standing variation and because selection is stronger than drift, it can decrease previously maintained variation.

A potential candidate for an ancestrally neutral psychological trait may be our preference for rising early or late: Our circadian rhythm is entrained to a universal source of light, the sun, in areas with little artificial light, where little time is spent indoors. With more artificial light, individuals' circadian rhythms become more variable (Wright et al., 2013), and such differences are moderately heritable (Barclay, Eley, Buysse, Archer, & Gregory, 2010). Possibly what we see here is cryptic genetic variation, revealed only under artificial light. Without it, the lack of variation in light exposure within populations might have meant that heritable differences were not visible, even though psychological differences that would have influenced self-exposure to artificial light already existed.

MECHANISMS IMPLICATING MORE THAN ONE TRAIT A TIME

In this section, we consider mechanisms that lead to the impression that there is heritable variability in a trait, but which are best understood in conjunction with other mechanisms and traits.

Mechanisms Related to Pleiotropy and Hitchhiking When genes are pleiotropic (affect multiple traits) or in linkage (in close proximity to each other on a chromosome), genetic correlations among traits can appear. There are ways to discover genetic correlations and to analyze contemporary selection on multiple correlated traits (Stearns, Byars, Govindaraju, & Ewbank, 2010), but few studies have tried to do so for human evolutionary history.

The best-characterized examples of antagonistic pleiotropy arise in conjunction with biological sex. Traits like facial masculinity may be more adaptive in one sex than the other, but the respective alleles spend half their careers in each sex (A. J. Lee et al., 2014). Another important class of pleiotropic interactions may arise through the body's limited energy budget, especially that available for immune, brain, and gut functions. As a consequence, selection cannot optimize either trait, eventually resulting in a continuum of equally fit trait combinations maintained in the population.

Reactive Heritability Not every trait with heritable individual differences needs to be subject to some sort of balancing mechanism itself. Instead, it could be calibrated to another heritable trait (Tooby & Cosmides, 1990). For example, Lukaszewski and Roney (2011) posited that extraversion might be calibrated to one's physical attractiveness and strength. Hence, we would find the signature of mutation-selection balance when studying extraversion in isolation, but would come to different conclusions when examining developmental and situational calibration of extraverted behavior to one's relative strength and attractiveness.

If they are not fixed at birth, we should not presume the primacy of physical traits. For example, we know that myopia appears to be linked to the amount of time children spend outdoors (Sherwin et al., 2012), but the substantial heritability estimates for myopia have led some researchers to downplay environmental explanations for the recent increase in myopia incidence (Mingroni, 2004). But if myopia heritability is partly reactive to children's heritable proclivity for outdoor play and if some children spend less time outdoors in recent times, which is plausible, these findings could be reconciled.

THE EVOLUTIONARY GENETICS TOOLKIT

In this section, we introduce the growing toolkit that is available to evolutionary geneticists. These tools were assembled from both quantitative and molecular genetics, as well as evolutionary psychology. We note what these tools can be used for, and how they are sometimes misused, but acknowledge how all of these methods make their contributions.

TWIN AND FAMILY STUDIES

Twin studies are one of the oldest tools available and have withstood the test of time (Conley, Rauscher, Dawes, Magnusson, & Siegal, 2013). They rely on the key difference between monozygotic (identical) twins and dizygotic (fraternal) twins: Identical twins share all of their genes, while fraternal twins share on average half of the genes that were variable between their parents. A central result from twin studies is usually a heritability estimate, though the rich data from twin and family studies can answer many other questions too. The concept hails from plant and animal breeding, where it is used to predict response to artificial selection.

Estimates of heritability derived from twin studies have held up remarkably well when reexamined using different family relationships (e.g., parents, siblings, half- and adopted siblings) and can be easily extended to novel data such as the sometimes numerous offspring of sperm donors. In cases where selection is fairly clear-cut, estimates of heritability have borne out their usefulness as predictors of the response to selection. For example, children of sperm donors are taller in a manner consistent with their mothers' selection on donor height (J. C. Lee, 2013).

Usually things are not so tidy: Heritability estimates from twin studies often include some nonadditive variation, that is, variation that will not "breed true" to the next generation. Moreover, environmental confounds can make it hard to isolate an effect of selection, as the initiators of the Scottish Mental Survey discovered in 1947 when they attempted to show a decline of intelligence through differential fertility and found an increase instead (Ramsden, 2007). Humans simply do not behave like crops on a field or cattle in a breeding facility; they actively choose mates and both choose and modify their environments. This decreases the value of heritability estimates as more than a proof that genetic differences play a role in observable phenotypic variation (Johnson, Penke, & Spinath, 2011).

High heritability in twin studies has often been misunderstood to imply that a trait cannot be changed. To the contrary, species-typical universals such as two-leggedness have virtually zero heritability, because the underlying genes rarely vary. On the other hand, some gene-environment interactions were not apparent before the relevant environment changed: For example, developing phenylketonuria, a disease causing intellectual disability, depends on consuming phenylalanine, which was a universal part of our diet before its damaging effects in some individuals became known.

Linkage Studies

Linkage studies, which identify larger genetic segments that segregate according to disease status in a pedigree, have been useful tools in the identification of "simple" Mendelian disorders, where single genes have major effects. They might also help once we learn to tell apart phenotypically similar diseases that we now group as complex psychiatric disorders (Mitchell, 2012). Linkage studies for most psychological variation have been characterized as a let-down. Still, they ruled out a suggested genetic architecture: If there were, for example, a single genetic locus causing human psychopathy (i.e., an exploitative social strategy) in analogy with the aforementioned sneaky side-blotched lizard, linkage patterns would have led to its identification.

Candidate Gene Studies

Candidate gene studies look for the association of a specific genetic locus with the trait of interest. By hypothesizing which locus may be involved *a priori*, they avoid correcting for multiple comparisons and can thus use smaller samples than the similar, but exploratory genome-wide association paradigm. They have come under intense criticism because of nonreplications and general doubts whether there is sufficient theory to predict candidate genes (Ioannidis, Trikalinos, Ntzani, & Contopoulos-Ioannidis, 2003).

Some recent studies, however, successfully employ candidate gene approaches, implicating candidate gene sets and apparently building on stronger theory than before. For example, W. D. Hill et al. (2014) reported and replicated an association of intelligence with variation in genes involved in one of the postsynaptic density complexes that have been implicated in cognitive functioning. Through preregistration of candidate genes, researchers could easily end disagreements and distrust whether their studies deserve the label of confirmatory research and concomitant relaxation of false discovery rates. Unfortunately, this is seldom done.

Genome-Wide Association Studies (GWAS)

GWAS assess the status of individuals on around a million genetic loci across the genome that are commonly variable in the population. While GWAS directly assess only around 0.033% of the human genome this way, linkage disequilibrium makes the assessed variants fairly exhaustive markers of common genetic variation, which is then related to the variation in the trait of interest. GWAS require large samples and have been early adopters of harsh significance thresholds to account for the number of multiple comparisons (Ioannidis et al., 2003).

GWAS have been successful in the identification of some of the genes that matter for pigmentation, some medical disorders, height, and recently, schizophrenia (Schizophrenia Working Group of the Psychiatric Genomics Consortium, 2014). Yet, for most psychological traits, especially normal variation, they rarely identified replicable associations (Chabris et al., 2012, 2013). This is often framed negatively, but GWAS effectively ruled out genetic architectures involving few common variants of medium-to-large effects for all psychological traits studied this way so far. Some researchers have advocated ever larger samples in order to potentially identify huge sets of genetic variants with individually miniscule effect sizes, while others argue that theory predicts only effects of questionable practical relevance and that family-based designs are better suited (Mitchell, 2012).

USING SEQUENCED EXOMES AND GENOMES IN ASSOCIATION STUDIES

Sequencing refers to identifying every single base pair in someone's genome, not just a few commonly polymorphic loci, as in GWAS. When sequencing is limited to protein-coding genes (ca. 1%–2% of the whole genome), this subset is called the exome. The exome constitutes a more manageable amount of data and has been considered promising for clinical variation. However, much of it is conserved between species and a lot of recent selection has operated on promoters outside the exome (Enard et al., 2014; The 1000 Genomes Project Consortium, 2012), making exome variation a less likely candidate for contributing to the genetic architecture of psychological traits in the normal range (Marioni et al., 2014).

With the amounts of data generated by genome sequencing, entirely exploratory research would not be useful due to the sample sizes required to filter chance findings. Integrating prior knowledge, such as annotations on regions with a signature of recent selection or expression in the brain (Ma et al., 2013), or alternatively relying on summary indices of rare genetic variants, a direct operationalization of mutation load (Marioni et al., 2014), may make such data manageable.

GENOMIC PREDICTION AND GENOME-WIDE COMPLEX TRAIT ANALYSIS (GCTA)

A method formerly used primarily to predict breeding value in domestic animals has recently become popular in human genetics under the name GCTA (Yang et al., 2011). The general method estimates distant relatedness (less than fourth cousins) between individuals in the general population on the basis of common genetic variants, as provided by GWAS. Unlike GWAS, this method does not identify individual important loci. Instead, the distant relatedness is used to infer a heritability score akin to that known from twin studies, but based solely on molecular data. After many GWAS failed to identify loci associated with psychological traits, GCTA provided a means of showing that the genotype data was actually informative: It can validate heritability estimates and be used to enable marker-assisted breeding (though this application is unlikely in humans), even if it does not identify causative genes and hence provides no foothold to find biological pathways. A frequently raised objection is that GCTA heritability estimates might be spurious, driven by the resemblance of distantly genetically related individuals for nongenetic reasons, such as similar environments because of shared ancestry and migration history. Researchers working with GCTA acknowledge such confounds, and the discussion revolves mostly about whether the corrections are sufficient (Conley et al., 2014; Yang et al., 2011).

Some researchers also doubt whether finding high GCTA heritability implies that the infinitesimal model of many common variants of tiny effect applies, especially when debilitating disorders are under study (Mitchell, 2012). Maybe more agreement can be fostered by a shift to delineating a fully featured genetic architecture, acknowledging the balanced forces enumerated in this chapter.

Paternal Age Effects

By sequencing and comparing the genomes of both parents and an offspring, Kong et al. (2012) convincingly demonstrated that the number of newly occurred single nucleotide variants in offspring can almost entirely be accounted for by the father's age at conception. Thus, paternal age can be used as a proxy variable to infer the effect of new mutations. To isolate this effect, the fact that human reproductive timing is not governed by chance has to be statistically controlled. Initially reported negative associations between paternal age and intelligence in the normal range (Malaspina et al., 2005) have not been replicated in later studies. Controlling parental intelligence, an important predictor of reproductive timing, may account for some of the observed heterogeneity of effects (Arslan, Penke, Johnson, Iacono, & McGue, 2014). Employing sibling comparison designs also led to the disappearance of paternal age effects on intelligence, while a strong association with attention deficit hyperactivity disorder became visible only with sibling controls (D'Onofrio et al., 2014).

Properly isolated, paternal age effects can provide evidence for a trait being under mutation-selection balance. In addition, they can be useful to predict the effect of increasingly delayed reproduction in the industrialized world on average mutation load (Sartorius & Nieschlag, 2010).

Genome and Exome Triplets and Quads

When the entire exomes or even genomes of parent-offspring trios are sequenced, it becomes possible to count new mutations, that is, alleles that neither parent carried. By assessing which haplotype a mutation lies on, it is also possible to identify the parent of origin. Then, mutation counts can predict, for example, intellectual disability (Rauch et al., 2012) and recurring mutations can be used to zero in on causative genes.

Exome quads (both parents and two offspring) have been used in autism genetics. Using genome annotations, Iossifov et al. (2012) estimated which mutations interrupted genes. By also sequencing unaffected siblings whose genomes were recombined from a common parental pool, they could isolate the effect of having more disrupted genes. Studies on autism genetics tried to isolate the effect of new mutations from assortative mating by considering only families without a familial history of autism and through sibling comparisons. These molecular genetic studies corroborate earlier results of autism increasing with paternal age.

Inbreeding Depression and Outbreeding Elevation

Inbreeding depression refers to a fitness decrease in offspring of consanguinous unions. Consanguinous parents (second cousins and closer) and their offspring make up about 10% of the world's population, though their prevalence has been predicted to decline (Bittles & Black, 2009). Franssen (2009) reported a linear negative relationship between offspring mental ability and consanguinity ranging from second-cousin marriages to incest. Such associations are confounded by many unobserved common causes. For example, lower parental education can, via lower mobility, increase the likelihood of marrying relatives and thus inflate estimates of inbreeding depression. The family history and cultural prevalence of consanguinity (e.g., in clans and castes) affect inbreeding coefficients too, so that estimates based on just two generations can be off (Bittles, 2010).

Outbreeding elevation, also known as *hybrid vigor* or *heterosis*, refers to the increased phenotypic quality of the offspring of genetically more distant parents. This phenomenon is very familiar to plant and animal breeders. Mules may be the most iconic hybrids and hybrid maize the most frequently consumed. The *vigor* does not necessarily translate to evolutionary fitness: Mules are valued beasts of burden but are frequently infertile. This is because too-distant genetic relationships between parents can break up co-adapted gene complexes during recombination, hence breaking vital functions such as the ability to reproduce. A bit of both may have happened when modern humans and Neanderthals interbred (Sankararaman et al., 2014). Hybrid vigor can also occur when inbreeding ends: Mixed-breed dogs have higher life expectancy than most purebreds (O'Neill, Church, McGreevy, Thomson, & Brodbelt, 2013). Mingroni (2004) proposed that urbanization and generally less sedentism led to decreased inbreeding and might be partial causes for the recent increases in height and intelligence in industrialized countries.

RUNS OF HOMOZYGOSITY

Analogously to GCTA, which employs DNA-based subtle relatedness to validate twin studies' estimate of heritability, runs of homozygosity (ROH) are an attempt to characterize subtle inbreeding on a molecular level. If long stretches of a diploid genome are homozygous, that is, both strands of DNA have the same variants, we can infer that closely related individuals have bred. If many shorter stretches are homozygous, we can infer ancient relatedness (Kirin et al., 2010). The genomic approach has the benefit that inbreeding over several generations can be characterized, though it is important to supplement this with knowledge of the history of endogamous marriage, founder effects, and population bottlenecks (Bittles, 2010). Homozygosity appears to play a role not only in well-characterized recessive disorders such as cystic fibrosis, but also for traits like personality (Verweij et al., 2012, 2014). Power et al. (2013) found a zero-to-slightly-positive association between ROH burden and intelligence, which conflicts with (possibly more biased) pedigree-based estimates of inbreeding effects (Franssen, 2009).

RELATIONS WITH FITNESS (LIFETIME REPRODUCTIVE SUCCESS) AND MATE PREFERENCES

It may seem as if we have so far neglected the obviously relevant effects of traits on fitness measures in this chapter. This is because, with some exceptions (e.g., pervasive developmental disorders), it is difficult to establish that the same association has persisted over evolutionary time and is thus indicative of the balancing mechanism that primarily upheld variation in a trait. We lack historical data for psychological traits, and many associations between normal variation and fitness estimated nowadays could be fickle. Contemporary selection on human individual differences is interesting in itself (Stearns et al., 2010), but we expect evolutionary genetics, among other disciplines, to answer the question "Why did humans evolve to be this way?"

In the age of widespread, effective contraception, it can be argued that mate preferences and choices are better-preserved indicators of sexual selection than correlations with reproductive success. In addition to being more immediately assessable than lifetime reproductive success, mate preferences have been shown to be relatively culturally invariant (Buss, 1989), unlike total fertility. Perinatal and postnatal survival selection plausibly have decreased in intensity since the advent of hygiene, modern health care, less frequent infanticide, and lower infant and maternal mortality. Still, a large number of pregnancies are not carried to term and many debilitating, previously lethal genetic conditions, such as severe disability, may now be sexually selected against owing to lower attractiveness in the mating market.

Correlations With Indicators of Developmental Stability

Bilateral fluctuating asymmetry (FA) of the body is presumed to be an indicator of developmental stability, operating under the assumption that mutation-free organisms in good condition will be more symmetrical (Polak, 2003). Correlations with FA are thus assumed to provide an indirect way to tap a trait's association with mutation load. This paradigm is prevalent in evolutionary psychology and somewhat plagued by publication bias (Van Dongen & Gangestad, 2011). Hardly any studies take a molecular or population genetic approach to fluctuating asymmetry in humans. Future studies should more directly examine an association of developmental stability indicators with rare genetic variant burden, paternal age, or consanguinity before correlations with FA can be deemed valid proxies for tapping "good genes." Preregistration of studies could foster greater trust, especially that of scientists in adjacent domains such as genetics.

CONCLUSION AND OUTLOOK

Evolution by natural selection occurs as long as there is heritable variation related to differential fitness in the population. The evidence for both is ubiquitous even today, posing the question why so much genetic variation persisted. Genetic variance is influenced by mutation, selection, drift, and migration, and combinations of these four forces can yield balanced states in which it is maintained. This has been known since the modern synthesis in the 1930s, but our understanding of the molecular genetics underlying these processes has radically progressed. We are increasingly able to learn about the genetic architecture underlying psychological traits. Although the resulting picture will not be as simple as most researchers assumed even a few years ago, it can eventually provide insights about the evolutionary history and the selective pressures currently acting on these traits (Penke et al., 2007).

The evolutionary genetic toolkit includes complementary tools from molecular, behavior genetics and classical evolutionary psychology. Every available method has so many caveats that only converging evidence can enable us to single out theories as tenable. Unfortunately, even closely neighboring disciplines do not often lend each other tools and insights. For example, pure life history models of psychopathology (Del Giudice, Klimczuk, Traficonte, & Maestripieri, 2014) are inconsistent with the accumulating evidence that mutation load plays a major role in the autism and schizophrenia spectra (Andreassen et al., 2014). Research on runs of homozygosity and mutation load could verify assumptions inherent in studies on fluctuating asymmetry. We need to subject our favored evolutionary explanations to tools from outside our own respective fields. Different disciplines can find it hard to properly evaluate and trust results outside their own field, especially if there is publication bias. Data and discussion brought to bear on the matter may have ideological baggage and bias (Ramsden, 2007), as researchers on, for example, intelligence or inbreeding, where science is easily conflated with moral judgments, know well. However, we can restore trust in areas plagued by bias (e.g., candidate gene and fluctuating asymmetry studies) through preregistration, replication, collaboration in consortia, and greater transparency. Such quality badges can be recognized even if the exact details are beyond us (Miller, 2011). By embracing such superior scientific standards we can protect our theories from the charge of being "just-so stories."

It is encouraging, however, that all these approaches share a common evolutionary meta-theory, which could help to integrate knowledge acquired using diverse tools and build a common understanding. We have referenced numerous positive examples throughout this chapter. Mutual assistance and understanding should lead not only to agreement on the existence of heritable individual differences, but on the *mechanisms* maintaining them. Even where we identify genetic architectures that make it hard for us to detect important causative genes (e.g., an infinitesimal number of causative genes of small effect, genetic heterogeneity, or epistasis), there is a lot to be gleaned from understanding maintaining mechanisms. These mechanisms are not idle theory; they have practical applications. Policy and mores already exert influence on demography, reproductive timing, and selective pressures. We do not need to know specific genetic variants to predict what will happen to autism incidence if people reproduce later, nor to characterize the role of assortative mating and consanguinity in the age of online dating, nor to understand the impact of anciently constant selective forces suddenly swayed by new technology.

Where we identify traits with a genetic architecture conducive to identifying causative genes, many doors open for vertical integration (Y. W. Lee, Gould, & Stinchcombe, 2014) with biology and neuroscience: We can study pathways, develop drugs and genetic screenings, examine molecular signatures of selection and demographic history (Enard et al., 2013), use Mendelian randomization techniques (Smith & Ebrahim, 2004) to identify modifiable causes of disease, and make inferences about earlier hominids' psychological characteristics on the basis of shared polymorphisms.

Darwin knew nothing about the genetics underlying evolution, but our ever more detailed understanding allows us to fully embrace the potential of merging evolutionary theory with genetics. Evolutionary genetics enriches evolutionary psychology by providing a theoretical framework and tools to integrate individual differences and recent evolution (Penke, 2010), and thus ultimately an understanding of why we are the way we are and how we became that way.

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CHAPTER 46

Evolutionary Psychology and Endocrinology

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OVERVIEW: THE ROLE OF ENDOCRINOLOGY IN HUMAN EVOLUTIONARY PSYCHOLOGY

Evolutionary psychology posits that the human mind in its basic design is composed of a collection of specialized processing mechanisms that were naturally selected to address specific adaptive problems, such as mate choice, food choice, social exchange, and parenting (Buss, 2012; Tooby & Cosmides, 1992; chapters in this *Handbook*). The primary empirical project for psychological science entailed by this perspective is the discovery and characterization of the functional information-processing features of each of these specialized mechanisms. Although the information-processing (or "cognitive") level of explanation may be privileged since natural selection will act primarily on the functionality of mappings between stimulus inputs and behavioral outputs (see Tooby & Cosmides, 1992), a complete understanding of human psychology also requires empirical characterization of each mechanism's ontogeny, phylogenetic origins, and neurobiological implementation (see Tinbergen, 1963). The systematic mapping of these four levels of explanation on a mechanism-by-mechanism basis comprises a method for the cumulative construction of an increasingly complete model of human nature.

Research that investigates endocrine signals may be especially productive in promoting the comprehensive mapping of psychological adaptations, for two basic reasons. First, knowledge of endocrine mechanisms typically cuts across the four types of explanation for biological traits such that characterization of the functional roles of hormonal signals holds the potential to produce unusually complete explanations for specific psychological adaptations. Endocrine signals are known to be produced and received by specific brain structures, the phylogeny and ontogeny of which are often

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well characterized; as such, research demonstrating that hormonal signals can produce functional linkages between contextual circumstances and behavioral outputs often carries implications for the neurobiology, ontogeny, and phylogeny of the relevant mechanisms.

Second, endocrine signals may play an especially important role in solutions to the adaptive problem of mechanism coordination that arises as a consequence of the modular organization of the mind. A collection of mechanisms specialized for the solution of different types of adaptive problems raises the problem of determining which problems are currently most pressing in order to assign priority to the processing algorithms of those mechanisms that best solve those problems, while inhibiting mechanisms the outputs of which would disrupt such solutions (see Cosmides & Tooby, 2000). Hormonal signals are ideally suited to contribute to mechanism coordination since they are often released into the general circulation and can thereby simultaneously broadcast information to mechanisms distributed throughout the brain and the rest of the body. In effect, endocrine signals may announce the present importance of specific adaptive problems, and prime organism-wide configurations of mechanism settings that tended to facilitate solutions to those problems over the course of human evolution.

In this chapter, I describe one specific example of how endocrine signals may produce functional linkages between specific situations and specific configurations of mechanism settings. The example concerns the suite of physiological and psychological changes that occur when individuals are exposed to potential mates. The chapter is not intended as a literature review of human endocrine research in general, but instead as an example of how research in this area might contribute to the empirical project of mapping the set of human psychological adaptations.

ENDOCRINE SIGNALS AND MATE PURSUIT

EMOTIONS AND THE PROBLEM OF MECHANISM COORDINATION

Cosmides and Tooby (2000) proposed a functional account of emotions as superordinate programs that address the adaptive problem of mechanism coordination. These programs detect ancestrally recurrent cues indicative of a fitness-relevant problem, communicate the presence of this problem via an internal signaling system, and via this communication prime and inhibit distinct mechanisms based on their relevance to solving the problem in question. On this account, emotions may be much more numerous and specific than the traditional set of emotion terms used in language, including emotions such as "being stalked by a predator" that were designed to address recurrent adaptive problems in the ancestral past. In the stalking example, a large number of mechanisms related to other adaptive problems may be inhibited (e.g., those pertaining to food or mate search, sleep, digestion, etc.), while a specific suite of programs and subprograms calibrate attention, motivation, behavioral thresholds, and physiological patterns toward those settings that on average facilitated escape from danger in this situation.

"Mating opportunity" may comprise an emotion in the sense proposed by Cosmides and Tooby (2000). In sexually reproducing species, the presence of a potential mating partner who exhibited signs of accessibility or interest would have been a recurrent and highly fitness-relevant situation. The fitness benefits of successful mate pursuit likely made it functional for organisms to shift attentional, motivational, physiological, and behavioral priorities away from other adaptive problems and toward mate acquisition upon detection of this situation. The relevant emotion program should implement decision rules regarding whether and how intensely to activate particular mechanism settings based on input cues related to the specific opportunity (e.g., what is the mate value of the potential partner?), the internal state of the organism (e.g., am I in good enough physical condition to engage in mate competition?), and other aspects of the social context (e.g., are competitors present who could thwart efforts at mate attraction?). These decision rules may in effect calibrate the intensity of the internal signals sent to mechanisms throughout the brain and body in order to determine the degree to which the organism is snapped into configuration settings geared toward mate pursuit.

Hormones may be used by many emotion programs as important internal signals that link detection of an adaptive problem to the organism-wide coordination of mechanism settings designed to address that problem. This appears to be especially true for the problem of mate attraction, as specific hormonal responses to cues from potential mates have been demonstrated in a wide array of vertebrate species. In what follows, I first review evidence for these responses in nonhuman species, with an emphasis on how hormone increases may index decision rules regarding behavioral pursuit of mating opportunities. The nonhuman literature provides a model for the possible design of human mechanisms. I then review evidence that humans express homologous emotion programs that use similar endocrine signals to activate a suite of mechanisms directed toward the problem of mate acquisition.

Endocrine Signals and Mate Pursuit in Nonhuman Species

Males Across a wide range of nonhuman vertebrate species, males respond to females or their stimuli with reactive increases in testosterone and corticosterone concentrations that appear to help signal the current importance of mating as an adaptive problem (for a review, see Meisel & Sachs, 1994). These effects are rapid but transient, being first detectable within 10 to 60 minutes of exposure to female stimuli (often peaking near 30 minutes) but with concentrations returning to baseline within 1 to 2 hours. The responses do not require physical contact, as they can be induced via proximity to females placed behind transparent barriers (e.g., Amstislavskaya & Popova, 2004; Batty, 1978; Bonilla-Jaime, Vazquez-Palacios, Artega-Silva, & Retana-Marquez, 2006; Popova & Amstislavskaya, 2002; Purvis & Haynes, 1974) and in some cases by chemosensory stimuli such as urine or vaginal secretions (e.g., Cerda-Molina et al., 2006; Pfeiffer & Johnston, 1994; Ziegler, Schultz-Darken, Scott, Snowdon, & Ferris, 2005). Finally, these responses are absent after comparable exposure to conspecific males (e.g., Amstislavskaya & Popova, 2004; Macrides, Bartke, & Dalterio, 1975; Pfeiffer & Johnston, 1992), which argues for their functional sensitivity to mating-relevant stimuli.

Male behavioral and hormonal responses to females are regulated by a phylogenetically conserved limbic-hypothalamic pathway (for reviews, see Meisel & Sachs, 1994; Paredes & Baum, 1997). Lesions to key structures within this pathway—such as the medial amygdala and especially the medial preoptic area—have been shown to abolish or significantly reduce male sexual (Paredes & Baum, 1997), courtship (e.g., Lloyd & Dixson, 1988; McGinnis & Kahn, 1997; Riters & Ball, 1999), and hormonal (Kamel & Frankel, 1978) responses to females. These structures express the highest density of androgen receptors of any brain region (Pfaff, 1981) and the signaling properties of this pathway are clearly regulated by androgens like testosterone: Castration (and thus removal of testosterone) eliminates or severely reduces male courtship responses to conspecific females, but selective implantation of testosterone into pathway structures such as the medial preoptic area can restore such behaviors to normal levels in castrated males (e.g., Matochik, Sipos, Nyby, & Barfield, 1994; Nyby, Wysocki, Whitney, & Dizinno, 1977; Sipos & Nyby, 1996). Likewise, pharmacological blockade of androgen receptors in this pathway eliminates or reduces male behavioral responses to females (Harding & McGinnis, 2004; Raskin et al., 2009). In sum, a conserved limbic-hypothalamic pathway appears to act as a type of gating mechanism that implements decisions rules about the extent to which cues from females trigger coordinated behavioral and hormonal responses in males. This gating mechanism is in turn modulated by androgens via the androgen receptor such that males are less responsive to female stimuli when testosterone falls to very low concentrations or when the number of occupied androgen receptors is otherwise low.

The signaling properties of the limbic-hypothalamic gating mechanism produce functional modulation of male responses to females under a range of natural conditions. Seasonally breeding species often undergo a type of reversible castration, for instance, in which testosterone falls to castrate levels during the nonbreeding season (in response to cues such as reduced photoperiod) concomitant with an absence or reduction of male behavioral and hormonal responses to females (e.g., Anand, Losee-Olson, Turek, & Horton, 2002; Riters et al., 2000). Likewise, male rodents that have reached a state of sexual satiety via frequent ejaculation fail to respond both behaviorally and hormonally to novel females (Bonilla-Jaime et al., 2006; Bronson & Desjardins, 1982), and the behavioral effects of satiety are strongly correlated with changes in the density of androgen receptors within the limbic-hypothalamic pathway. Receptor density drops as satiation sets in but then recovers with the resumption of sexual responses to females (Fernandez-Guasti, Swaab, & Rodriguez-Manzo, 2003; Romano-Torres, Phillips-Farfan, Chavira, Rodriguez-Manzo, & Fernandez-Guasti, 2007). These patterns suggest the functionality of this emotion program's decision rules: Under conditions in which pursuit of mates is less functional—as when females are not fertile during the nonbreeding season or when sexual exhaustion has produced sperm depletion—this pathway is down-regulated such that cues from females are no longer mapped onto behavioral and hormonal responses in males.

Various social conditions are also modulators of male hormonal responses to cues from females. In cynomolgus macaques, for instance, an estrous female introduced into a group of males for 20 minutes triggers testosterone and cortisol increases in dominant but not in subordinate individuals; however, subordinates exhibit hormonal responses to females under experimental conditions in which the dominant male was removed from their group (Glick, 1984; for similar effects on longer time scales in squirrel monkeys, see Mendoza, Coe, Lowe, & Levine, 1979). Among male marmosets, who form pair-bonds and provide paternal care for offspring, the vaginal secretions of novel females triggered testosterone increases in unpaired and pair-bonded males without offspring, but failed to trigger hormonal responses in males who were currently caring for juveniles (Ziegler et al., 2005); paternal males will often respond to novel females with aggression, furthermore, suggesting the absence of testosterone responses when males are not treating females as potential mating partners.

Overall, the literature on hormonal responses to potential mates in vertebrate males suggests an endocrine code that indexes a motivational state directed toward mate acquisition. When males respond to females with courtship and sexual behaviors, they also tend to exhibit transient, rapid increases in testosterone and glucocorticoid concentrations. These hormonal responses are diminished or absent under those circumstances in which males do not pursue mating opportunities: during the nonbreeding season when baseline testosterone is very low, when in a state of sexual exhaustion, when in the presence of dominant males who are likely to attack subordinates who make mating attempts, and when engaged in paternal care for offspring. While other signals may also be implicated in this motivational state, testosterone and corticosterone appear to be consistent components of responses to mates across many species, and are thus phylogenetically conserved components of an internal signaling system that broadcasts the current pursuit of mating opportunities.

Reactive hormone increases, in turn, have been implicated in a wide range of downstream effects, consistent with their proposed role as calibrators of organism-wide mechanism settings. Testosterone injections that experimentally simulate reactive increases, for instance, have been shown to have a number of rapid effects (for reviews, see Gleason, Fuxjager, Oyegbile, & Marler, 2009; Nyby, 2008). Male mice injected with testosterone mount females faster than do control males at 30 minutes post-injection, which approximates the time delay between first encounters with females and onset of copulation (James & Nyby, 2002). Testosterone injections likewise induce preferences for places in which they occurred (e.g., Alexander, Packard, & Hines, 1994), rapidly reduce males' risk aversion (Aikey, Nyby, Anmuth, & James, 2002), and increase the probability of attacking other males (Gleason et al., 2009). In addition to these behavioral effects mediated via brain mechanisms, testosterone has been shown to rapidly promote both penile reflexes (reviewed in Nyby, 2008) and glucose uptake in muscle cells (Tsai & Sapolsky, 1996), with such effects occurring within 1 to 10 minutes of hormone administration.

A simple example may help clarify the functions of hormonal responses in non-human males. Rodents are typically averse to open spaces as a predator avoidance tactic. Exposure to female urine triggers both reactive testosterone increases and increased exploration of open spaces in male mice, with such exploration being reproduced by testosterone injections alone (Aikey et al., 2002). In effect, the testosterone increases act as an internal signal for a mate pursuit emotion program that reduces aversion to predation risk when cues of mating opportunities alter the likely cost-benefit profile of exploratory behaviors. This assignment of relative priority across mechanisms with incompatible behavioral outputs (e.g., avoidance vs. exploration of open spaces) is the general function of emotion programs, and all of the downstream effects of reactive testosterone increases reviewed above appear consistent with assignment of priority to those mechanisms that facilitate the successful pursuit of mating opportunities.

Females Emotion programs related to mating behaviors appear to be activated differently in females than in males across many vertebrate species. Rather than being cued by stimuli from potential mates, such programs appear to respond primarily to internal signals associated with ovulation and thus current fecundity. Interactions with males or their stimuli are the proximate triggers of ovulation in a minority of species (such as rabbits, ferrets, and cats) with induced ovulation (for a review of such cases, see Bakker & Baum, 2000). In the vast majority of mammals, however, females ovulate according to cycles of endogenous signals with sexual receptivity and proceptivity restricted to fertile regions of the cycle characterized by elevated estrogen (for reviews, see Blaustein, 2008; Carter, 1992).

The likelihood of ovulation occurring within a given time period is in turn a function of energetic variables for most vertebrate and especially mammalian species. The high energetic costliness of mammalian gestation and lactation have led to the evolution of mechanisms that suppress ovulation (and thus fecundity) under conditions in which energy availability is below that necessary for successful gestation (for a review, see Wade & Jones, 2004). Conditions of low energy availability occur regularly during events such as lactation or seasonal drops in food supply, and during such times it is clearly functional for females to allocate priority to mechanisms addressing adaptive problems such as maternal care, foraging, or thermoregulation. The general chain of causation in female mating programs appears to run from energy availability to ovulation and its associated release of hormones to prioritization of mating mechanisms in response to such hormones.

Ovarian hormones act as internal signals for female mating programs in ways analogous to the effects of testosterone in male mating programs. A similar limbic-hypothalamic circuit to that involved in males has been shown to regulate female responses to potential mates, with key structures such as the ventromedial nucleus of the hypothalamus directly affecting behavioral indicators of receptivity (such as the lordosis posture) under the influence of estradiol (for a review, see Pfaff & Schwartz-Giblin, 1998). Estradiol has been shown to have positive effects on female sexual motivation across a broad range of vertebrate species (Blaustein, 2008; Carter, 1992), though evidence occasionally supports positive effects of testosterone in some species, especially with respect to proceptive behaviors (Fernandez-Guasti, Vega-Matuszczyk, & Larsson, 1991) or preferences for gonadally intact males in partner preference experiments (e.g., Xiao, Kondo, & Sakuma, 2004). Consistent with a mechanism coordinating function for hormones, the increased sexual motivation associated with fecund regions of the estrous cycle appears to be coupled with reduced motivation for other behaviors, as exemplified by substantial drops in foraging and eating when sexual receptivity is heightened near ovulation (for reviews, see Fessler, 2003; Schneider, Wise, Benton, Brozek, & Keen-Rhinehart, 2013).

Rapid hormonal responses to interactions with potential mates as demonstrated in males have rarely been tested in nonhuman females, probably because of the known effects of endogenous changes in hormones on female sexual motivation. In humans, however, the common formation of long-term pair bonds in mating relationships may have selected for rapid hormonal responses as a means of activating mate acquisition programs independent of time in the menstrual cycle. Given that long-term mates could be met at any time of the cycle and not just on fecund days, reactive hormone increases may have allowed phylogenetically conserved brain structures that respond to ovarian hormones to be activated even outside of the fertile window when women met men who were perceived as attractive potential mates. This logic underlies the prediction that both men and women will exhibit hormonal responses to potential mates as internal signals that coordinate mechanism settings associated with a mating opportunity emotion program.

ENDOCRINE SIGNALS AND MATE PURSUIT IN HUMANS

Males The limbic-hypothalamic structures that regulate male hormonal and behavioral responses to potential mates exhibit extensive neuroanatomical and functional homology across vertebrate species (e.g., Baum, 1992), which raises the possibility that human males have likewise inherited homologous structures that play similar regulatory roles in a mating opportunity emotion program. Two general empirical patterns are expected if human males express homologous mechanisms. First, men should exhibit hormonal responses to potential mates that are similar to those exhibited in nonhuman vertebrate males. Second, the reactive hormone increases should produce organism-wide downstream effects on mechanism settings that are consistent with facilitation of mate pursuit. Evidence supports both of these patterns.

With respect to hormonal responses to potential mates, controlled laboratory experiments have demonstrated that young men exhibit rapid increases in concentrations of both salivary testosterone (Roney, Lukaszewski, & Simmons, 2007; Roney, Mahler, & Maestripieri, 2003; Roney, Simmons, & Lukaszewski, 2010; van der Meij, Buunk, van de Sande, & Salvador, 2008) and cortisol (Roney et al., 2007, 2010; van der Meij, Buunk, & Salvador, 2010) after brief social interactions with female confederates. These responses are absent after similar interactions with male confederates. Field studies have also demonstrated reactive increases in testosterone after exposure to or social interaction with women under more ecologically realistic circumstances: after dancing with a woman versus engaging in the same movements without a partner (Murcia, Bongard, & Kreutz, 2009), after performing skateboard tricks in the presence of a young woman versus in the presence of a young man (Ronay & von Hippel, 2010), after engaging in sporting events with a greater versus lesser ratio of women to men present (Miller, Maner, & McNulty, 2012), and after naturally occurring social interactions with young women in a Dominican village (Flinn, Ponzi, & Muehlenbein, 2012). Finally, men's testosterone (Cerda-Molina, Hernández-López, de la O, Chavira-Ramirez, & Mondragón-Ceballos, 2013; Miller & Maner, 2010; cf. Roney & Simmons, 2012) and cortisol (Cerda-Molina et al., 2013) concentrations may undergo more positive changes after exposure to olfactory stimuli collected from women near ovulation than after exposure to various types of control odors.

The hormonal responses in human males exhibit many parallels to those demonstrated in nonhuman species. The effects occur on a similar time scale, being first detectable on average within about 15 to 30 minutes; both testosterone and cortisol (corticosterone in nonhuman species) are released, and responses are absent after comparable exposure to other males. One study demonstrated that testosterone responses to conversations with women were larger among men with more sensitive androgen receptors as indexed by shorter CAG codon repeat lengths in the androgen receptor gene (Roney et al., 2010). This is consistent with regulation of the hormone response by similar limbic-hypothalamic structures as in nonhuman species, given the known role of androgen receptors in modulating the responsiveness of this brain pathway to cues from females among male rodents. Taken together, these similarities with nonhuman responses argue for the likely phylogenetic conservation of the same basic system across human and nonhuman species.

Other lines of evidence suggest that the probability and size of men's hormonal responses to potential mates are modulated in functional ways by other variables, and, as in nonhuman males, the hormone increases may comprise an endocrine code that indexes a motivational state directed toward mate pursuit. Flinn et al. (2012), for instance, demonstrated that men did not exhibit reactive testosterone increases after interacting with young women who were mates of their friends, which suggests the absence of hormonal responses under conditions in which men are unlikely to behaviorally pursue a mating opportunity. Likewise, men who self-reported higher dominance were found to exhibit larger testosterone responses to interactions with young women (van der Meij et al., 2008), which suggests parallels to nonhuman primate studies that have reported larger responses among dominant males (e.g., Glick, 1984; Mendoza et al., 1979), and is consistent with modulation of mating effort by relative levels of intrasexual competitiveness. Such modulation suggests that the decision rules that determine courtship effort are sensitive to the possible costs as well as the benefits of pursuing mating opportunities.

Perhaps consistent with such cost sensitivity, Roney et al. (2010) found that higher baseline cortisol concentrations predicted smaller testosterone responses to interactions with young women. Many of the conditions that cause elevated baseline cortisol (e.g., energy shortage, immune activation, psychosocial stress; see Dickerson & Kemeny, 2004; Peters et al., 2004) may make mate competition temporarily less functional, explaining the relative suppression of a mate pursuit emotion program when baseline cortisol is elevated. In sum, conserved brain structures appear to implement decision rules regarding mate pursuit based on various costs and benefits associated with specific opportunities, and when decisions are positive, cause reactive increases in hormone concentrations as internal signals of those decisions.

Although the precise functions of reactive hormone increases in humans have not been definitively determined, a number of lines of evidence suggest that such increases have a range of downstream effects that are consistent with an organism-wide orientation toward courtship and mate competition. Cortisol increases are known to promote short-term glucose availability (for a review, see Peters et al., 2004) and can facilitate enhanced attention, concentration, and memory consolidation in response to motivationally significant events (for a review, see Erickson, Drevets, & Schulkin, 2003). Cortisol increases in response to interactions with potential mates may therefore act as rapid energy mobilizations in support of courtship efforts. High baseline cortisol, however, may indicate poor condition for mate competition given its elevation during energy shortages, such that baseline cortisol could negatively index the energetic resources currently available for mating effort, while cortisol responses to potential mates may represent the marginal increases in energetic resources that can be devoted to such effort.

Reactive testosterone increases in humans have been associated with a range of effects that are logically related to willingness and ability to compete for mating opportunities. van Honk and colleagues in a series of experiments have induced large spikes in testosterone in women via exogenous hormone delivery and then measured psychological and behavioral outcomes within a few hours of drug administration. These studies demonstrated that testosterone administration relative to placebo triggered reduced fear responses (Hermans, Putnam, Baas, Koppeschaar, & van Honk, 2006; Hermans et al., 2007; van Honk, Peper, & Schutter, 2005), reduced empathy and sensitivity to others' facial expressions of emotion (Hermans, Putnam, & van Honk, 2006; van Honk & Schutter, 2007), and increased risk-taking and reward sensitivity (van Honk et al., 2004). Although the extent to which such effects would generalize to men is uncertain, all of these outcomes are consistent with a general orientation toward greater boldness and competitiveness. In addition, a number of studies have tested correlations between the size of men's testosterone responses to experimental manipulations and the magnitudes of behaviors performed just after the hormone responses. These studies have found that the size of hormonal responses to competitive tasks positively predicts self-reports of willingness to compete again (Carre & McCormick, 2008; Mehta & Josephs, 2006), the magnitude of aggressive behaviors directed toward other participants (Carre, Campbell, Lozoya, Goetz, &

Welker, 2013; Carre, Putnam, & McCormick, 2009; see also Klinesmith, Kasser, & McAndrew, 2006), and the magnitude of courtship-like behaviors directed toward a young woman (van der Meij, Almela, Buunk, Fawcett, & Salvador, 2012). Finally, a recent study reported that the size of testosterone responses to short film clips, including an erotic film, positively predicted subsequent weight lifting performance among trained athletes (Cook & Crewther, 2012). As in nonhuman species, then, evidence supports organism-wide changes in response to transient hormone increases, ranging from adjustments in behavioral tendencies to possible increases in physical strength.

In summary, there is now fairly strong evidence for the expression of a mating opportunity emotion program in human males. Upon exposure to stimuli from potential mates, men exhibit reactive hormone increases that are highly similar to the responses found among nonhuman vertebrate males, which argues strongly for their regulation by homologous brain structures. These hormone increases, likely in conjunction with other signals, appear to act as an endocrine code announcing the present importance of mate pursuit as an adaptive problem. Consistent with this, the reactive hormone increases have been associated with a range of downstream effects that logically would have facilitated courtship effort and intrasexual mate competition, including increased competitiveness, boldness, aggressiveness, physical strength, and expressions of courtship-like behaviors directed toward young women. Although many details of this emotion program remain to be worked out, the evidence to date suggests positive prospects for achieving a fairly complete description of an adaptive psychological system in which endocrine signals play a central role.

Females Little research has assessed reactive hormone changes in women after exposure to potential mates. Most instead has assessed effects of menstrual cycle phase on specific aspects of women's sexual psychology and behavior. In an important exception, Lopez, Hay, & Conklin (2009) tested and found evidence for reactive increases in women's salivary testosterone and cortisol concentrations after viewing a video of a physically and behaviorally attractive man who was directing courtship behaviors toward a woman (the subjects were instructed to imagine themselves in place of the target woman). These effects were detected at 30 minutes after the onset of the video and were absent among women in control groups who viewed a nature documentary, a video containing an attractive woman, or a video containing an unattractive man. Furthermore, among the women who viewed videos containing a man, magnitudes of changes in both testosterone and cortisol were significantly positively correlated with ratings of the man's attractiveness, desire to have sex with the man, and desire for a relationship with the man.

The results of the Lopez et al. (2009) study suggest that the same hormones that serve as internal signals of a mating opportunity emotion program in men may play similar signaling roles in women. Increases in testosterone and cortisol may help signal the presence of an attractive mating opportunity and cause downstream adjustments in mechanism settings that on average facilitated successful efforts at mate attraction. Experimental manipulations of testosterone pulses in women suggest in particular that reactive testosterone increases may reduce fear responses (Hermans, Putnam, Baas, et al., 2006; Hermans et al., 2007; van Honk et al., 2005) and increase risk-taking and reward sensitivity (van Honk et al., 2004), all of which might plausibly increase the display of receptive and proceptive signals to prospective partners, although future research is necessary to specifically test links between hormonal changes and behaviors directed toward potential mates. Baseline concentrations of testosterone (and in some cases cortisol) have also been linked to some measures of aggressive and competitive behaviors in women (e.g., Cashdan, 2003; Denson, Mehta, & Tan, 2013), such that reactive increases in these hormones might prime competition with intrasexual rivals for the attention of a highly desirable potential partner. In short, the Lopez et al. (2009) study provides an important proof of concept for women's hormonal responses to potential mates, but as the only study of its kind there is a clear need for further research that both replicates the effect in actual social interactions and tests downstream consequences of the reactive hormone changes.

Emotion programs related to mate choice and mate pursuit appear to be calibrated by endogenously generated shifts in ovarian hormones associated with cycle phase physiology in women, in addition to being triggered by exposure to attractive potential mates. Women tested during the fertile window relative to other times in the cycle tend to express stronger attraction to putative heritable fitness indicators in men, such as more masculine or symmetrical features (for reviews, see Gildersleeve, Haselton, & Fales, 2014; Jones et al., 2008; Thornhill & Gangestad, 2008); may exhibit increased sexual desire and initiation of sexual behavior (for a review, see Wallen, 2001); and appear to increase their proceptivity in the form of adopting more attractive and revealing clothing choices (Durante, Li, & Haselton, 2008; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007). Less research has addressed the endocrine signals that may regulate such shifts, although studies have supported elevated testosterone as a predictor of preferences for more masculine faces (Bobst, Sauter, Fopp, & Lobmaier, 2014; Welling et al., 2007), elevated estradiol as a predictor of preferences for cues of higher circulating testosterone in men (Roney & Simmons, 2008; Roney, Simmons, & Gray, 2011), and the combination of elevated estradiol and low progesterone as a predictor of within-cycle increases in subjective sexual desire (Roney & Simmons, 2013). The theorized functions of these cycle phase shifts have been covered in detail elsewhere (e.g., Gangestad, Thornhill, & Garver-Apgar, Chapter 14, this *Handbook*, Volume 1; Thornhill & Gangestad, 2008; cf. Roney, 2009). The key point here is that the diverse effects associated with ovulatory timing are consistent with endogenous hormonal changes acting as internal signals for mating-related emotion programs. Essentially, endocrine signals associated with current fecundity may broadcast the current importance of mating as an adaptive problem in the service of calibrating mechanism settings such that preferences for specific cues are sensitized, behavioral proclivities toward display of attractiveness is increased, and motivation for contact with mates is elevated.

An interesting direction for future research is the investigation of how endogenously generated endocrine signals associated with cycle phase dynamics may affect and interact with more transient hormonal responses to potential mates. Hormonal signals associated with high current fecundity may create a baseline motivational state directed toward mate search and mate evaluation, with hormonal responses to actual potential partners then triggering a more specific emotion program (or subprogram) directed toward pursuit of a particular target partner. Whether reactive hormone responses to attractive potential mates may be more likely or larger in magnitude depending on baseline hormone concentrations is largely unknown since the Lopez and colleagues (2009) study was underpowered to address this question. However, Lopez et al. (2009) did report that testosterone responses to the attractive man video were absent among women using hormonal contraceptives, which is consistent with the inhibition of reactive hormone responses to potential mates when baseline hormones are reduced due to the absence of dominant follicle maturation. If lower baseline ovarian hormone concentrations are associated with a higher threshold for activation of mate pursuit emotion programs, this may have evolved to allocate greater priority to adaptive problems other than mate attraction during natural conditions associated with suppressed fecundity, such as during lactational amenorrhea or after menopause (see Roney, 2015). Future research could directly assess whether reactive hormone responses to potential mates are larger or more likely in ovulatory as opposed to anovulatory natural cycles (or in cycles with higher vs. lower estradiol concentrations) as a first step toward testing more complete models of the possible roles of endocrine signals in women's reactions to potential mates.

FUTURE RESEARCH IN EVOLUTIONARY ENDOCRINOLOGY

The mate pursuit examples described above were intended to demonstrate the potential heuristic value of treating endocrine signals as important components of evolved emotion programs as defined by Cosmides and Tooby (2000). This framing, in fact, may be the key to understanding the functions of hormones in general. Other endocrine signals share with sex hormones the property of release into the general circulation and thus the ability to manipulate organism-wide parameter settings that determine the relative priority of distinct mechanisms based on the current importance of particular adaptive problems. This makes other hormonal signals—such as oxytocin, vasopressin, and prolactin—ideal messengers to act as internal signals in various emotion programs. Development and empirical testing of theories regarding the design of the emotion programs that use such signals may thus be the best method for elucidating the evolved functions of human hormones. Conversely, the relatively unique ability of hormones to simultaneously activate and inhibit multiple mechanisms throughout the brain and body suggests that endocrine signals will often have key roles in adaptive emotion programs such that knowledge of endocrinology may be crucial for achieving a full understanding of the design of many human psychological adaptations.

The emotion program framing is not widespread in the extant literature on human hormones, however, which has often focused on attempting to derive the most parsimonious descriptions of the functions of endocrine signals. Historically, for example, testosterone has at various times been proposed as a status or dominance or aggression hormone, with debates regarding which description best describes its effects and an implicit appeal to a parsimony principle in which the most encompassing description is considered scientifically superior. Similar arguments exist in the expanding literature on oxytocin, with proposals for general descriptions of oxytocin as a bonding or trust hormone.

The argument that hormones play key roles as internal signals in emotion programs does not suggest that these general descriptions of hormones are necessarily inaccurate, but instead that they are likely to be incomplete given that the very function of such signals is the simultaneous calibration of multiple mechanism settings. Testosterone, for instance, has wide-ranging physiological effects in addition to calibration of behavioral tendencies, including influences on immune function, fat catabolism, blood hemoglobin, muscle anabolism and glucose uptake, and rates of spermatogenesis (for reviews, see Ellison, 2001; Ellison & Gray, 2009; Muehlenbein &

Bribiescas, 2005). These multiple diverse effects resist simple reduction to a broad category such as status or aggression, but may make functional sense as coordinated components of emotion programs activated under specific circumstances. These considerations recommend an empirical shift of emphasis away from attempting to find the most generalized descriptions of specific hormones' effects and toward the systematic mapping of the broader emotion programs that use hormones as signals and are activated in response to cues of ancestrally recurrent adaptive problems. This shift would seamlessly integrate the study of human endocrinology with the adaptation-mapping project of human evolutionary psychology.

An interesting question concerns the potential breadth of this integration of endocrinology with evolutionary psychology. While hormones clearly play important roles as internal signals with respect to mating adaptations, is this also the case for many other adaptive problems? In theory, hormones might be expected to act as signals whenever the broad coordination of multiple mechanisms is an adaptive response to ancestrally recurrent cues of specific problem domains. Such coordination is clearly important in response to events such as the birth of a child, and in fact a variety of hormonal signals have been studied as intermediaries between perception of this event and diverse psychological and behavioral responses (for reviews, see Fleming & Gonzalez, 2009; Rilling, 2013; Saltzman & Maestripieri, 2011). Parenting adaptations thus represent another example in which the emotion program approach is likely to productively integrate evolutionary psychology with endocrinology.

Even beyond the broad motivational categories typically associated with behavioral endocrinology research (e.g., mating, parenting, feeding, aggression), it is possible that endocrine signals have specific coordinating roles associated with many psychological adaptations. In social exchange, as just one example, information indicating that an exchange partner has cheated or benefited you may have cascading implications both for your relationship with that particular partner and for your broader position within a social group. An adaptive response to those implications might then entail the adjustment of multiple mechanism settings related to levels of vigilance, proclivities toward risk-taking, levels of sociality, thresholds for aggression, and so on. Perhaps consistent with an endocrine signal of such adjustments, recipients of even a brief expression of trust in a neuroeconomics experiment demonstrated rapid increases in serum oxytocin (Zak, Kurzban, & Matzner, 2005). Future research will be necessary to determine how widespread endocrine signals actually are in psychological adaptations, but the diffuse messages carried by hormones suggest that they are likely to be common devices for recalibrating diverse mechanism settings in response to cues of functionally relevant circumstances.

Specific hormonal signals could play roles in multiple emotion programs, such that an additional empirical task for a field of evolutionary endocrinology may be the discovery of how emotion programs interact with each other or are differentiated from one another. The types of testosterone responses exhibited after interactions with potential mates have also been demonstrated after aggressive and competitive interactions in both human and nonhuman species (for reviews, see Archer, 2006; Gleason et al., 2009; Mazur & Booth, 1998), which suggests use of similar internal signals by multiple emotion programs. A possible explanation for this is that similar downstream mechanism settings are functional after both exposure to potential mates and events such as competitive victories. Competitive victories may prime mating motives secondary to increased attractiveness and mating opportunities may prime increased competitiveness in the service of potentially defending a valuable reproductive resource (see Ainsworth & Maner, 2012; Gleason et al., 2009). This is not to say that mate pursuit and competitive interaction emotion programs are identical. They are presumably activated by distinct cues with distinct decision rules regarding the release of internal signals for production of specific mechanism settings. Some of these downstream settings, however, may in fact be overlapping. Furthermore, hormones are very unlikely to be the exclusive signals employed by emotion programs—hormone-mediated communication is slow compared to most neurotransmitter-mediated signals and many emotion programs will require very rapid effects (see Cosmides & Tooby, 2000)—such that mate pursuit and competitive interaction programs probably involve the rapid activation of distinct neural networks via transmitter-based signaling, with the common downstream modulation of mechanism settings via testosterone responses occurring at a more delayed time-scale. Another possibility, however, is that distinct combinations of hormonal responses may act as de facto endocrine codes that distinguish specific emotion programs. If, for instance, exposure to mates was associated with oxytocin increases but competitive interactions were not, or specific combinations of catecholamines accompanied testosterone release in one case but not the other, then even the downstream mechanism settings associated with reactive testosterone increases might be differentiated in subtle ways across the two emotion programs. These types of issues present challenging empirical problems for future investigation.

The emotion program approach to understanding hormones almost necessarily requires collaborative and interdisciplinary approaches to future research in evolutionary endocrinology. Understanding whole organism calibration of mechanism settings, for instance, requires either collaboration between scholars with expertise in different types of psychological and physiological mechanisms or uncommonly broad interdisciplinary training in individual researchers. Future research in this area may entail teams of scholars mapping out distinct pieces of emotion programs in order to collaboratively build models that specify specific activating cues, release of endocrine signals in response to those cues, and, finally, the set of downstream mechanism settings triggered by endocrine signals and directed toward the solution of specific adaptive problems.

In conclusion, endocrine signals are likely to play important explanatory roles in the expanding field of human evolutionary psychology. A modular collection of specialized processing mechanisms requires functional means of coordinating when specific mechanisms are activated and inhibited, and hormonal signals are ideally suited to act as messengers of such coordination. In effect, hormones act as conductors of the real-time symphony of mechanism activation and inhibition that links patterns of behaviors to the specific circumstances in which those behaviors were most functional over the course of human evolution. No model of human nature will be complete without a clear understanding of the functional roles of these chemical messengers.

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CHAPTER 47

Evolutionary Political Psychology

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SOCIAL LIFE—WHEN ORGANISMS designed for propagation of their own genes come to depend on each other—inevitably leads to conflict. Different individuals have different interests and as a consequence, conflicts about their prioritization arise. Politics is the process of determining this prioritization. Human ancestors lived in groups for millions of years and politics have most likely constituted an evolutionarily recurrent phenomenon throughout the evolution of the genus Homo. Humans are not just social animals; they are political animals.

Evolutionary political psychology is the field concerned with the application of evolutionary psychology to the study of politics and the nature of the human political animal. Empirical work within evolutionary political psychology is accumulating at a fast pace. This chapter reviews this work. At the same time, evolutionary political psychology is a very recent field and the available theory outweighs the available data. The chapter therefore also provides descriptions of the research avenues ahead and outlines evolutionarily informed hypotheses that have yet to be tested.

The study of politics is traditionally considered the topic of the field of political science and evolutionary political psychology is an interdisciplinary endeavor seeking to answer the questions raised within political science with the analytical tools provided by evolutionary psychology. This also raises important challenges for evolutionary psychology. Humans evolved in small social groups and evolutionary psychologists have most often analyzed modern behavior that happens within small groups, such as mating, cooperation, and forms of social conflict. Modern politics, however, happens within mass societies where millions of anonymous individuals interact with each other to shape political outcomes. As reviewed below, evolutionary political psychology therefore entails a two-step approach: First, dissecting the adaptive problems of conflicts of interests and building testable predictions on the structure of the corresponding adaptations for political behavior. Second, analyzing about how these adaptations operate under the evolutionarily novel conditions of mass politics.

WHAT IS POLITICS?

If we think of social life as a game, political behavior aims to negotiate the rules of that game: Who is entitled to get what, when, and how (Lasswell, 1950)? In its prototypical form, political behavior targets shared expectations about entitlement (Easton, 1981). For example, when a hunter obtains and eats meat during a solitary hunting expedition, this is a pursuit of the hunter's interests. But eating this meat is not necessarily a political action. Even if the hunter's band has a rule saying that all meat should be shared, it might not be a political action. The hunter's action could go unnoticed, leaving the rule unchallenged in the eyes of others. Politics enter the scene when another individual comes by and makes a claim on the meat (e.g., that he should have it or that it should be shared with the rest of the group). If the hunter refuses, perhaps stating that he is entitled to the animals he himself kills, his action becomes political. Rather than being an unnoticed rule violation, it aims to challenge and change others' expectations about entitlement.

Politics is produced by adaptations designed to solve the coordination problems that emerge from group living. There are multiple ways to organize life within and between groups. If expectations about the rules of social life are not shared this creates transaction costs such as costs from fighting and opportunity costs from constant negotiations. This sets up a selection pressure for the evolution of adaptations designed to coordinate expectations (referred to as a "sense of social regularity" by de Waal, 1996). Yet, each potential rule entails different costs and benefits to different individuals (DeScioli & Kurzban, 2013). This entails a selection pressure for the evolution of adaptations designed to change the content of coordinated rules into alignment with the interests of the self. Politics is the output of these sets of adaptations.

While the folk concept of "politics" often restrictively refers only to the business of professional politicians, evolutionary psychology advances a concept that is applicable to groups at all levels. Ancestrally, it was played out within and between families, bands, and tribes. Today, it is played out across a larger number of levels. This includes local groups such as the family, workplaces and communities. But it also includes the mass level such as municipalities, states, and the global world.

PRINCIPLES OF EVOLUTIONARY POLITICAL PSYCHOLOGY

Evolutionary political psychology is concerned with analyzing political behavior at all levels. At the same time, the mass level is of particular interest due to the formal concentration of power and political scientists have mainly focused on this level. In this section, I review the key principles guiding an evolutionary approach to the study of politics in general and of mass politics in particular.

Principle 1. Evolved political psychology is designed to operate adaptively within and between small-scale groups. In a large number of territories, mass societies only emerged within the past 500 years (Diamond, 1998), too recently for the evolution of dedicated adaptations. Accordingly, any species-typical feature of human political psychology is designed by the selection pressures operating within evolutionarily recurrent groups of between 25 and 200 individuals (Kelly, 1995). This predicts that this psychology attends to factors that were adaptive to consider under ancestral, small-scale circumstances. Similarly, this psychology motivates solutions that worked under these circumstances. In other words, when modern individuals reason about mass political issues such as criminal justice, social welfare, and immigration, they reason about them using psychological mechanisms designed to handle related adaptive problems such as counterexploitation, cheater-detection, and newcomers in the context of small-scale, ancestral group life.

Principle 2. Evolved political psychology provides a "default" structure to mass politics. The evolved, universal human political psychology is predicted to provide an underlying structure for political processes and institutions in modern mass societies. Institutions that "fit" or resonate with evolved psychology will be more likely to emerge. Accordingly, politics across societies is predicted to share key commonalities and to be oriented towards solving similar problems (Boyer & Petersen, 2012). This does not mean that an evolutionary psychological approach entails that political institutions are everywhere the same. First, adaptive responses are context-dependent responses. Human psychology is designed to calibrate responses to the contingencies of the individual and situation in ways that would have been fitness enhancing over human evolutionary history. While the structure of social welfare institutions everywhere might emerge from a universal psychology designed to regulate help-giving and guard against cheaters, the generosity of these institutions will differ dramatically depending on whether people in specific countries perceive the number of cheaters as high or low (Aarøe & Petersen, 2014). Second, it is most accurate to think of evolved psychology as a "rubber cage" (Boyer & Petersen, 2012). The evolution of improvisational intelligence (Cosmides & Tooby, 2002) allows human organisms to invest cognitive effort in down-prioritizing the immediate solutions motivated by this psychology and engineer alternatives suited to fulfill these motivations in light of novel environmental contingencies. This implies that the architecture of evolved political psychology provides the researcher with a set of default expectations about how political processes and institutions are structured. Many divergences occur, providing important objects for explanation: How are the cognitive demands of this divergence mitigated and how are people incentivized to meet them? What are the cultural transmission processes that brought the processes and institutions into existence? The existence of mass society itself is an example of such institutional divergence.

Principle 3. Politics is an informational arms race and evolved political psychology reflects the coevolution of informational strategies and counterstrategies. Political behavior targets people's sense about who is entitled to what. As a consequence, the psychology of other humans constituted the core environment that has selected for psychological adaptations for politics. In terms of selection pressures, politics has created an evolutionary arm's race between strategies (enacted by psychological adaptations) designed to down-regulate the sense of entitlement in other's and counterstrategies designed to avoid nonadaptive down-regulations. Many of the key parameters that determine relative entitlement in humans are exceptionally difficult to assess; for example, "Am I stronger than my competitor?," "Is my group more numerous than the competing group?," "Are my group's members more committed and loyal than our rivals?," and "Do we have better leadership than our rivals?" Setting such parameters accurately cannot be done without relying intensely on information, including signals from others. Hence, offensive and defensive political strategies are informational strategies. A key goal in politics is to broadcast information that sets these parameters in one's favor; for example, signaling that members of the ingroup are highly committed to a common cause (hence deterring outgroups and galvanizing commitment among the ingroup). The goal of counterstrategies is to evaluate this information and only integrate it into decision-making parameters when is evaluated to be accurate. In modern politics, the strategic use of information is clear in everything from military parades (signaling superior strength) to denigration of leaders of rival political parties (signaling superior leadership). For the evolutionary political psychologist, the symbols, parades, and debates that surround politics are not merely "theater" or "cheap talk," as a rational choice theorist would argue. These are the very strategies through which political interests are pursued, designed to tap into human psychology and mobilize support or counter the mobilization of support.

Principle 4. In mass politics, evolved political psychology is responding to events and groups without direct experience but on the basis of mental simulations aided by information from others. Information matters even more in large-scale relative to small-scale politics. Today, people pass judgments on people, events, and groups they have no direct experience with. For example, when a crime occurs in a small group, people will often have lived together with the offender and his family for years. Today, people pass judgments on criminals on the basis of what they can piece together about motivations, background, and so forth from divergent information from political elites, the media, and their social network. Given that the mechanisms of the mind—including dedicated political adaptations—are information-processing mechanisms, how and whether evolved political psychology is aroused depends critically on the content of this information. Political issues are almost always multifaceted (Chong & Druckman, 2007), involving multiple adaptive problems. Evolutionary political psychology endeavors to dissect not just the structure of adaptations for political judgment and behavior but also analyze the flow of information from elite debates and social networks and how this flow activates some adaptations and keep others from being activated. At times, the information provided will fail to activate any high arousal reasoning mechanisms. Under such circumstances, the human political animal is found to be ignorant of and uninterested in mass politics (Petersen & Aarøe, 2012).

ADAPTATIONS FOR POLITICAL JUDGMENT

To engage in political behavior, an actor needs to be able to solve two overarching adaptive problems. One problem is an evaluation problem: Political behavior requires abilities to pass judgments on resource distributions and the rules giving rise to them. Another problem is a behavioral problem: Political behavior requires power to change the rules into alignment with ones evaluation. I consider these in turn.

At the most general level, the evolutionary approach entails the prediction that an individual's political judgments track whether the rule under ancestral circumstances would involve fitness benefits or costs for the individual given his or her individual and situational characteristics. This is not because humans—or other organisms—are designed to consciously strive to maximize fitness, but because natural selection has sculpted human psychological adaptations to utilize input and produce output that were fitness-enhancing under ancestral circumstances (Tooby & Cosmides, 1990).

Fitness interests are at the core of virtually all evolutionary theories. Accordingly, the study of political judgments involves the application of any available mid-range evolutionary theory (about kin selection, reciprocity, coalitions, life history, parent-offspring conflict, etc.) to the particular problem of politics. Correspondingly, individual differences in political judgments emerge through multiple developmental pathways, including genetic heritability (Hibbing, Smith, & Alford, 2013). Navigating through this multitude of causes, this section reviews the general factors shaping political judgments: how a rule affects the self, how it affects others valuable to the self, and how coalitional allies judge the rule.

HOW DOES THE RULE DIRECTLY AFFECT THE SELF?

An evolutionary approach predicts that individuals favor policies that favor the individual. Ancestrally, favored resources would be, for example, food, help, and mating opportunities. In modern politics, a favored resource is money (which can translate into the just mentioned resources) and, hence, one source of conflict in politics is differences in economic interests. People who are at the receiving end of an economic policy should favor it. While a classical position in political science is to argue against the role of self-interest (Sears, Lau, Tyler, & Allen, 1980), economic self-interest does indeed have substantial effects on political judgments (Weeden & Kurzban, 2014).

An evolutionary approach expands the notion of self-interest beyond the economic domain. Human psychology is expected to attribute value to all resources that would enhance fitness under ancestral circumstances, and evolutionary psychological research has documented multiple sources of self-interested, political conflict. People's positions on rules that regulate reproduction have been found to track mating strategies such that individuals seeking committed relationships tend to favor rules that constrict sexuality, while individuals seeking multiple, short-term partners oppose such rules (Kurzban, Dukes, & Weeden, 2010). Also, people who are highly motivated to avoid pathogens are more likely to oppose policies that would bring them into contact with individuals who could be bearer of pathogens, such as outgroups from distant countries (Faulkner, Schaller, Park, & Duncan, 2004). Finally, concerns about food have been shown to shape political judgments. In many modern democracies, hunger has been abolished. Short-term fluctuations in hunger nonetheless shapes how people think about democratic politics. When hungry, people are much more likely to approve of redistributive policies that involve transferring resources from the rich to the needy (Aarøe & Petersen, 2013). This is not because hungry people want to share *their* resources with others but because they want to acquire the resources *from* others.

HOW DOES THE RULE AFFECT OTHERS VALUABLE TO THE SELF?

Mechanisms for political judgment should also process how rules affect others. Humans are a social species and depend critically on others. The resource states of specific others have had repercussions for the fitness of the self, and human psychology is designed to factor this into political judgments.

An important way through which others are valuable to the self is through genetic relatedness. Kin are inherently valuable to us from a fitness perspective, and mechanisms for political judgment should intuitively up-regulate support for rules that benefit kin. One interesting example of this comes from research on court rulings demonstrating that judges with female offspring are more likely to rule in favor of positions that favor females (Glynn & Sen, 2014).

Unrelated others also have provided humans with fitness benefits over human evolutionary history. In general, we should expect that individuals are more supportive of rules that benefit individuals that expose features that ancestrally would have made them valuable to the self. One line of research has focused on political attitudes about criminal justice. In small-scale societies, fewer cooperation partners are available, and hence, killing or ostracizing potentially valuable individuals involves fitness costs. Reflecting this small-scale social calculus, people are motivated to rehabilitate criminals who they perceive as productive, independently of the seriousness of the crime (Petersen, Sell, Tooby, & Cosmides, 2012). Also, across cultures, there is much consensus about what counts as crime and how serious different crimes are, tracking their fitness consequences to a significant degree (Robinson, Kurzban, & Jones, 2007).

Research has also explored how the psychology of social exchange shapes political judgments (Petersen, 2015). The key selection pressure involved in the evolution of social exchange relates to reciprocity: Adaptive exchange is reciprocal and human psychology includes sophisticated mechanisms for detecting cheaters (i.e., nonreciprocators) (Cosmides & Tooby, 1992). This psychology has been demonstrated to powerfully shape opinions about the most sophisticated modern group-wide exchange system: the welfare state. Across the world, people are motivated to support welfare for needy individuals who put in an effort to find a job and contribute to society but oppose welfare to individuals who are unmotivated to do so (those who are "lazy") (see, e.g., Petersen, 2012; for an overview, see Petersen, 2015). Essentially, people's support for the rules governing welfare institutions seems to be regulated by a psychology designed to scan partners for reciprocal exchanges of help. When the rules are seen to support such partners, people support the rules.

Research on coalitional psychology provides a final illustration of how political judgments are shaped by adaptive concerns about unrelated individuals. Coalitions are groups of individuals that engage in repeated, delayed, and reciprocal exchanges of help and resources (Tooby & Cosmides, 2010). Due to the selection pressure for directing resources into the exchange system that the self participates in, coalitional psychology evolved to generate preferences for directing resources towards people that are represented as fellow group members (Yamagishi & Kiyonari, 2000). This shape political judgments such that people judge rules and institutions (related to, e.g., criminal justice or social welfare) more negatively when these primarily benefit outgroup members such racially or ethnically different others (e.g., Gilens, 1996). This also helps explain cross-country variation in political institutions. Differences in ethnic and racial heterogeneity across countries are major causes of differences in the size of welfare states, with more heterogeneous countries having smaller welfare states (Alesina & Glaeser, 2004).

How Do Others Judge the Rule?

The importance of coalitional psychology for political judgments extends beyond being motivated to support rules that favor ingroup members. In coalitions, the self supports other members when their interests are at stake in exchange for support when the self's interests are at stake. A crucial part of coalitional behavior is therefore to adopt and advance the judgments of comembers of coalitions and to counter the judgments of members of competing coalitions. These strategies extend to mass politics. When people form opinions on new policies, people are likely to simply adopt their preferred political party's position and reject the opposing party's position, independently of policy content (e.g., Cohen, 2003).

Political judgments are accordingly informed by at least two general types of evolved mechanisms: first, adaptations designed to judge the fitness consequences for the self of the content of rules (in part, due to the effects on valuable others) and second, adaptations designed to coordinate judgments with other coalitional members, independently of rule content. Because of the lack of perfect alignment between the interests of coalitional members, inputs from these sets of adaptations can lead to divergent conclusions and need to be traded off. For example, when parties change positions on an issue, their supporters tend to change their positions as well. Importantly, however, this happens only among supporters who do not consider the issue important. Those who consider the issue important tend to change their party preference rather their issue position (Carsey & Layman, 2006).

ADAPTATIONS FOR POLITICAL BEHAVIOR: PHYSICAL DOMINANCE

One adaptive problem is to form an adaptive representation about the political interests of the self and how they relate to the rules of the community. Another problem is to engage in political behavior to change shared rules and expectations into alignment with the self's political interests. This section reviews how adaptations relating to physical dominance, coalitions, and persuasion have helped solve this adaptive problem of acquiring political power.

POLITICAL POWER AS STATUS

One of the most fundamental features shaping expectations about resource access across animal species is hierarchy (Sidanius & Pratto, 2001). Many animals recognize that certain individuals have higher status and priority access to resources such as food and mates. For humans, this also includes a privileged access to determining the rules of resource access themselves.

A general framework for understanding status is provided by the asymmetric war of attrition model, designed to describe the adaptive problems associated with relative asymmetries between contestants in conflict situations (Hammerstein & Parker, 1982). The model predicts that organisms with higher fighting ability (i.e., larger size or greater strength) will escalate conflicts whereas organisms with lesser fighting ability will withdraw. Because fighting ability determines the likelihood of prevailing, a selection pressure is created for adaptations designed to regulate conflict behavior merely on assessments of relative fighting ability. Such adaptations are fitness-enhancing because they allow organisms to avoid costly fights in which resources most likely would be seized anyway. From these adaptations grow the existence of dominance hierarchies: Motivations to cede resources without fighting are triggered in less dominant individuals in the face of more dominant individuals (Cummins, 1996). Given this, adaptations designed to solve the adaptive problem of acquiring dominance are key for political behavior, as are adaptations for adaptively pursuing the flipside of dominance, subordination, when dominance is not possible.

PHYSICAL DOMINANCE AND STATUS

Dominance is related to the physical capabilities of organisms. In humans, upper-body strength is particularly important (Puts, Bailey, & Reno, Chapter 13, this *Handbook*, Volume 1; Sell, Hone, & Pound, 2012) and males' political pursuit of their self-interests has been found to be shaped by their strength. Stronger males are more likely to advocate war as a means to solve international conflicts of interest (Sell, Tooby, & Cosmides, 2009), they are more likely to advocate for policies that favor their own group over other groups (Price, Kang, Dunn, & Hopkins, 2011), and they are more likely to support policies that are aligned with their economic self-interest. For poor males, strength increases support for redistributive policies whereby resources are transferred to the self from the rich; for rich males, strength increases opposition against such politics (Petersen, Sznycer, Sell, Cosmides, & Tooby, 2013). Consistent with the evolutionarily recurrent association between physical strength and political power, research has also shown that the desire for your own group to dominate other groups predicts a desire to gain greater muscularity (Swami et al., 2013). Those who seek to impose their interests on others are cognizant and desirous of increased fighting ability.

ADAPTATIONS FOR POLITICAL BEHAVIOR: COALITIONAL PSYCHOLOGY

Status has the particular quality that it is zero-sum: If A has more, B has less. Accordingly, one essential part of status seeking is competitions aimed at enhancing one's own status and reducing the status of competitors. For humans, strength does not constitute the primary tool for status competitions (von Rueden, Gurven, & Kaplan, 2008). The key tool for political power is to form and join coalitions with others. To achieve such strength through numbers, humans have evolved a sophisticated coalitional psychology (Tooby & Cosmides, 2010).

Coalitional Competition

Modern politics is permeated by multilayered sets of nested coalitions from the global level and down: international alliances, states, political parties, factions within parties, and so forth. In international politics, coalitions in the form of states are the key actors (Lopez, McDermott, & Petersen, 2011). For domestic politics, coalitions in the form of political parties similarly play the major role in deciding political outcomes. Also outside professional politics, coalitions are exceptionally salient. For many, the provisioning of coalitional support in the form of voting is the primary form of political action, and the most important determinant of the likelihood of voting for a particular candidate is whether the candidate is a member of the party that people identify as "their" party (Miller, 1991). Consistent with a coalitional perspective, such party affiliations are mentally represented using the psychological mechanisms that represent other, key coalitional identities such as race (Pietraszewski, Curry, Petersen, Cosmides, & Tooby, 2015).

Just as dominance hierarchies between individuals are set by individual abilities to impose costs, hierarchies between coalitions are set by corresponding collective abilities. Coalitions therefore compete by utilizing a range of different strategies to signal relative coalitional formidability. Collective violence constitutes the most direct and hard-to-fake expression of such signaling, and the available evidence suggests that humans have adapted to engage in violent collective action (Wrangham & Glowacki, 2012). Coalitional dominance, however, is also acquired by another mean: informational warfare. Because status often grows from assessed but not utilized fighting ability, fights over status often occur without resorting to physical violence but by emitting relevant information that can change the landscape of affiliations in favorable ways for the self's coalition. In mass politics, such informational warfare in coalitional competition is routinely present in the context of so-called negative campaigning. In political campaigns, candidates spend large amounts of resources on broadcasting information about the competence of opposing candidates. A coalition without competent leadership is a weak coalition and such information could down-regulate the assessed status of the party in the eyes of the ingroup, the outgroup, and those unaffiliated.

The literature on negative campaigning also shows the complexities involved in informational warfare where counterstrategies for evaluating information play a significant role. Because people (presumably) recognize that negative campaigning is strategically motivated, negative campaigning is only partially effective. Among those who support the attacked candidate, informational attacks might even backfire and prompt supporters to rally around their candidate in anger (Ansolabehere & Iyengar, 1995).

JOINING COALITIONS

Forming coalitions is a complex coordination task: Like-minded individuals need to be located and joint attention and trust needs to be created. This adaptive problem has selected for psychological adaptations designed to motivate the individual to join coalitions independently of the existence of conflicts and prepare for the rapid activation of these coalitions when conflicts arise (Tooby & Cosmides, 2010).

Adaptations for joining coalitions should estimate and trade off two parameters: First, within the landscape of available coalitions, which coalition is most formidable? Coalitional competition influences the landscape of affiliations because the broadcasted information about relative formidability serves as input to adaptations for joining coalitions.

Second, which coalitions have an agenda that is closest to the self? Lasting coalitional affiliations do not tend to be formed on the basis of shared interests on a narrow agenda—such as an interest in changing one particular rule—but on the basis of interest similarities across a broader set of agendas such that the particular coalition can be activated across a range of different projects. Coalitional psychology is accordingly predicted to contain mechanisms for identifying cues to the broader agendas of others and for evaluating whether the agenda of a coalition is likely to lead to support for rules and institutions that match the narrow interests of the self. Some evidence for the existence of abilities for evaluating the alignment between the political agendas of coalitions and the self comes from the voting literature. While many voters lack political knowledge, voters are at the same time surprisingly adept at "voting correctly," that is, voting for the party or candidate that best matches their values and issue positions (Lau & Redlawsk, 1997).

In modern politics, the key broad agenda utilized to make decisions about coalitional affiliation is political ideology. Ideology works as a coalitional sorting mechanism because it predicts a number of narrow-issue positions among both individuals and parties and also predicts a number of basic personality constructs (Hibbing et al., 2013) and even cooperation and mating strategies (Weeden & Kurzban, 2014). Commonalities at this level between coalitional members suggest that their interests will be aligned in a large number of concrete cases.

Signaling Coalitional Membership

A key adaptive problem in the context of coalitions is to ensure that fellow coalition members aid the self when needed. Because there is not perfect alignment of interests within a coalition, it is most accurate to think of a coalition as an exchange system where the exchanged resource is coalitional support: An individual provides support to other coalitional members when their key interests are at stake in exchange for support when his or her own key interests are at stake.

This sets up a selection pressure for adaptations designed to send signals of commitment to the system of coalitional exchange and attend to such signals from others. Hard-to-fake signals of commitment provide information that the self will reciprocate coalitional support, which in turns incentivizes other members to provide coalitional support to the self. Over human evolutionary history, signals of coalitional allegiances have taken the form of clothing, tattoos, facial paint, participation in group rituals, and so forth (e.g., Legare & Watson-Jones, Chapter 34, this volume). Because coalition members share political judgments (due to both a shared broad agenda and direct coordination) this has opened for another type of coalitional signal: signals of judgments. In essence, people can express side-taking in coalitional status competitions merely be expressing an opinion.

This has multiple consequences. First, people should be sensitive to express political judgments when they are motivated to establish new relationships and are unsure about the coalitional affiliation of others. Although political views—consistent with a coalitional perspective—are widely shared between spouses, in short-term dating contexts, people are highly motivated to withhold political allegiance or describe themselves as centrist (Klofstad, McDermott, & Hatemi, 2012). Second, it creates incentives for members of competing coalitions to take opposing positions merely for purposes of signaling differentiation, saying, "I am not one of them." People are prone to support policies—independently of their content—if they are promoted by their party and oppose policies if the opposing party promotes them (e.g., Cohen, 2003). That people from the same political party share an ideology is not just a reflection of deeper commonalities in, for example, cooperation and mating strategies but is also an effect of the coordination of coalitional signals. While the need to signal allegiance might seem overly sensitive, such signals would have been important under ancestral, small-scale conditions. Signals of allegiances convey information to bystanders and the enemy about the numeric strength of the coalition and under ancestral conditions a change in allegiance of one or two persons could determine outcomes (Wrangham & Glowacki, 2012).

The resulting motivations are important for understanding modern political dynamics. They explain why it is extremely difficult for candidates from different political parties to express agreement on issues and why people readily respond to intense disagreement with declining political trust (Mutz & Reeves, 2005), interpreting it as reflections of self-interested coalitional strategies. It also helps explain why politically engaged individuals are highly motivated to follow political news. Coalitional signals are dynamic and change when new issues emerge. To keep up with the game of coalitional signaling, one needs to constantly attend to the signals emitted from coalitional leaders. News programs are like fashion shows to the evolved mind: information about how to signal your identity.

COALITIONAL LEADERS AND FOLLOWERS

Due to the broad-agenda nature of coalitions, member interests are not completely overlapping. This has created a selection pressure for solutions that help coordinate which of these interests to collectively pursue and how. The formation of within-coalition hierarchies is one important evolved coordination device. In humans, hierarchies have evolved into complex exchange relationships between leaders and followers (Price & van Vugt, 2014). Human leaders enjoy benefits such as power and privileged access. In exchange, human leaders are expected to coordinate solutions to collective problems of the coalitions.

The precondition for the evolution of this leader-follower relationship is the sophisticated coalitional psychology of humans. Because humans can readily form coalitions and engage in coalitional action, no individual would ancestrally have been able to completely dominate a collective of individuals. In humans, exploitive behavior in a higher-ranking individual can be held in check by the possibility of the formation of coalitions between lower-ranking individuals. Because of this, human coalitional psychology has coevolved with a psychology of counterdominance (Boehm, 2000). This psychology imposes important constraints on the extent to which leaders can utilize coalitions to pursue their own narrow interests: Leaders need to cater to the interests of the followers or be overthrown.

The psychology of counterdominance structures modern politics in multiple ways. First, humans have adapted to influence leadership through side taking between competitors for leadership position. This implies that key features of democratic elections fit evolved intuitions. Voting, for example, is essentially a coalitional action and equivalent to taking sides in a competition. This might also help explain the public appetite for news that portrays politics as a strategic competitive race between candidates (see Iyengar, Norpoth, & Hahn, 2004).

Second, humans intuitively recognize a division of labor between leaders and followers. The evidence for acceptance of political authority is overwhelming (Tyler, 2006). This resonates with the representational aspect of representative democracy. It also provides a psychological basis for limited political participation because it sets up motivational incentives to lean on competent leaders for routine collective decisions and only become engaged when key interests are at stake (see Hibbing & Theiss-Morse, 2002).

Third, counterdominance psychology motivates a follower to only view political authority as legitimate to the extent leaders pursue the follower's interests: We evolved to monitor our leaders and keep them accountable (Bøggild & Petersen, in press). This is reflected in the dispersion of democracy through the world. Stable democracies are more likely to appear in resourceful countries with low rather than high levels of ethnic heterogeneity (Jensen & Skaaning, 2012), suggesting that people primarily accept political authority that benefits their own ethnic coalition. People, however, also attend keenly to motivations in ingroup leaders and withdraw support from self-interested decision makers (Tyler, 2006). One reflection of these motivations is the massive public attention to political scandals. When politicians' personal choices are at odds with their political positions—reflecting a self-interested attempt to constrain the actions of the others but not the self—outrage ensues.

Because followers expect service in return for bestowing prestige on leaders (Price & van Vugt, 2014), a key input to the psychology for aligning the self with particular within-group leaders is their problem-solving competence. Perceptions of the competence of political candidates are one of the strongest predictors of vote choice in modern elections (Kinder, Peters, Abelson, & Fiske, 1980). Furthermore, voters in modern elections utilize a range of physical cues that would have been recurrently available over human evolutionary history to make such competence judgments, including facial and voice-related features of the candidates (Todorov, Mandisodza, Goren, & Hall, 2005). For example, people generally perceive low-pitched voices as indicative of physical prowess and strength (Puts, 2010; Puts, Bailey, & Reno, Chapter 13, this *Handbook*, Volume 1) and, in political elections, this leads voters to prefer candidates with low-pitched voices (Tigue, Borak, O'Connor, Schandl, & Feinberg, 2012). Importantly, preferences for physical features are adaptively calibrated by contextual factors. People favor features that ancestrally would have increased the leader's ability to solve the problems facing the coalition (Laustsen & Petersen, 2015). In times of war, people prefer a leader with masculine, dominance-related physical traits. In times of peace, such features could potentially increase the likelihood of exploitation and accordingly, people exhibit greater preferences for competent-looking, feminine individuals (e.g., Little, Burriss, Jones, & Roberts, 2007).

ADAPTATIONS FOR POLITICAL BEHAVIOR: PERSUASION AND INFORMATIONAL VIGILANCE

Another set of adaptations for political behavior is designed to enable humans to pursue their interests by persuading others that their interests are aligned. Political science has offered ample evidence that modern-day politicians routinely use persuasion strategies to promote their policies, and that information communicated by media and political elites can induce opinion change among the public (Chong & Druckman, 2007).

Persuasion strategies involve the communication of two information types to the receiver(s) (see, e.g., Griskevicius et al., 2009). First, information serving as input to psychological mechanisms that activate motivational goals aligned with support for the political rule the communicator wants to promote. If communicators, for example, seek to increase opposition to generous social welfare, relevant information includes that welfare recipients are lazy, ungrateful, and outgroup members (i.e., cheaters rather than reciprocators). Second, information revealing how the preferred rule supports the fulfillment of those motivational goals. If the communicators seek to promote a specific policy that tightens the eligibility criteria for welfare benefits, they need to provide information that this policy guards against cheaters and encourages reciprocation. As a consequence, the success of political communication is constrained by the evolved, human psychological architecture. The fit between the communication and the input conditions of relevant psychological mechanisms determines whether a piece of information activates appropriate motivational goals. The fit between the communication and the outputs of these mechanisms determines whether the motivations translate into support for the rule that the communicator wants to promote (Arceneaux, 2012).

PERSUASION STRATEGIES

There are a number of persuasion strategies, such as logically deducing a specific rule from other rules that are supported or exposing expertise in the specific domain of the rule. Here, two particular strategies—framing and moralization—are reviewed, both designed to activate relevant motivations in a receiver.

Most political decisions are complex: It is difficult to keep all relevant features accessible in working memory, and most decisions involve trade-offs. In such cases, framing is a frequently used strategy (Chong & Druckman, 2007). Framing seeks to flood the working memory of the receiver with those features that would generate support for the promoted rule by emphasizing certain features at the expense of other features of a decision situation. For example, by emphasizing information suggesting that many social welfare recipients are cheaters and downplaying information to the contrary, communicators can exploit cheater-detection mechanisms to increase support for policies that impose costs on welfare recipients (for an empirical demonstration, see Slothuus, 2007). Similarly, when mobilizing for war, communicators often emphasize past grievances and downplay cooperative relations with the opposing group in order to portrait the relationship as one of zero-sum competition (see Lopez et al., 2011). In the lead up to the Balkan war between Serbia and (Muslim-dominated) Kosovo, Serbian leaders continuously referred to lessons from the lost Battle at Blackbird Field between the Serbian and the Ottoman army, a battle that took place 700 hundred years earlier.

Another strategy is moralization. Morality is produced by adaptations designed for coordination of judgments (DeScioli & Kurzban, 2013). In conflicts, humans have adapted to side against individuals violating the set of rules that are recognized as “moral” within the particular community. This coordinated side-taking across the entire community hinders conflicts from escalating along, for example, coalitional lines. However, due to the strong motivational force of morality (motivating observance of rules and outrage against violations; Fiske & Tetlock, 1997), moral psychology becomes an obvious target for persuasion strategies. Because a large range of rules can, in principle, be included in the set of rules considered “moral” (as demonstrated by the vast variation in moral rules across societies), the content of this set is not static, and people can seek to strategically broadcast information that promotes the inclusion of a preferred political rule into the set of moral rules (DeScioli & Kurzban, 2013; Petersen, 2013). While a communicator might be motivated to promote a rule due to narrow self-interest, the task when moralizing is to remove this self-interest from the argumentation and broadcast information that makes the rule a likely coordination point for the entire collective. One commonly used tactic is to recast the rule as being in the interests of everybody or, at least, of the majority. For example, the moralization of smoking in politics and beyond was significantly advanced by information of the negative effects of secondhand smoking (Rozin & Singh, 1999). Another tactic is to recast the rule as moral by linking the specific rule to more general moral taboos (“abortion is lack of respect for life,” “the death penalty is lack of respect for life,” “homosexuality is a sin in the eyes of God,” etc.) (Fiske & Tetlock, 1997).

COUNTERSTRATEGIES: INFORMATIONAL VIGILANCE

Persuasion potentially involves broadcasting false information. As a consequence, the existence of persuasion strategies has created a selection pressure for the evolution of defensive mechanisms designed for countermanipulation through informational vigilance.

Humans seem to have rapidly operating mechanisms for identifying self-interested motivations behind moral rhetoric and for, upon the detection of such hypocrisy, triggering anger (Monin & Merritt, 2012). One feature of these mechanisms that makes them effective is that they are designed to presuppose the existence of self-interested motivations (Ybarra, 2002). Consistent with the involvement of these mechanisms in modern politics, people have very clear perceptions about the different interests to which different political parties cater (Stubager & Slothuus, 2013).

Humans also engage in motivated reasoning—they discount information (facts, arguments, etc.) that goes against the position they are currently endorsing (Kunda, 1990), something that also occurs in modern politics (Taber & Lodge, 2006). By operating under the presumption that one's original position is valid, motivated reasoning increases the threshold that persuasion attempts need to meet in order to generate a change in positions. Hence, while motivated reasoning is often portrayed as a faulty aspect of human reasoning, an evolutionary perspective suggests that one of its core adaptive functions is to set up an effective shield against manipulation (see also Mercier & Sperber, 2011).

MASS POLITICS IS A BOTH STRANGE AND FAMILIAR PLACE TO THE EVOLVED MIND

The psychological mechanisms reviewed above evolved to promote adaptive political judgments and behavior under evolutionarily recurrent circumstances. Given the recent transition from small-scale to large-scale societies, these mechanisms do not necessarily operate adaptively in the context of modern, mass politics. Mass politics is a phenomenon that is both familiar and strange to the evolved mind: familiar because mass politics is about core problems that we have adapted to solve, strange because we today need to solve them in a radically different context. In this final section, a range of implications is reviewed.

The Myth of the (Ir)rational Voter

One key difference between ancestral and modern politics is about the factors that are rational to consider. For example, in the context of ancestral interpersonal interaction, differences in upper-body strength were important. Today, in the context of mass politics, differences in upper-body strength continue to shape male political judgments, but it is hardly rational to base modern views on military strength (Sell et al., 2009) or personal benefits from redistribution (Petersen et al., 2013) on one's individual strength. The continuous influence of ancestrally relevant factors in modern politics reflects the design of the political mind and the structure of available cues in modern politics. The human mind is an adaptation-executor (Tooby & Cosmides, 1990), continuously scanning for cues that ancestrally would, on average, predict the presence of an adaptive problem in order to automatically bring adaptations for solving the problem online. Today, the cues that surround mass politics often resemble evolutionary recurrent cues sufficiently to activate evolved political psychology that, as a consequence, comes to guide subsequent processing. Despite all the legal complexities of the modern welfare state, for example, political debates about welfare still revolve around needy individuals and requests for help, arousing our evolved help-giving psychology and the related cheater-detection mechanisms (Petersen, 2012). When new problems emerge in mass politics with no direct ancestral parallel, our evolved psychology will latch on to any available cue and interpret the novel problems as if they contained ancestral risks. For example, in modern politics, judgments on the novel issue of genetically modified products are processed by adaptations for pathogen avoidance due to the cues inherent in tinkering with food (Prokop, Ozel, Usak, & Senay, 2013), giving rise to intuitions about contamination risk.

As a consequence of the activation of adaptations designed for small-scale politics, modern political judgments will often disregard modernly rational factors and prioritize ancestrally rational factors. In this way, evolutionary political psychology parts with two major strands in political science research. One strand argues that people's political decision-making mechanisms are well matched to mass politics because they have been "learned" from exposure to mass political debates (e.g., Lau & Redlawsk, 1997). Another strand argues that people are "muddle-headed" and incapable of coherent political reasoning (e.g., Converse, 1964). Against these strands of argument, an evolutionary perspective suggests that human political psychology is *ecologically rational*. When factors such as upper-body strength or short-term hunger influence modern political attitudes, it is not because humans are irrational but because our political psychology evolved to operate efficiently in the ecology of small-scale ancestral life. When the cognitive demands of small-scale and large-scale politics diverge, it will give rise to biased judgments and apparently irrational responses in the context of mass politics. This is not all bad. For example, high levels of participation in elections are often deemed normatively desirable, but voting has often been viewed as irrational because the influence of a single vote is so miniscule. Seemingly, however, the desired participation is brought about by coalitional motivations to support one's party (Smirnov, Dawes, Fowler, Johnson, & McElreath, 2010), adapted to small-scale circumstances in which the support from everyone were vital for coalitional success.

THE POVERTY OF ECOLOGICALLY VALID STIMULI

Another, important difference between ancestral and mass politics relates to the informational context. Ancestrally, adaptations for politics would (mostly) process information relating to familiar, concrete individuals in face-to-face interactions. Today, most political debates focus on individuals, groups, and events that are removed from the individual and, furthermore, on abstract, social categories ("criminals," "welfare recipients," "immigrants") rather than concrete others. In mass politics, the input to political adaptations accordingly comes from decoupled mental simulations (Petersen & Aarøe, 2013). Furthermore, these decoupled simulations are built on the basis of information provided by others (political elites, social networks, media) rather than directly experienced cues.

One consequence is that the window for persuasion strategies and informational warfare becomes larger as people are not able to routinely check assertions against personal experiences. A related consequence is that the potential for conflict is increased. The mental representations underlying mass political judgments are (a) less constrained by shared direct experiences and (b) rely heavily on internally generated representations. Accordingly, each psychological difference that influences the default expectations people have about the world will come to influence these representations and provide a basis for conflict. Political conflict primarily exists in the abstract debates, but less so in relation to concrete cases (e.g., Peffley, Hurwitz, & Sniderman, 1997; Petersen, Slothuus, Stubager, & Togeby, 2011). For example, while liberals and conservatives disagree about welfare polices in general, this disagreement is dramatically decreased in debates about specific welfare recipients when evolutionarily relevant cues are available. Liberals and conservatives are equally supportive of providing welfare to reciprocators and equally likely to reject welfare to cheaters (Petersen et al., 2011). They differ primarily in their decoupled stereotypes about whether most welfare recipients are one or the other (Aarøe & Petersen, 2014).

The absence of direct, ecologically valid information in mass politics (in addition to the legal and technical complexities of many modern issues) also means that mass political issues at times fail to activate relevant psychological mechanisms (Petersen & Aarøe, 2012), and it is important to acknowledge the widespread nature of public ignorance of and disinterest in mass politics (Carpini & Keeter, 1996). Hence, forming political judgments on mass political issues is only an interesting and effortless affair to the extent the underlying adaptations have been locked onto the mass political level.

Both contextual and individual factors influence whether people utilize evolved political psychology to reason about mass politics. One factor is developmental context. Exposure to politically engaged parents—and, hence, cues that partisanship and political judgments are important coalitional markers—has been found to increase political attention and learning (Jennings, Stoker, & Bowers, 2009). Another contextual factor is current media framing. When media and political elites convey information in formats that fit evolved psychological mechanisms—through vividly described case stories rather than abstract but objectively more relevant statistical information—people become more emotionally engaged in the issue at hand (e.g., Aarøe, 2011).

One important individual difference relates to abilities for decoupled cognition. People who are more imaginative and better able to generate vivid, engaging mental pictures of absent events and groups are more likely to form extreme political judgments, to hold emotion-infused attitudes, and, of particular relevance, to utilize evolutionarily relevant cues in opinion formation (e.g., cheater-detection relevant cues in the case of social welfare attitudes), suggesting that vivid, decoupled representations fuel a stronger activation of the underlying psychological adaptations (Petersen & Aarøe, 2013). Hence, in the context of mass politics, researchers cannot understand the formation of political judgments by just considering the structure of adaptations for politics. In addition, researchers need to dissect the pathways—such as mental simulations, medias stories, and political campaigns—through which ecologically valid information is (or fails to be) transmitted to those adaptations.

CONCLUSION

Humans are political animals, designed by natural selection to navigate the conflicts of interests pervading human evolutionary history. Politics is the process of settling these conflicts by negotiating the rules of social life. According to the present review, the related adaptive problems have selected for a political psychology designed to, first, judge how the rules of resource access align with evolutionarily recurrent fitness interest and, second, transform rules into alignment with those interests through dominance, coalition formation, and persuasion.

Evolved political psychology guides conflict behavior in both the politics of everyday life (in the family, local communities, and so forth) and politics at the level of modern mass society. Human political psychology evolved to operate within ancestral small-scale groups. The context of everyday politics resembles this social ecology, and in that context, we should expect humans to be as skilled as the best-paid spin doctor. The context of large-scale politics is, in contrast, radically different, and the activation of evolved political psychology is dependent on the flow of evolutionarily recurrent cues from political elites. Without these cues, the political animal is partially a political ignorant.

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CHAPTER 48

Evolutionary Literary Study

JOSEPH CARROLL

INTRODUCTION

Evolutionary literary study has emerged only in the past 20 years or so, and its practitioners still constitute a relatively small community on the margins of the academic literary establishment. That establishment is oriented to poststructuralist ideas and thus repudiates the ideas both of human nature and of objective scientific knowledge (Carroll, 1995; Carroll, Gottschall, Johnson, & Kruger, 2012, pp. 1–6; Culler, 2011). Evolutionary literary critics embrace the notion of “consilience,” affirm the cogency of evolutionary theory, and assimilate the findings of the evolutionary social sciences. They would agree with E. O. Wilson that the world is a unified causal order and that knowledge forms an integrated field encompassing the physical sciences, the social sciences, and the humanities (Carroll, McAdams, & Wilson, in press; Slingerland & Collard, 2012; E. O. Wilson, 1998). They affirm that human mental and cultural activity is constrained by the principles that regulate all biological activity, that life has evolved through an adaptive process by means of natural selection, and that complex functional structure in living things has been produced by adaptation. They argue that the adapted mind produces literature and that literature reflects the structure and character of the adapted mind.

In the 1990s and early 2000s, much of the work done in evolutionary literary study was polemical and programmatic. Scholars attacked the cultural constructivist ideas prevailing in the academic literary establishment, rehearsed the basic logic of the adaptationist program, and made exploratory efforts to formulate principles of interpretation that could be linked to specifically evolutionary ideas (B. Boyd, 1998; Carroll, 1995, 2004; Cooke, 2002; Cooke & Turner, 1999; Easterlin, 2000, 2001, 2004; Gottschall, 2001, 2003a, 2003b; Gottschall, Martin, Quish, & Rea, 2004; Headlam Wells, 2005; Jobling, 2001; Love, 1999a, 1999b, 2003; Scalise Sugiyama, 1996, 2001a, 2001b, 2001c; Storey, 1996; Thiessen & Umezawa, 1998). Over the past decade, polemics and programmatic rehearsals have diminished while literary theory and interpretive literary criticism have matured (Anderson & Anderson, 2005; B. Boyd, 2008, 2009; B. Boyd, Carroll, & Gottschall, 2010b; Carroll, 2011b, 2012b, 2012c, 2013a, 2013c, 2013e, 2013f; Clasen, 2010, 2012a, 2012b, 2012c, in press; Duncan, 2010; Dutton, 2009; Easterlin, 2012; Gansel & Vanderbeke, 2012; Gottschall, 2008b, 2012; Gottschall & Wilson, 2005; Headlam Wells, 2011; Jonsson, 2012, 2013; Keener, 2010; Martindale, Locher, & Petrov, 2007; Nordlund, 2007; Saunders, 2007, 2009, 2012a, 2012b; Swirski, 2006, 2010, 2011; Vermeule, 2010).

Most evolutionary literary study still uses the discursive, speculative methods characteristic of the humanities. A few evolutionary literary scholars have assimilated empirical methods from the social sciences and a few evolutionary social scientists have taken literature as their subject matter (Carroll, Gottschall, et al., 2012; Carroll, Johnson, Gottschall, & Kruger, 2012; Gottschall, 2008a; Johnson, Carroll, Gottschall, & Kruger, 2008, 2011; Kruger, Fisher, & Jobling, 2003; Mar, 2004; Mar & Oatley, 2008; Mar, Oatley, Djikic, & Mullin, 2011; Mar, Peskin, & Fong, 2011; Miall & Dissanayake, 2003; Oatley, Mar, & Djikic, 2012; Whissel, 1996).

HUMAN NATURE, CULTURAL NORMS, AND THE ARTS

Over the past several decades, the evolutionary human sciences have gradually developed a good working model of human nature. The early sociobiological emphasis on reproductive success was modified by the evolutionary psychologists' insistence on "proximate" or mid-level motives (Laland & Brown, 2002). Evolutionary psychologists, emphasizing "modules" or hard-wired bits of cognitive machinery, sometimes left out "general intelligence," but a broader conception of human cognitive architecture has corrected that mistake (Chiappe & MacDonald, 2005; Geary, 2005; Geary & Huffman, 2002; MacDonald, 1991; MacDonald & Hershberger, 2005; Mithen, 1996). Early sociobiologists tended to limit human social interaction to kinship and the exchange of favors, but evolutionary biologists and social scientists have been developing more complete and adequate accounts of specifically human capacities for cooperative group endeavor (Boehm, 1999, 2012, in press; Buckholtz & Marois, 2012; Carroll, 2015; Chudek & Henrich, 2011; Fukuyama, 2011, pp. 339–440; Gintis, 2003, 2011; Gintis & Van Schaik, 2012; Haidt, 2012; Henrich et al., 2010; Hill, 2007; Nowak, 2006; Nowak & Highfield, 2011; Nowak, Tarnita, & Antal, 2010; Simpson, 2011). Evolutionists in the humanities have been making increasingly effective arguments that forms of imaginative culture—the arts, religions, ideologies—are integral parts of the human adaptive repertory (B. Boyd, 2005; Carroll, 2008a, 2012a; Dissanayake, 2000). Those arguments converge with the now rapidly developing concept of "gene-culture co-evolution"—the idea that humans are genetically disposed to produce culture, and that over evolutionary time culture alters the human genome (Carroll, 2011a; Chudek & Henrich, 2011; Chudek, Zhao, & Henrich, in press; Cochran & Harpending, 2009; Gintis, 2003; Irons, 2009; Lumsden & Wilson, 1983, 2005; Richerson & Boyd, 2005). Early evolutionary psychology grouped its mid-level or "proximate" motives into open-ended lists (Carroll, 1999). Those lists are now being replaced with "human life history theory": the idea of a systemic organization of all the components of human nature (Burkart, Hrdy, & Van Schaik, 2009; Burkart & van Schaik, 2010; Carroll, 2011a; Foley & Gamble, 2009; Gintis & Van Schaik, 2012; Hill, Barton, & Hurtado, 2009; Hrdy, 2005, 2009; H. Kaplan, Gurven, & Winking, 2009; H. S. Kaplan, Gurven, & Lancaster, 2007; H. S. Kaplan, Hooper, & Gurven, 2009; Klein, 2009; Lancaster & Kaplan, 2007; Muehlenbein & Flinn, 2011; Wade, 2006; Wrangham, 2009; Wrangham & Peterson, 1996). Beneath all variation in the details of organization, the life history of every species forms a reproductive cycle. In the case of human beings, successful parental care produces children capable, when grown, of forming adult pair bonds, becoming functional members of a community, and caring for children of their own. Human life history theory thus integrates the sociobiologists' "ultimate" level of casual explanation—reproductive success—with the evolutionary psychologists' mid-level explanations focusing on immediate motives such as mating, parenting, and striving for social status.

In literature and in casual conversation, when people use the phrase "human nature," they usually have in mind basic human motives: survival, mating, parenting, favoring kin, and acting as members of a social group (Carroll, 2012e). Human nature is important in fiction because most stories are built out of basic human motives and emotions. Stories are about struggling to survive, seeking romantic love, maintaining family relationships, satisfying ambitions, making friends, forming coalitions, and striving against enemies.

Human nature manifests itself in basic human motives that are channeled into specific cultural norms (Buckholtz & Marois, 2012; Carroll, 2015; Chudek & Henrich, 2011; Haidt, 2012; Sripada & Stich, 2005; Tomasello, 2009). Those norms are articulated in imaginative form through myths, legends, rituals, images, songs, and stories. Humans universally regulate their behavior in accordance with beliefs and values that are made vividly present to them in the depictions of art, including fictional narratives, dramatic representations, films, and poetic verses.

Literature is the written version of an oral behavior—the verbal representation of imagined actions—that is universal in preliterate cultures. Whenever the word "literature" appears in this chapter, it may be taken tacitly to signify the larger concept, "literature or its oral antecedents."

IMAGINATIVE VIRTUAL WORLDS AND THE ADAPTIVE FUNCTION OF THE ARTS

All of us, at all times, inhabit imagined worlds. An imagined world is an emotionally and aesthetically modulated vision of oneself and the world one inhabits (Carroll, 2012e; McAdams, 2006, 2008, 2009, 2011, in press; McAdams & Olson, 2010). Emotional modulation involves basic emotions such as disgust, joy, and sorrow (Ekman, 1999). Aesthetic modulation involves sensory feeling tones such as coarse, fine, ugly, or beautiful (Carroll, 2013b; Davies, 2012; Dutton, 2009). An imagined world contains the present within a temporal continuum that includes the past and the future. The past is not only the personal past but the historical or mythic past. The future is not only one's own personal future but the future of the world; it can contain an eternity of punishment or bliss, or a perpetual shadowy semi-existence in a ghostly limbo. An imagined world contains communities—all the people with whom one shares beliefs, values, and experiences.

The imagined worlds we inhabit overlap with the imaginative virtual worlds created by artists or by collective cultural efforts extending over generations or centuries. Imaginative virtual worlds feed into our imagined worlds, profoundly influencing the way we imagine our own actual lives. For instance, the Biblical myth of the creation of the world is, for many people, part of the imagined actual world that they inhabit. So also with Islam, Hinduism, the communist world vision that occupied half the world just a couple of decades ago, and with every set of cult beliefs that leads people to radically alter their life trajectories, prompting them sometimes even to mass suicide. On a more local level, people who read novels, watch films, listen to popular music, or attend operas assimilate images of personal and social identity that they incorporate into their own sense of who they are (Carroll, Gottschall, et al., 2012; Dissanayake, 2000; Gottschall, 2012; McAdams, 2011; Tooby & Cosmides, 2001).

In many forms of art, multiple arts are combined to fashion imaginative virtual worlds. Operas and musicals integrate dramatic depiction, music, costume, and setting. Films integrate dramatic depiction, music, and the visual characteristics of camera work, lighting, and editing. Songs integrate instrumental music with lyric and narrative poetry; music videos integrate those art forms with the arts of film. A church is an institution designed to give official housing to a shared imaginative virtual world that contains supernatural agents, immortal souls, a mythic beginning of the world, a final day of judgment, and an eternity of blisses and torments. Churches use architecture, statuary, painted images, colored glass, instrumental music, choral song, ritualized movements and vocal utterances, costumes, and even perfumed smoke to create a sensory surround giving concrete aesthetic form to the beliefs invested in doctrine and myth. In many societies, rituals also include dance and chanting (Dissanayake, 1992, 2000).

We are not always reading a novel, attending the opera, watching a movie, sitting in church, looking at pictures in a museum, or listening to music. But we are always conscious of emotionally and aesthetically modulated images of ourselves and of the world we inhabit (McAdams, 2011). We designate such consciousness by terms such as moods, feelings, beliefs, values, memories, associations, projections, goals, self-images, and world views. When we sing, draw, play an instrument, or dance, we are giving expression to the subjective sensations that inform our everyday lives. The imagined worlds we inhabit are imbued with our experience of music, painting, architecture, dance, drama, narrative literature, poetry, and film.

THE DEGREE OF CONSENSUS ABOUT THE ADAPTIVE FUNCTION OF THE ARTS

Steven Pinker argues that the arts are pleasure technologies like recreational drugs or pornography; the arts, he says, are used to exploit brain mechanisms that evolved for adaptive functions unrelated to the arts (Carroll, 2012a; Carroll, Johnson, et al., 2012, Ch. 5; Pinker, 1997, 2007). Geoffrey Miller argues that the arts are forms of sexual display—costly signals that have no primary adaptive functions (2000). Hypotheses by other theorists have converged toward a common point: the idea that literature and the other arts affect cognitive and emotional organization, influence motives, and help regulate behavior (B. Boyd, 2009; Carroll, 2008a, 2008b, 2012a; Carroll, Gottschall, Johnson, & Kruger, 2010; Carroll, Gottschall, et al., 2012; Deacon, 1997; Dissanayake, 1992, 2011; Dutton, 2009; Easterlin, 2012, 2013; Gottschall, 2012; Mar & Oatley, 2008; Panksepp & Panksepp, 2000; Salmon & Symons, 2004; Tooby & Cosmides, 2001; E. O. Wilson, 1998, Ch. 10). Many biocultural theorists would agree that basic human motives are channeled into specific cultural norms and that specific cultural norms are articulated in imaginative form through myths, legends, rituals, images, songs, and stories. They would agree also that humans universally regulate their behavior in accordance with beliefs and values that are made vividly present to them in the arts. Those points of agreement are signified by the term "imaginative virtual worlds." The theory of imaginative virtual worlds subsumes more particular ideas that the arts can provide practically useful information (Scalise Sugiyama, 1996, 2001a, 2001b, 2004, 2006), offer game-plan scenarios to rehearse potential adaptive challenges (Pinker, 1997), provide means for sexual display (Dutton, 2009; Miller, 2000), enhance pattern recognition and stimulate creativity (B. Boyd, 2009), and provide a medium for shared social identity (B. Boyd, 2009; Carroll, Gottschall, et al., 2012; Dissanayake, 2000).

The human disposition to inhabit imaginative virtual worlds evolved through gene-culture coevolution. The theory of gene-culture coevolution was first proposed by Lumsden and Wilson more than three decades ago, but it has begun to emerge as a robust and integrative theory only within the past few years (R. Boyd, Richerson, & Henrich, 2011; Carroll, 2011a, 2012a; Carroll et al., 2010; Chudek & Henrich, 2011; Chudek et al., in press; Cochran & Harpending, 2009; Lumsden & Wilson, 1981, 1983; Richerson & Christiansen, 2013; E. O. Wilson, 1998, Ch. 10). As evolutionists in the social sciences continue to develop the theory of gene-culture coevolution, it seems likely that they will increasingly recognize that the arts are integral parts of the uniquely human adaptive repertory. Evolutionists in the humanities can draw on findings from research into gene-culture coevolution and can also contribute directly to that research.

THE GOALS OF BIOCULTURAL RESEARCH

Even 20 years ago, we understood far less than we now do about the human evolutionary trajectory, and especially less about the uniquely human, biocultural character of that trajectory. Many researchers in both the evolutionary human sciences and the evolutionary humanities have not yet caught up with the most advanced thinking about gene-culture coevolution, and that thinking is itself still in its beginning phases. One important area for future research is the study of specific periods in history: research that integrates ecological, reproductive, social, religious, ideological, economic, political, literary, and artistic aspects of biocultural thinking. A few scholars have already begun contributing key elements to that kind of integrative research (Carroll, Gottschall, et al., 2012; Fukuyama, 2011; Gat, 2008; Gottschall, 2008b, 2012; Oakley, 2007; Pinker, 2011; Turchin, 2006; D. S. Wilson, 2002). The cultural imagination interacts causally with material conditions and forms of social organization. Consequently, findings about social and cultural dynamics in specific historical periods should constrain and stimulate evolutionary social theory. Working cooperatively toward common goals, evolutionary social theorists, historians, and scholars of literature and the other arts can produce results more satisfactory than could be produced by researchers remaining within the boundaries of their own disciplines.

A major goal for integrative biocultural research would be to create, collectively, a total explanatory grid for every specific culture—every society located in a particular ecology, organized by a specific socioeconomic and political structure, and informed by specific religious, ideological, and aesthetic traditions. That grid would extend in two directions. For ultimate causal explanation, it would extend toward basic, universal principles of biology and evolutionary psychology. In the other direction, the grid would extend toward finely nuanced detail in understanding the evocation of subjective particularities of experience for individuals within any given culture. The analysis of specific historical cultures would thus form the pivotal link between universal causal explanation, the aim of the sciences, and the analysis of particularistic subjective evocation, a chief activity in the humanities. The explanatory continuum would be unbroken. Knowledge and imaginative experience would form a seamless web of knowledge.

ANALYZING MEANING IN LITERARY REPRESENTATIONS

Both actual human experience and depicted human actions have three main components: individual persons (characters), a surrounding world (setting), and sequences of events connected by emotionally meaningful concerns (plots). Literary authors can seek to give exact and faithful accounts of what actual experience is like in a concretely detailed physical and social world occupied by ordinary people engaged in activities that are constrained by commonplace conditions. We call that kind of literature "realism." Authors can also depict imagined situations in which characters exemplify elemental emotions and abstract ideas; in which settings exemplify emotional or imaginative aspects of experience; and in which plots fulfill the inner logic of some emotional or imaginative process relatively unconstrained by ordinary physical conditions. We call that kind of literature "symbolism." Myths and fairy tales offer examples. Realism and symbolism represent not mutually exclusive alternatives but polar points on a continuum, and all literature has some measure both of realism and of symbolism (Carroll, 1995, Ch. 3) Dickens, for example, both depicts the actual conditions of Victorian urban life and also creates characters and plots that often seem more like those of myth or fairy tale than those of simple realist fiction.

Every author has a culturally modulated identity, an idiosyncratic temperament, and a unique set of personal experiences (Bauer & McAdams, 2004; Carroll, in press; Habermas & Bluck, 2000; McAdams, 2001, 2006, 2009, 2011, in press; McAdams & Bowman, 2001; McAdams, Josselson, & Lieblich, 2001, 2006; McAdams & Olson, 2010). The author can only envision depicted events from within the author's own world view. Readers responds to depicted events and also to the personality and manner of the author. This interaction between authors and readers is a fundamental part of the total literary experience and is an indispensable part of what a literary interpretation takes into account (Carroll, Gottschall, et al., 2012; Gibbs, 2013; Gottschall, 2012; Mar & Oatley, 2008; Oatley, 1999).

Interpretive criticism characterizes the author's conception of his or her subject (themes), the orchestrated sequence of emotions expressed and evoked by the work (tone), and the organization of verbal components in the work (form and style). These three categories of interpretive criticism can be lodged within an evolutionary conception of human nature. The subject matter of literature are human motives and behavior. Human life history theory and evolutionary social psychology identify the main phases and concerns of human life and thus also of literature (Carroll, 2012e; Figueredo & Wolf, 2009; H. Kaplan et al., 2009; Lancaster & Kaplan, 2007; Muehlenbein & Flinn, 2011). Orchestrated sequences of emotions can best be understood by appeal to universal emotions and affective neuroscience (Carroll, Gottschall, et al., 2012; Carroll, Johnson, et al., 2012; Ekman, 2007; Panksepp, 2011; Panksepp & Biven, 2012; Plutchik, 2003). Formal structures derive from and reflect the properties of our evolved cognitive architecture. The "cognitive rhetoricians" have suggested some avenues of approach into formal organization but have stopped short of connecting formal analysis with a larger model of human nature (Hogan, 2003; Turner, 1991, 1996; Zunshine, 2006, 2008, 2010). Brian Boyd has made evolutionary formal analysis a salient aspect of his work (B. Boyd, 2009, in press).

Thematic, tonal, and formal criticism cover the whole spectrum of internal structure in a literary work. A full understanding of a literary work situates analysis of internal structure within larger contexts: the interactions among authors and readers and the cultural complex within which that interaction takes place. At the highest level of criticism, structural and contextual criticism is lodged explicitly within explanatory terms from some specific theory about literature (Bordwell, 2008, p. 46; Carroll, Gottschall, et al., 2012, pp. 59–69; Hirsch, 1967). Such theories necessarily include ideas about human psychology, language, representation, and the basic causal forces that shape the world in which represented actions and communicative social relations take place.

Ideally, an evolutionary critique of any given literary work or set of works would analyze thematic, tonal, and formal organization; locate the work or works in a cultural context; explain that cultural context as a particular organization of the elements of human nature within a specific set of environmental conditions (including cultural traditions); register the responses of readers; describe the sociocultural, political, and psychological functions the work fulfills; locate those functions in relation to the evolved needs of human nature; and link the work comparatively with other artistic works, using a taxonomy of themes, formal elements, affective elements, and functions derived from a comprehensive model of human nature.

WORLD VIEWS OF AUTHORS AND CRITICS

Literary theorists and critics ultimately reduce depicted events to thematic structures that reflect their own beliefs about psychological and social processes. In that respect, evolutionary critics are like critics of any other school—Marxists, Freudians, deconstructionists, feminists, and Foucauldian cultural critics. What distinguishes an evolutionary approach is that evolutionary critics use evolutionary social science as the common frame within which they assess the conceptual order of any depicted action (Carroll, 2013a, 2013c; Gottschall, 2008b; Saunders, 2009, 2010, 2012a).

Most authors have a strong intuitive understanding of human nature. That understanding is one of the prerequisites for being an author. Evolutionary critics analyze the way the intuitive understanding of any given author is made to fit within the author's world view. Authors sometimes give depictions of human behavior in which some personal bias or some religious, ideological, or theoretical preconception interacts with his or her intuitive understanding. Such interactions are also materials for an evolutionary interpretive analysis (Carroll, 2013a).

Evolutionists need not make the naïve mistake of assuming that authors share an evolutionary viewpoint. Historically, for authors writing before the publication of *The Origin of Species*, that is not even possible. What evolutionary critics assume is that all world views can ultimately be explained within an evolutionary framework. Christians, Hindus, Muslims, Buddhists, Marxists, Scientologists, and practitioners of Voodoo all have world views, and those world views can all be explained by causal forces operating within the adapted mind.

THE FUTURE

Literary Darwinists have emerged and survived on the margins of the literary establishment, like small early mammals creeping about nocturnally among the feet of sleeping dinosaurs. The dinosaurs in this case consist of two populations. One population is composed of the last lingering elements—most of them gray, stiff, and fragile—of old-fashioned, humanist critics—belle-lettristic, archivalist, and a little lost and disoriented in the modern world of progressive empirical knowledge (Abrams, 1989, 1997; Carroll, 2004, pp. 29–39; Carroll, Boyd, & Deresiewicz, 2009; Carroll, Gottschall, et al., 2012, pp. 171-173; Crews, 1986, 2006, 2008; Deresiewicz, 2009; Goodheart, 2007, 2009; Patai, 2005; Pigliucci, in press). The other population is composed of the postmodern establishment, no longer revolutionary but fully ensconced in all the precincts of academic power (B. Boyd, 2006; B. Boyd, Carroll, & Gottschall, 2010a; Crews, 2001; Culler, 2011; Headlam Wells, 2005; Menand, 2005). This population can be compared to an invading army that has conquered a vast district, ravaged it, left it destitute, and has thus deprived itself of the resources necessary to maintain itself on the ground it has conquered. The purely theoretical impulses animating postmodernism inspired the first wave of invaders, the deconstructionists, but that wave had already subsided by the late 1980s and had been superseded by the much more heavily political criticism of the Foucauldians, supplemented by their auxiliaries of gender, postcolonial, and ethnic critics. That secondary political wave has now also exhausted its momentum, and the literary establishment finds itself in a period of stasis and fatigue, isolated both from the progressive empirical sciences and from the interests and tastes of educated public opinion (Bérubé & Nelson, 1995; Carroll, Gottschall, et al., 2012, pp. 1–9; Feal, 2005). The intellectual works that appear on nonfiction bestseller lists are not the works of Althusserian Marxists, Lacanian psychoanalysts, or Kristevan feminists. They are the works of primatologists such as Frans de Waal and Richard Wrangham, biologists such as Edward O. Wilson and Richard Dawkins, and evolutionary psychologists such as David Buss, Steven Pinker, Jonathan Haidt, and Daniel Goleman.

In the future, academic literary study could take any of three possible paths. Along one path, evolutionary literary study would remain on the margins of the academic establishment, ignored or rejected (Carroll, 2012d; Carroll et al., 2009; Carroll & Gottschall, 2008; Crews, 2008; Dawson, 2006; Deresiewicz, 2009; Goodheart, 2007, 2009; Kramnick, 2011; Menand, 2005; Peterson, 2008; Spolsky, 2008). In a second path, evolutionary criticism could be incorporated as just another of many different "schools" of literary theory (B. Boyd, 2013; Gottschall, 2013), with no one school claiming any particular priority over other schools. If academic literary study took this path, casebooks of essays would include a Darwinist essay along with essays by Marxists, Freudians, feminists, and Foucauldians. In the third path, the evolutionary human sciences would fundamentally transform and subsume all literary study (Carroll, 2011b, pp. 71–87; 2013d).

Which path is most likely? If one were to base predictions on the current status of evolutionary study in the humanities, the first or second path might seem the most likely. If one bases prediction on the inherent appeal of developing knowledge, the third will seem most likely. No other currently active theory lodges itself in a biological view of the human mind. No other theory thus makes it possible to integrate literary study with the rapidly developing body of knowledge from evolutionary biology and the evolutionary social sciences. If consistency with empirically grounded forms of knowledge is the criterion by which we assess the validity of literary theories, the currently active alternatives to evolutionary literary study willingly disqualify themselves. Only the evolutionary understanding of literature offers the prospect for a cumulative development of literary research consistent with a broad range of scientific knowledge.

Knowledge about human behavior is set inexorably on a course toward integration from within evolutionary theory (Carroll, in press; E. O. Wilson, 1998). As research in human behavior molds itself to the inherent structure of reality, the disciplinary organization of higher education will need to adjust itself to the actual shape of knowledge. The current organization of segregated disciplines will have to become more fluid and flexible. Already, researchers in the vanguard of the evolutionary human sciences regularly cross disciplinary boundaries in order to integrate information from primatology, evolutionary anthropology, evolutionary psychology, behavioral ecology, comparative ethology, cognitive and affective neuroscience, behavioral genetics, personality psychology, social psychology, and other such disciplines. Evolutionary humanists draw on all this information and insistently point toward the evolutionary significance of their own subject matter—the products of imaginative culture.

For evolutionary social scientists, institutional adjustments within the social sciences will require no great alteration in outlook—in the scope of subject matter, in methods, or in standards of validity. The greatest impediment to a full integration of knowledge about human behavior remains the gap between the social sciences and the humanities. Many humanists are intimidated by science or regard it as inherently antipathetic to the subject matter of the humanities; many scientists tacitly dismiss the subject matter of the humanities as trivial or regard it as beyond the reach of scientific method. All of that will have to change.

To bring about a large-scale transformation in the institutional structures that separate the humanities and the social sciences, it would be helpful to create programs designed specifically for that purpose. A prototype already exists in the evolutionary studies programs initiated at SUNY Binghamton by D. S. Wilson and copied at many other colleges and universities (EvoS: http://evostudies.org/). Along similar lines, a recently created program at Aarhus University in Denmark, the Center for Biocultural History, focuses specifically on the biocultural history of Denmark, from prehistoric times to the present (http://bioculture.au.dk/). The EvoS programs offer certificates at the undergraduate and graduate level, but they work within the current structure of academic departments, requiring students to select a distribution of courses from within those departments. For the most part, the work of synthesis is left up to the student himself or herself. A more radical approach would be to establish programs designed specifically for integrative biocultural research.

In one possible model for an institute of biocultural research, students would be required to take a distribution of courses designed to parallel main areas of emphasis from within an evolutionary view of human life. Topics for such courses might include basic evolutionary theory, the course of human evolutionary history, human life history theory, hunter-gatherer ecology, evolutionary behavioral psychology, cognitive and affective neuroscience, the evolution of human sociality, biocultural aesthetic and literary theory, and biocultural courses in specific historical periods. In this hypothetical model, students would be trained in ways that cancel or at least diminish the basic differences in research methods in the social sciences and the humanities. Students could be required to take or to test out of an introductory year-long course in statistics and empirical methods. Students coming into the institute from biology or the social sciences would already have that background and would have the option of taking more advanced statistical courses when they needed them.

The pedagogical outcomes envisioned for this program would extend across a range occupied by polar extremes: at one extreme, pure empirical social science oriented to the study of literature—the kind of thing being done now by researchers like Raymond Mar and Keith Oatley; and at the other extreme, purely discursive, essayistic commentary on literature, like that produced now by the majority of literary Darwinists. Students engaging in predominantly empirical, quantitative research would also have taken intensive courses in cultural history and literature. Students engaging in predominantly discursive forms of commentary would have taken courses that involve hands-on empirical research. They would thus at the least have expertise sufficient to evaluate the results of empirical research and to engage in collaborative work with empirical researchers. Much of the work done in any such biocultural institute would perhaps fall somewhere in between the polar extremes.

David Sloan Wilson conducted a survey in which he asked contributors to the journal *Behavioral and Brain Sciences* whether evolutionary ideas had been a significant part of their graduate training (2007, pp. 6–7). The majority of the respondents said no. They had been credentialed within some established discipline and then later, as established scholars, had incorporated evolutionary thinking in their research. Now, of course, robust programs in evolutionary psychology and evolutionary anthropology are in place at major universities in many countries. Graduate students in psychology and anthropology have been trained in specifically evolutionary ways of thinking, have gained tenured positions, and now have graduate students of their own.

The first generation of evolutionary social scientists faced stiff resistance from within their own fields (Kenrick, 2011; Segerstråle, 2000). Evolutionary scholars in the humanities face opposition even more stubbornly entrenched. By filtering admissions into graduate study, two or three generations of poststructuralists have perpetuated themselves. Institutional inertia is a political reality. At present, students of literature who overtly profess sympathy for evolutionary psychology find most graduate programs closed to them (Carroll, 2013e; Gottschall & Wilson, 2005, pp. xvii–xxvi; Kean, 2011). Consequently, in the short term, one can reasonably anticipate only very limited movement from within departments of literature. A graduate institute designed specifically to train doctoral candidates in biocultural research could serve as the thin end of a wedge ultimately transforming the character of research in the humanities.

The Darwinian revolution that has taken place in the social sciences will in all likelihood ease the way for evolutionary humanists. So long as the social sciences followed the standard social science model (Tooby & Cosmides, 1992), humanists could comfortably presuppose that culture, independently of biology, creates all content of human minds and has sole causal power over human behavior. The larger intellectual context within which the humanities operate has now fundamentally changed. The humanities are increasingly isolated from other fields in the university and from generally educated people. Institutional inertia within the humanities is in tension with the pressure exerted by the mass and creative energy of serious intellectual life outside the humanities. Continued stasis, isolation, degeneration? Or a gradual breaking up of stubbornly retrograde intellectual commitments? The answer to this question matters a great deal to young people who have talents and interests leading them toward research about imaginative culture. It matters a great deal also for the whole community of scholars who wish to achieve a full, complete understanding of human nature.

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PART IX

PRACTICAL APPLICATIONS OF EVOLUTIONARY PSYCHOLOGY

DAVID M. BUSS

In addition to informing basic scientific research, evolutionary psychology is increasingly being used for practical applications, from the business world to public policy to the courtroom. This final section of the *Handbook* captures four of these new trends—public policy, consumer behavior, organizational behavior, and legal issues. Three chapters are entirely new, and the fourth is an updated chapter from the first *Handbook of Evolutionary Psychology*.

Nicolas Baumard kicks off this section with an outstanding chapter on *evolutionary psychology and public policy*. At a fundamental level, public policies carry assumptions (implicit or explicit) about human nature. Baumard contrasts traditional public policy assumptions about that nature with those of evolutionary psychology. He illustrates that these assumptions matter a great deal by highlighting empirical research on more effective means to gently nudge people to adopt behaviors that are more environmentally friendly (in this case, by invoking social norms). Public policies, in short, work better with an accurate model of human nature, and Baumard's chapter provides the first extant road map for this important set of evolutionary psychological applications.

Gad Saad, a leader in *applying evolutionary psychology to human consumer behavior*, provides a compelling chapter about applications to the world of marketing. Understanding human adaptations for survival, mating, reciprocity, and kinship, he argues, is critical to effective marketing in a world where so many products compete for our attention. Although business schools have traditionally been slow to utilize evolutionary psychology for these practical applications, Saad's pioneering efforts, as summarized in this chapter, will be seen in retrospect as showing the light and the way.

Nigel Nicholson extends *an evolutionary analysis to organizations*, with a special focus on organizational leadership. His chapter addresses these key questions: What does the history of our species teach us about the essence of leadership? What are the gaps in knowledge that an evolutionary approach might fill? How can an evolutionary approach shed light on the key processes of leadership emergence, effectiveness, and failure? Leaders in organizations worldwide would do well to read Nicholson's important chapter and use a deep understanding of human evolved psychology to inform their own and their organization's behavior.

The final chapter in this section, by law professor Owen Jones, offers a penetrating *evolutionary analysis of the law*. The legal system, Jones argues, is designed to affect human behavior in certain ways, such as deterring certain forms of behavior—theft, rape, and murder. Simultaneously, it is designed to encourage other forms of behavior, such as persuading people to further public goals. Insights from evolutionary psychology offer tools for making the legal system more efficient in attaining these goals. It can do so, Jones argues, by discovering useful patterns of regulable behavior, identifying policy conflicts, exposing unwarranted assumptions in the law, revealing deep patterns in legal architecture, and assessing the comparative effectiveness of legal strategies, among others. Jones's analysis—prudent, judicious, and careful—promises to revolutionize the legal system. Indeed, after reading Jones's chapter, it is difficult to imagine how the legal system can accomplish its aims in ignorance of our evolved psychological mechanisms.

These four chapters signal the dramatic infusion of evolutionary psychology into practical applications with real-world consequences: How to formulate public policies to maximize their effectiveness? How to market to consumers in a world of information explosion? How to more effectively lead organizations? And how to devise laws as effective levers of human behavior?

CHAPTER 49

Evolutionary Psychology and Public Policy

NICOLAS BAUMARD

INTRODUCTION

Human beings seem to be at once a feat of engineering and a miserable technological failure. People may recognize the face of someone they met in passing years ago, but forget the three-digit security code of the credit card and the email password that they use all the time. Sometimes people may be generous, generating flows of billions of dollars after a hurricane or contributing large fractions of their income to finance public goods. At other times, people may be selfish, focusing on their own careers, family, and friends, and having no empathy for others. People can be very patient, spending thousands of hours in training that yields benefits only after many years. Yet the same people may be unable to resist the temptations of junk food and whim purchases and find themselves, years later, overweight and without savings for their old age.

How can we make sense of these paradoxes? It is not enough to conclude that human nature is flawed, or that humans are simply "not that smart" or "not very generous." They are sometimes incredibly intelligent or exceedingly generous, and sometimes incredibly stupid or desperately greedy. More importantly—to echo a popular presentation of behavioral economics—they are *predictably* intelligent and *predictably* stupid, *predictably* altruistic and *predictably* selfish. Their achievements and their failures follow certain patterns, which are specific to humans. Uncovering the logic behind these patterns can enable us to design better policies, policies that account for the built-in constraints of human nature (shortsightedness, greed, cognitive biases), while using its core features (generosity, endurance, natural social expertise) as levers to achieve goals that cannot be achieved using standard approaches.

BEYOND THE CONTRADICTIONS OF HUMAN BEHAVIOR: EVOLUTIONARY CHALLENGES AND PSYCHOLOGICAL MECHANISMS

This chapter is based on the idea that the logic of human behavior lies in the psychological mechanisms that produce it (Cosmides & Tooby, 1997; Pinker, 1997).

In short, by understanding the mechanisms that constitute our nature and why they were selected by evolution, we will be able to make sense of the apparent inconsistencies of human behavior.

This approach differs markedly from the classical economic approach, which is based on a highly idealized view of human behavior rather than on the more realistic portrait painted by behavioral economists. But this psychological and evolutionary approach *also* differs importantly from the standard approach in behavioral economics. While behavioral economics aims to document the ways in which the behavior of *Homo sapiens* departs from that of *Homo economicus*, the aim of psychological and evolutionary approaches is to understand *why* modern humans differ from "economic man": why they are both nicer and dumber than classical economics would have us believe, and more fundamentally, why sometimes they are kind and sometimes petty, sometimes clever and sometimes stupid.

For evolutionary psychologists, humans are neither smart nor dumb. Instead, they are adapted to certain situations that posed recurrent challenges in the environment they evolved in (known in technical terms as the "environment of evolutionary adaptedness"—and which, importantly, differs from one psychological mechanism to the next). From this point of view, people's failure to behave "efficiently" may not be due to intrinsically weak faculties, but rather to mismatches between the situations their brain has evolved to deal with and the specific situations that they actually find themselves in today. Put in another situation that more closely resembles the problems their ancestors solved, they may prove extremely capable indeed.[1]

FROM *HOMO ECONOMICUS* TO *HOMO SAPIENS*: THEORETICAL AND PRACTICAL IMPLICATIONS

Comparing two visions of humans, *homo economicus* and *homo sapiens*, may seem like a rather theoretical exercise. But throughout this chapter, we will see that such theoretical differences can have important practical consequences (see Figure 49.1). For instance, while the evolutionary and psychological approach agrees with the behavioral approach that humans are "dumber" than they are assumed to be in the classical model, in the evolutionary approach they are not understood to be dumber *in general*. Instead, humans are assumed to have evolved specific mechanisms to deal with the challenges that they faced in their environment. True, they sometimes seem unwise, but this is not because their capacities are intrinsically weak. It is because their brain is wired to solve certain types of problems—interacting in a small-scale society, choosing the most caloric food, or saving for the future without the help of the state or financial markets—but not all the problems that people typically face in a modern industrialized society, such as saving for retirement, understanding medical statistics, or refraining from eating too much fatty food.

From an evolutionary perspective, each problem is different and requires different solutions. Building a supercomputer that can solve any kind of problem would be enormously costly, and probably much less efficient. It is better to build lots of small devices specialized for specific tasks (eating, mating, detecting dangers, etc.). The downside of such a strategy is that sometimes, particularly when the environment changes quickly, these devices become less adapted to the challenges facing

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[1] Note that adaptations are selected because they solve adaptive problems, *on average*, better than competing designs extant at the time. There are lots of cases in which properly functioning adaptations fail, even if situations closely match those in which they evolved.

Type of Approach	**Object of Study**	**View of Individuals**	**Usual Problems for Policies**
Classical Approach	Homo economicus	Humans are selfish and rational.	Market failure Institutional failure
Behavioral Approach	Human behavior	Humans are “nicer and dumber.”	Limited rationality Weakness of will
Evolutionary Approach	Psychological mechanisms selected by evolutionary pressures	Humans are nicer and dumber, *depending of the evolutionary relevance of the situation*.	Gap between the environment of evolutionary adaptedness (EEA) and the current situation

Figure 49.1 Theoretical Differences and Their Consequences

individuals. The job of an evolutionary and psychological perspective is precisely to help us better understand these situations.

So why we are so good at remembering faces and so bad at remembering credit card codes? Is it because we are irrational? Is it because our brain is suboptimal? More likely, it is because our brain was designed by evolution to deal with particular challenges. We are sometimes very smart—when a task is similar to one that our ancestors faced, like the challenge of recognizing a friend—and sometimes very dumb, when the task does not correspond to such an evolutionary challenge, like reading a text. The evolutionary psychological approach allows us to understand what cognitive constraints need to be taken into account when choosing a policy in a given context: The further away its goal is from the challenges that evolution adapted humans to facing, the harder it will be to implement.

Having brains specialized in performing specific tasks is not just an unfortunate constraint, however. It also means that we can use our very well-designed adaptations to develop new “tricks.” For instance, although learning how to read is difficult, painful, and slow, learning how to use smileys only takes a few seconds, because smileys tap into our face processing skills. In contrast to letters, we can use and remember dozens of smileys very quickly and effortlessly. More generally, marketing research has shown that using images rather words is a more efficient communication strategy, because faces, objects, and colors are more attractive and natural to humans than written words. Human nature can be both a constraint *and* a lever.

WHY SOMETIMES GENEROUS AND SOMETIMES GREEDY?

One puzzling aspect of human nature is how variable the tendency to cooperate seems to be. On one hand, humans appear to be far more generous than other animals. On the other hand, they often seem to be motivated only by selfishness. This creates important problems for policy design, because these contrasting aspects of human nature seemingly entail opposite policies. If people are greedy, then ensuring cooperation and protecting public goods always require very costly enforcement mechanisms. But if people are very generous, policies need to focus on inspiring generosity rather than on monitoring treacherous behavior.

How can we make sense of the apparent inconsistency of human cooperation? Here again, the solution lies in understanding the evolutionary challenges that humans faced in their ancestral environment. During most of human history, humans lived without institutions and the rule of law (Diamond, 2012; Hoebel, 1954). There were no state, no police, and no courts. This means that cheaters could take advantage of cooperative situations. Because they could not be sent to jail or even fined, honest cooperators ran the risk of being exploited: They might pay the cost of cooperation, while their partners could take the benefits and never pay them back.

On the surface, these conditions seem very detrimental to cooperation. If people can cheat without facing punishment, their best strategy should be to defect as often as possible, as in the famous Prisoner's Dilemma. And this is indeed what classical economic models predict. Fortunately, humans lived in a more complex environment than the prisoners of the dilemma. They could choose their partners. If someone cheated, they could always walk away and choose someone better to cooperate with (Aktipis, 2004; Baumard, 2010; Kaplan & Gurven, 2005).[2]

When partner choice is possible, being good becomes advantageous: By cooperating, you send others a signal that you are a good cooperator, and you attract good partners. The possibility of choosing partners and the consequent competition among individuals to be chosen as a partner by others made it possible for cooperation to emerge (Roberts, 1998; Baumard, André, & Sperber, 2013). Cheaters were not punished by external institutions, but ultimately they were punished nevertheless, because in time fewer and fewer people would cooperate with them.

This evolutionary approach explains the apparent inconsistency of human cooperation. In reality, people are not inconsistent cooperators—they are *conditional* cooperators (Trivers, 1971). Their strategy is the following:

- If others cooperate, they cooperate (otherwise they run the risk of being seen as a cheater).
- If others do not cooperate, they do not cooperate (otherwise they run the risk of being exploited by cheaters).

This conclusion has important consequences for policy design. It means that others' behavior is crucial: People are ready to abide by a social norm if they believe that others do the same. By contrast, if they think that they are the only ones who are complying with the norm, they are likely to stop respecting it. Similarly, this conclusion entails that trust is paramount: People are willing to cooperate a lot if they think that others are also honest cooperators. On the other hand, if they think that others are dishonest or lazy, they might stop contributing to the common good. A third consequence is that reputation can be a strong incentive in motivating people to cooperate. Finally, we will see that the evolutionary approach explains why fairness is so important to people and why, as a large number of empirical studies have shown, fairness is a prerequisite for any public policy.

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[2] Another possibility was for people to rely on kin, friends, and coalition to resolve conflict and deter defection.

SOCIAL NORMS MATTER

Two experiments illustrate the importance of the behavior of others in promoting or hindering cooperation. In the first, scientists compared two ways of asking clients to reuse their towels in a hotel. In half of the rooms, they left a card saying:

HELP SAVE THE ENVIRONMENT

You can show your respect for nature and
help save the environment by reusing
your towels during your stay.

In the other half the card said:

JOIN YOUR FELLOW GUESTS IN
HELPING TO SAVE THE ENVIRONMENT

Almost 75% of guests who are asked to participate
in our new resource savings program do help by
using their towels more than once. You can join your
fellow guests in this program to help save the
environment by reusing your towels during your stay.

Results showed that the second card increased the number of clients who reused their towels by 25% (Goldstein, Cialdini, & Griskevicius, 2008).

The second experiment studied the impact of messages stuck to the doors of a middle-class neighborhood in San Marcos, California. These messages all asked people to use fans rather than air conditioning, but various reasons were given: One group was told that using fans would allow them to save $54 per month in electricity, another was told that the change would prevent the release of more than 100 kilos of greenhouse gas, another read that this was the most socially responsible option, and a final group was told that 77% of their neighbors were using fans rather than air conditioning, and that therefore this practice was the "choice of your community." The reading of electricity meters showed that the first three conditions had very little or no impact on people's behavior. The last one, however, led to a 10% decrease in electricity consumption (Nolan, Schultz, Cialdini, Goldstein, & Griskevicius, 2008). In other words, people are happy to save the environment if they think others are doing it as well!

These results have obvious implications for policy design. Take the efforts of the U.K. government's Behavioural Insights Team (BIT), which is testing the efficiency of different messages in motivating people to pay their taxes. To do so, the BIT sent letters to 140,000 taxpayers. Residents received either a control letter (which contained no information about the behavior of others) or one of a number of different messages containing information about others' behaviors.

All of the social norm letters contained the statement that "9 out of 10 people in Britain pay their tax on time," but some also mentioned the fact that most people in the recipient's local area, or postcode, had already paid.

The results revealed a 15 percentage point increase of tax payment relative to the control letters (see Figure 49.2). Moreover, the more local the information was, the bigger its impact on taxpayers. Overall, the U.K. tax authority estimated that this

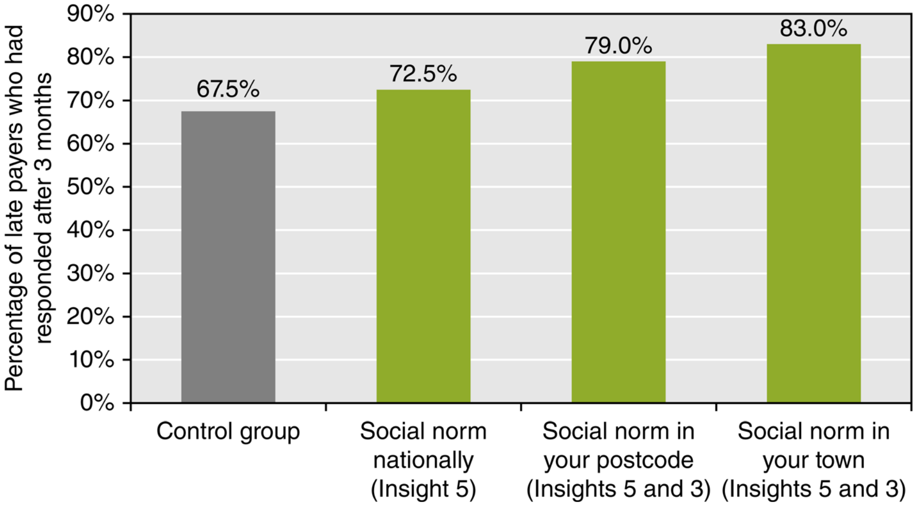

Figure 49.2 Percentage of Late Payers Who Had Responded After 3 Months

effect, if the same procedure were rolled out and repeated across the country, could lead to the payment of about £160 million in tax debts to the Exchequer over the 6-week period of the trial (Behavioural Insight Team, 2012). As this example shows, understanding the conditional logic of human cooperation can be a great lever in improving fiscal policy.

TRUST MATTERS

The conditional logic of cooperation means that trust is paramount in social interactions. In the same way that people do not want to be seen as cheaters (and thus cooperate if they think others are cooperating), they do not want to be cheated on (and thus are less likely to cooperate if they don't believe that others are doing so). In line with this idea, empirical data show that trust has an important impact on both economic development and generosity (Putnam, 2000; Uslaner, 2002). Economic exchanges are more difficult and riskier when people do not trust each other, and as a result low-trust countries tend to have lower GDP (Fukuyama, 1995). Similarly, it makes less sense to help your neighbors if you believe that they are not likely to reciprocate, and as a result, people help others less in low-trust countries (Willinger, Keser, Lohmann, & Usunier, 2003).

Trust not only affects economic exchanges and informal interactions, it also greatly influences public policies (Algan & Cahuc, 2006). Indeed, any kind of policy is likely to be sensitive to free riding. For example, many benefits are conditional on behaviors that are not easily observable, such as living together as couples, having income other than unemployment benefits, or suffering from some illness. As marital status, black market work, and health are not easy for public bureaucracies to observe, cheating can be relatively easy, and policies can only work if people refrain from doing it (Bjørnskov & Svendsen, 2012). Consequently, because they are conditional cooperators, people are likely to vote for welfare policies only if they think that others are going to respect the law.

In line with this idea, it has been observed that levels of trust largely explain differences of opinion on the welfare state in different countries. For instance, the United States and Europe differ greatly in the level of social benefits offered through the state. This divergence is often thought to be related to cultural differences in attitudes on the role of the state. Further analysis, however, reveals that Americans think that the welfare state has an important role to play. Seventy-one percent of Americans think that it is either an "essential" or an "important" responsibility of government to ensure that everyone who wants a job has one, and 78% of Americans think that providing good medical care is an "essential" or "important" government responsibility, while 81% think the government should provide adequate housing (Alesina & Glaeser, 2004).

The real cultural difference occurs not at the moral level ("Should the government help the people?") but at the level of trust. Indeed, Americans, just like Europeans (and humans everywhere), are conditional cooperators. They agree to help others, but only if others are good cooperators. In a modern state, this means that they agree to help others only if others work hard to get a job and contribute to the common good. However, Americans, in contrast to Europeans, have a very negative view of the poor. Indeed, while 60% of Europeans believe that the poor are trapped in poverty, only 29% of Americans agree with this idea. Similarly, 54% of Europeans think that luck determines income, compared to 30% of Americans. And while only 26% of Europeans think that the poor are lazy, 60% of Americans think so. In other words, both Americans and Europeans are happy to see the government help the poor if they believe that the poor deserve that help. However, Americans are much less likely than Europeans to believe that they do.

Statistical analyses suggest that this lack of trust has an important impact on the ability of the state to fund welfare programs to alleviate poverty. Indeed, both among U.S. states and European countries, the belief that luck determines income correlates with the level of social welfare spending. This contrast is all the more striking given that in reality, the level of social mobility is very similar on the two sides of the Atlantic (and if anything, mobility is slightly higher in Europe than in the United States). In other words, there is not so much differences between the American poor and the European poor. The poor in the United States are no lazier than those in Europe. What is detrimental to the establishment of public policies in the United States is thus not a general opposition to government intervention, but the cultural belief that others (and especially the poor and members of minorities) cannot be trusted. In the end, this state of mistrust prevents the investment of trillions in public policies and the development of effective poverty reduction policies.

In summary, trust is a central element for any policy. Because humans are conditional cooperators, they will be reluctant to cooperate, contribute to the public good, or help others if they think that others are not similarly well-intentioned.

Reputation Matters

Another consequence of the human propensity for conditional cooperation is that reputation is very important. In an environment where there are no institutions, reputation is an important guarantee that your partner is going to cooperate with you. If someone cheats, they lose their reputation as a good partner and thereby greatly decrease their chances of finding good partners in their turn. This explains

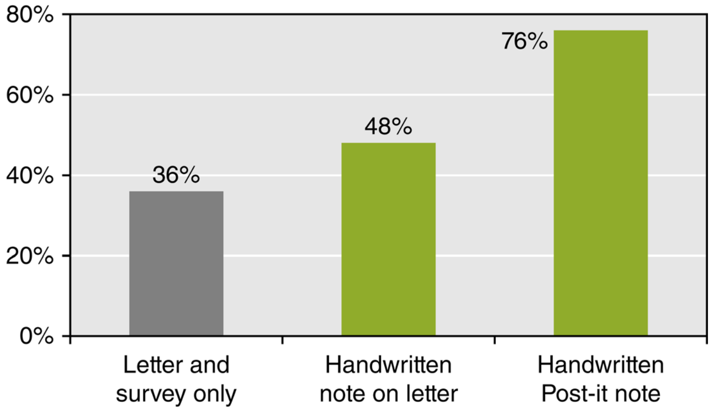

Figure 49.3 Response Rate to Survey When Testing a Handwritten Message

why people spend so much time gossiping, telling stories and exchanging strategic information about others. Reputation is one of the most important resources that an individual has in life. A good reputation can make a career, and a bad reputation can end it.

Public policies can easily make use of people's desire to protect their reputation. For instance, psychologists have observed that people are less likely to respond to a letter sent by a company than by a named individual working in the very same company. A U.S. study tested the impact of Post-it notes and handwriting on people's likelihood of completing a survey (Garner, 2005). When the survey was accompanied by a handwritten Post-it note requesting completion, three quarters of recipients completed it, compared with half when the handwritten message was directly on the cover page, and just over a third of those who received the survey and cover page with no handwriting. In addition, those who responded to the handwritten Post-it note returned the survey more promptly and gave more detailed answers. When the experimenter added his initials and a "Thank you," response rates increased even further (see Figure 49.3).

Getting people to commit is another way to increase cooperation. When people sign a document indicating that they will do something, they put their reputation more clearly on the line, because it is harder to plead ignorance in this case (Cialdini, 1993). In line with this idea, psychologists have found that that moving a signature box from the end of a form to the beginning can help promote more honest responses. Here, again, a psychological and evolutionary approach can help to make sense of apparently irrational behaviors. Why would adding a Post-it or moving a signature to the top of a letter increase cooperation? From a standard economic point of view, nothing has changed: The individual is still interacting with a large institution, and the incentives are the same (e.g., fees for late responses). But from a psychological and evolutionary perspective, paying attention to the person who sent the letter makes sense. Humans evolved in an environment where personal relationships were crucial for survival. They are equipped with a range of psychological mechanisms aiming at dealing with questions of reputation. Thus, they treat everything that puts their reputation at stake very seriously (Barclay, Chapter 33, this volume). Failing to consider social signals could compromise their reputation and the associated social benefits.

Humans are wired to pay attention to eyes, because the gaze can carry a great deal of relevant information: what others want, what they think, and also whether they are watching you. In a famous experiment, Gregory Bateson and his colleagues showed that this works in mostly automatical and unconscious fashion (Bateson, Nettle, & Roberts, 2006). In their experiment, they measured the amount of money that people put in a box to pay for milk at an unattended coffee machine. Every week, they alternated the image displayed on the wall above the box: either a pair of eyes or some flowers. They found that people put more money in the box when there was a pair of eyes rather than a picture of flowers on the wall above it. This is totally consistent with both people's motivation to project a good image of themselves and with their strong sensitivity to faces, and eyes in particular. The eyes on the wall activate mechanisms whose aim is to manage reputation. When people are alone in the room, parts of their brain (the mechanisms dedicated to reputation management) "believe" that they are actually being observed and that their reputation is at stake (see also Ernest-Jones, Nettle, & Bateson, 2011; Haley & Fessler, 2005).

WHY ARE PEOPLE SOMETIMES PATIENT AND SOMETIMES IMPATIENT?

In standard economic models, the aim of rationality is to maximize the fulfillment of preferences. The preferences themselves remain a given: They cannot be rational or irrational. But many human behaviors seem to reveal inconsistencies between their preferences: People want to enjoy ice cream, but do not want to gain weight; they want to buy fancy clothes, but also to save for their retirement; they would like to have a long life, but they smoke, drink, and refrain from exercise.

How can we make sense of these behaviors? Many economists have argued that humans just suffer from some sort of weakness of will. However, this idea seems to conflict with the many situations in which humans display extraordinary self-discipline, such as in courtship, parenting, or athletic training. Why is it that people are sometimes able to carry out long-term projects despite their short-term costs, while other times they fail completely?

Here again, an evolutionary perspective can make sense of an apparently contradictory pattern. Indeed, from an evolutionary perspective, not all goals are equally relevant (Cosmides & Tooby, 2013). Some goals, like raising a child, seeking social status, or eating sugary food are evolutionarily relevant (earlier humans with these goals had children who thrived, they had higher status and thus access to more resources, and they ate food that contained more energy). This means that, on average, individuals endowed with these "tastes" survived better over the generations than those who weren't.

By contrast, other goals, like saving for retirement or paying the bills, are almost totally irrelevant to the situations that faced our ancestors, and are experienced as either painful or boring. The evolutionary reason for this is obvious. For most of their history, humans lived in small groups of hunter-gatherers. In these small societies, there were no institutions, no market, no social security, and so on. The best way to save resources for the future was thus not to put these resources in a bank account or even to stockpile them (most resources were perishable), but rather to build a strong social network of friends and allies ready to extend help in case of illness, danger, or scarcity (Kaplan, Hooper, & Gurven, 2009). As Steven Pinker says:

> How can I store extra food in the fat weeks and draw on it in the lean weeks? Refrigeration is not an option. I could gorge on it now and store it as a bubbler, but that works only up to a point; I can't eat enough in a day to avoid hunger for a month. But I can store in the bodies and mind of other people, in the form of a memory of my generosity they feel obliged to repay when fortunes are reverse. (Pinker, 1997, p. 555)

In line with this idea, people spend an enormous amount of time seeking friends, cultivating their friendships, and exchanging gossip about their friends. We experience these things as highly rewarding because over the generations, humans who liked having friends fared better than others. By contrast, despite their huge impact on people's lives, many aspects of modern life (saving for retirement, paying the bills, receiving medical treatment) are felt as a burden and are often forgotten or neglected (Burnham & Phelan, 2012).

The evolutionary and psychological approach allows us to understand when humans are able to carry a long-term project through—when it is evolutionarily relevant and they are thus equipped with adequate motivation—and when they fail—when it is not evolutionarily relevant and people therefore tend to lack motivation. At first sight, this analysis seems like bad news. It means that the goals of some public policies are going to be enormously difficult to achieve, and people will clearly need a nudge. Nevertheless, this aspect of human psychology needs to be taken into account. In recent years, many government agencies have started using new technologies to distribute such nudges, for instance by sending text messages to people on their cell phones to remind them to pay their bills (Datta & Mullainathan, 2012). Indeed, while people rarely need to be reminded that they have a date with an attractive partner or that they need to pick up their kids (evolutionarily relevant goals), they definitely need reminders for most of their administrative duties (evolutionarily irrelevant goal).

Similarly, because people lack motivation to fill in tax forms, agencies have started prepopulating all the fields to alleviate the burden. A U.S. study on the Free Application for Federal Student Aid found that prepopulating the form with information already held by the system and streamlining the process involved in completing the form significantly increased submission rates and college entry (Bettinger, Long, Oreopoulos, & Sanbonmatsu, 2012). This is result is all the more interesting given that in a sense, students clearly have an interest in completing the process. Yet because completing a form is psychologically irrelevant to the situations that shaped human nature, they still need some help.

To sum up, the evolutionary perspective may help to understand the limits of traditional public policies and the power of choice architecture (setting the default choices right in an administrative scheme). Traditional public policies assume that people are rational and that the only reason they take bad decisions is that they are ill-informed or not incentivized enough. Indeed, why would one prefer to have less money than more money? But the reality may be pretty different, because human have not evolved to maximize their saving account or their electricity bills. In consequence, they may not be interested at all in thinking about their retirement scheme or in paying their bill on time, which does not make any sense form a standard rational choice perspective. Understanding human cognition, and the context in which it evolves, may help designing policies that consider that human behavior is not irrational, but just ill adapted to modern societies, and that nudging people by changing the default choice in their retirement scheme can have way more impact than incentivizing their decisions or providing more information. For instance, a recent study on the Danish retirement system has shown that giving people money has less impact on their decision than just changing the default option (Chetty, Friedman, Leth-Petersen, Nielsen, & Olsen, 2013). In other words, because people do not care very much about their retirement plan, money cannot work as a good tool. Better use the power of nudge!

LIVING, FAST AND SLOW

From an evolutionary perspective, humans do not suffer from a general weakness of will or lack of patience. They are sometimes very patient, and sometimes totally impatient. The explanation for this apparent inconsistency lies in the evolutionary history of the human species and the psychological mechanisms that were selected over the course of this history. Thus, humans are typically very strong when it comes to investing in their social network, finding a mate, or raising a child, but much weaker when it comes to saving for retirement, refraining from eating fat, or exercising to burn extra calories.

Understanding the evolutionary and psychological basis of human preferences is crucial. If we just stick to general behavioral explanations without examining the specific situations that are associated with different kinds of behavior, we may draw mistaken conclusions. Witnessing people's weak willpower in their daily lives, for example, we might think that humans cannot be trusted when it comes to long-term projects. But when we use evolutionary thinking to sharpen our focus on the conditions on this apparent weakness of will—seeing how it is present in some domains of human life, but absent in others—we find that only evolution can explain the underlying logic of this variability.

The evolutionary perspective also allows us to explain another apparent paradox: Why is it that people from different social backgrounds have different preferences? From an economic perspective, it might seem that people with a lower socioeconomic status should be particularly cautious about saving, they should invest a lot in schooling to have better opportunities, and in general they should take fewer risks. But in reality, people in less advantaged positions tend to save less, invest less in education, have children sooner, and take more risks (Nettle, 2010a).

This paradox is not specific to humans. All organisms face fundamental trade-offs when deciding how to allocate limited resources. For example, all multicellular organisms need to choose between reproducing now or later, between investing in a few children or having a large family, or between taking small risks (and obtaining small amounts of resources) and taking large risks (and getting either large amounts of resources, or nothing, or worse).

A part of evolutionary biology known as "life history theory" addresses how organisms allocate limited resources to maximize fitness (Roff, 2002; Stearns, 1992). Life history theory provides a framework for understanding people's patterns of decisions about trade-offs in very diverse areas, from investments and health to education and sexual behavior (Ellis, Figueredo, Brumbach, & Schlomer, 2009; Griskevicius et al., 2013; Nettle, 2010b). In particular, it describes these strategies along a slow-to-fast continuum (Chisholm et al., 1993; Griskevicius et al., 2013; Nettle,

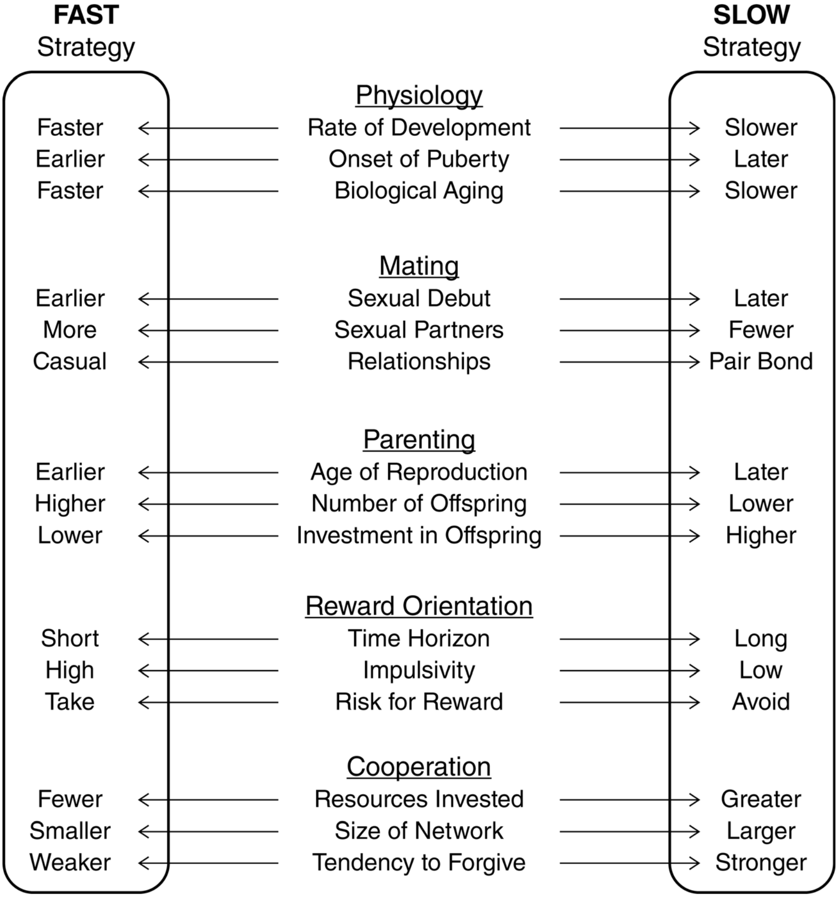

Figure 49.4 Illustration of Correlates of Fast and Slow Life-History Strategy

2010b) (see Figure 49.4). At the physiological level, faster and slower strategies are respectively associated with earlier and later physiological development and sexual maturity. At the psychological level, fast strategies are associated with short-term opportunism and taking immediate benefits with little regard for long-term consequences, whereas slow strategies are associated with long-term planning and delaying gratification to increase future payoffs.

Empirical studies show that, contrary to what might have been predicted from a standard economic point of view, harsher and poorer environments lead people to enact faster strategies, speeding up the timing of their physiological development and sexual maturation. This is because harsher environments are inherently more risky. As a result, organisms cannot expect to live as long as in a safer and richer environment. To increase their fitness, it is better for them to do less long-term investing, because their prospects of getting to reap the benefits of such investments are relatively poor. Similarly, they are better off reproducing as soon as possible, because the more they wait, the more they run the risk of dying or being injured or too poor to reproduce. Because harsher environments are less predictable, the best strategy is to take more risks and have more and earlier offspring. When the environment is more predictable, on the other hand, slower strategies associated with delaying reproduction and investing in future outcomes become adaptive. In line with life history theory, cross-cultural studies show that in environments characterized by higher mortality, people tend to have their first child at an earlier age. They also mature earlier, take more risks, and are more impulsive (Griskevicius et al., 2013; Nettle, 2010a).

From an evolutionary perspective, the faster strategies adopted by people living in harsh conditions are not irrational. Quite the contrary: In these contexts, they make perfect sense. The function of these behavioral strategies is to increase the chances of the organism to successfully reproduce itself despite a higher risk of death, injury, or accident. This does not mean, of course, that these mechanisms are always adaptive. Again, they evolved in a specific environment, in which there were no higher education, job markets, bank accounts, or policemen. It might be that today, they lead people to overreact to harsh environments in the same way that we overreact to the abundance of fat and sugar. If this is true, poor people may take too many risks, invest inadequately, and reproduce earlier than serves their interests or those of their children. The important point to understand, though, is that their decisions are not due to cognitive limitations or weakness of will. Instead they result from strong, context-sensitive feelings, which reflect evolutionary psychological adaptations aimed at allowing people to make the best trade-offs in a given type of environment.

From a policy perspective, this distinction is crucial. It means that people in lower socioeconomic strata might not need more *information* (about the advantages of saving or going to the health center, say). Increasing people's time horizon, for instance, may have drastic and long-lasting effects on people's preferences, without any need for change in their explicit beliefs.

IMPLICATIONS FOR THE GOALS OF DEVELOPMENT POLICIES

Evolutionary psychology not only explains why some policies are aligned with human psychology and others are not—it also gives us insights into what public policies should aim for. In other words, it is relevant both to the *means* by which development policies are pursued and their *goals*. Indeed, as we have seen throughout this chapter, human psychology—its cognitive systems, its heuristics, its reward systems—has been designed to fulfill certain goals, such as taking in energy-rich foods, avoiding pathogens, attaining social status, having friends and mates, and so on. That is why humans universally like sugar and fat; enjoy sex, parenting, and friendship; and seek social status and material resources.

This evolutionary perspective has profound implications for development policy. Policy makers often accept classical economic models, which hold that increasing income is the most efficient way to promote well-being. This "blank slate" approach is often preferred because it is supposed to be ethically neutral: Since there are many ways to be happy, this line of thinking goes, people should be left to choose which best fits their preferences. However, "maximum GDP" is not in fact a neutral measure. It assumes that money is always to be preferred to other kinds of goods, but this assumption does not hold from an evolutionary perspective. First, money—and more generally, cash economy—is a recent invention, and only appears a few thousand years ago. Second, although money can help us to achieve one kind of fitness-relevant goals, from an evolutionary perspective, many other goals such as children, friends, autonomy, dignity, and security also matter. Yet, most of the time, money cannot buy friendship, children, or security, and often maximizing GDP is actually detrimental to achieving these goals, as when increasing working hours and focusing on one's career translates into less time with friends and family and more stress.

Although the limits of maximum-GDP policy may seem more relevant in developed societies than for poorer ones, research on newly developed societies such as China suggest that development policies should take these effects into account in those cases as well. In the past 20 years, China has seen its GDP increase massively. But this increase has been associated with population movements, family breakdown, high unemployment, lack of solidarity, and higher inequality. In line with theoretical and empirical studies in psychology, this increase in GDP has been accompanied by a decrease in the reported well-being of most of the population, although it has risen somewhat at the upper end of the socioeconomic scale.

These empirical studies therefore raise a very important question: What is the point of developing the economy if all the benefits of a higher income come at the cost of higher levels of job-related stress, a shorter amount of time spent with family and friends, and decreases in self-esteem due to growing inequality?

In this last section, I review some parameters that are often undervalued or disregarded in development policy, and explain why, from an evolutionary perspective, they are crucial for well-being. Basically, what makes us happy is being in conditions that allow us to fulfill the goals that were important in environments of evolutionary adaptedness.

ABSOLUTE AND RELATIVE INCOME

A priori, maximizing GDP seems to be the most reasonable solution. Since, as is well known, money can buy everything, people will be better off with a higher GDP, whatever it is that they want. This idea, however, neglects the fact that humans are a special species. They live in groups, and their success in life depends on their position in their society. During most of human history (including the most egalitarian societies, such as those of hunter-gatherers, both ancient and modern), higher status has translated into more resources, more friends, more mates, more children, better health, and so on. In other words, fitness is highly correlated with status. This is the reason why people care a lot about their status and how well they fare in their society. It is a signal of their success as well as an end in itself, because it opens the way to a better life.

Because status is a good in itself, humans have evolved psychological mechanisms to evaluate their status and make it a reward in itself. For instance, brain imaging studies have demonstrated that social comparison activates brain areas associated with rewards, like the striatum. Doing better than others is intrinsically rewarding for humans. Conversely, doing worse than others is intrinsically painful.

Humans are so obsessed by social comparison that it is difficult to overestimate the importance of social status. A range of studies suggest that above a certain level of affluence, people care more about social comparison than absolute level of resources (Frank, 1985, 2007). In a famous experiment (Solnick & Hemenway, 1998), participants were given the choice to live in either situation A or situation B.

Situation A: Your current yearly income is $50,000; others earn $25,000.

Situation B: Your current yearly income is $100,000; others earn $200,000.

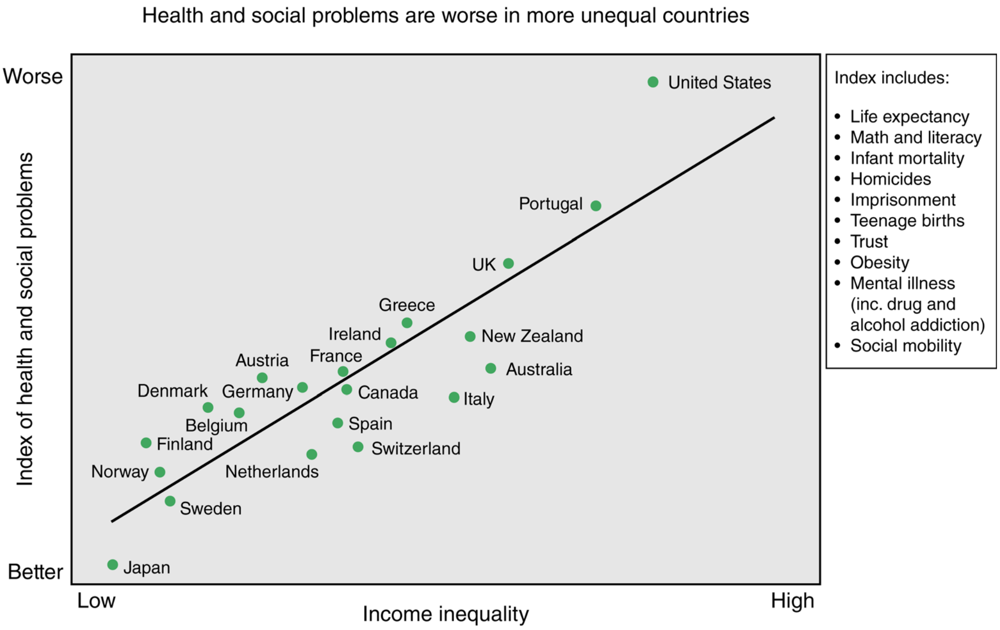

Figure 49.5 The effect of inequality (bottom) on health and social problems in developed countries. Income inequality is measured by the ratio of incomes among the richest 20% to those of the poorest 20% in each country.

Income inequality is measured by the ratio of incomes among the richest 20% to those of the poorest 20% in each country. *Source:* From Wilkinson and Pickett, 2008.

Participants were told that the prices were what they were currently and that therefore the purchasing power of money was the same in situations A and B. Despite the participants' 100% increase in income between society A and society B, many said they would prefer to live in society A because in this scenario they fare better than others.

The importance of social status has fundamental consequences for the organization of society. It means that, everything else being equal, it is better to live in a more equal society (Frank, 2007; Wilkinson & Pickett, 2008). Indeed, on average, because social status is a zero-sum game, the more unequal the society is, the less happy people will be. Note that this holds even for the richer part of the society, because people compare themselves to those who are closer to them—and the more unequal the society, the greater the distance between people, even among those with the highest incomes.

In line with this idea, epidemiological studies show that inequality has adverse effects on humans in a range of domains, such as trust, mental illness, life expectancy, infant mortality, obesity, educational performance, teenage motherhood, and homicide (see Figure 49.5). What is striking is that this effect cannot be explained by absolute income (through a link between a relatively low income and a relatively high level of inequality). Among developed countries, absolute income does not seem to play an important role in preventing social and health problems. The richest countries, such as the United States, are not specially immunized against homicide, teen pregnancy, or obesity. And the poorest, like Greece, New Zealand, and Spain, are not especially more prone to these problems. The main predictor of rates of obesity, teen pregnancy, or homicide is the level of inequality in a society.

It is important to note that a similar effect can be observed among U.S. states (Wilkinson & Pickett, 2008) Again, absolute income does not play an important role. By contrast, the more unequal the state, the higher the rates of obesity, homicide, and teen pregnancy.

From an evolutionary and psychological perspective, the link between inequality and health and social problems is straightforward. Indeed, for humans as well as for most nonhuman primates, social status is crucial for survival. Humans have thus evolved specific mechanisms to deal with the issue of status. The trade-off here is the same as between slow and fast strategies. Individuals choose between a slow strategy, with long-term investments and low-risk choices, and a fast strategy, with short-term investments and high-risk choices (Daly & Wilson, 2001). When status is low, individuals face the risk of being eliminated from the race (not having enough resources for their children, not finding a mate, etc.). In this situation, it is better to switch to a risky strategy.

In real life, this translates into specific evolved behaviors. For males, it often means choosing violence to protect one's status and gain respect from others. For females, it means reproducing earlier and having more children (Daly & Wilson, 2001; Nettle, 2010a, 2010b). In line with this evolutionary logic, epidemiological studies have shown that violence occurs mostly among young males from lower SES, those in the greatest need of status and respect, and that violence is strongly related to inequality (Daly & Wilson, 2001). Homicide rates, for instance, are higher in the most unequal US states, in the most unequal Canadian provinces as well as in the most unequal OECD countries. Similarly, teen pregnancy strongly correlates with inequality both among U.S. states and OECD countries.

These correlations do not necessarily make sense from a standard economic model. Indeed, from a purely rational standpoint, it would seem sensible for someone with a low status in a modern society to work hard, invest in education, and postpone reproduction. It is only from an evolutionary perspective that these effects make sense. In environments of evolutionary adaptedness, where violence was higher and education less important, violence and teen pregnancy were indeed successful strategies for low-status individuals. They increased their chances of dying young or having no surviving children, but on average, they also increased their chances of climbing the social ladder.

Evolutionary theory also explains other effects of inequality, such as obesity. Although it is natural to us to find eating, and especially eating highly caloric food such as ice cream or pizza, comforting, this behavior requires an explanation. Why is it that stress makes us eat more? Again, the response lies in the particular environment in which our tastes evolved. As discussed above, for most of human history, resources were relatively scarce. Since stress signals that things are not going well, the organism makes food a higher priority, because in the past, when things went badly, it usually meant that food was going to become even scarcer (Nesse & Young, 2000). Our preferences change with stress, but so does our physiology. For instance, it has been shown that stress makes the organism more likely to transform calories into abdominal fat, a good indication that the body is preparing itself for harder times.

In line with this idea, rates of obesity in developed countries are highly correlated with inequality (Wilkinson & Pickett, 2008). In developed countries, where food and calories are abundant and cheap, eating large amounts to stockpile calories no longer makes sense. Yet, because it made sense in the evolutionary past, people still eat to cope with stress. As a result, countries where stress is higher because of high inequality tend to have a higher rate of obesity as well.

Eating fattier foods and stocking calories in the abdomen is part of a more general stress system regulated by hormones like cortisol, which aim at elevating the level of resources available to the organism (like the fear system) at the cost of its less immediate needs. For instance, the activation of the immune defense system decreases, which explains why stressed people are more likely to get sick. Thus, in the short term, stress can render the organism more efficient or more alert or give it more endurance, because it makes more resources available, but in the long term, stress is highly detrimental to the organism, which explains why inequality and stress are associated to myriad health problems, such as atherosclerosis and cardiovascular diseases (Nesse & Young, 2000).

To sum up, the evolutionary and psychological approach allows us to understand why inequality is so harmful to humans. Because humans are a social species, they care a great deal about status, and being in an unequal society makes them both less happy and more prone to develop problematic behaviors. Again, this result cannot be derived from a traditional economic perspective, which makes no assumptions about people's preferences, and in particular their preference for a high social status. This result is fundamental for public policy. The main argument typically presented in favor of equality is based on considerations of social justice. The evolutionary and psychological approach suggests that there is another, more neutral argument in favor of equality, which is that most people, rich and poor, would be better off in a more equal and less stressful society.

The High Cost of GDP-Centered Policies

Social support is central for humans, and just as competition is stressful, lack of support is painful. As recently demonstrated by brain imaging (Eisenberger, Lieberman, & Williams, 2003), social exclusion activates the same neural network as physical pain. This result makes sense from an evolutionary point of view. Indeed, just as physical pain signals the presence of physical threats to the organism, so does social pain signal the existence of social threats to the organism. Being alone is very bad news for most animals because it increases the risk of getting caught by a predator and decreases the chance of finding food, but it is particularly bad for humans since we cannot survive without social cooperation and support.

In line with this idea, stress has been found to increase greatly when social support decreases (for a review, see Diener & Seligman, 2004; Layard, 2006). Men and women with more friends were found to have lower levels of mental distress than those with fewer friends. The highest rates of mental problems are found among unmarried people, single parents, and people living alone. Individuals with close social bonds suffer if they are separated for long periods of time. For example, the wives of men who work on submarines often experience increased physical illness and depression during their spouses' absences. Here, stress is a very clear indication that human psychology treats lack of social support as a threat for the survival of the individual. This, as we have seen, ultimately increases the occurrence of physical and mental disease.

These empirical results are of great importance for public policy. Indeed, they highlight that friends and family are crucial for human well-being. People cannot be happy if they lack social support. In the past 20 years, a large amount of data have shown that, indeed, very happy people are, on average, people who have more close friends and stronger family and romantic relationships (from Diener & Seligman, 2002).

Similarly, people's social relationships have an equal if not greater impact on their well-being than their economic situation. For instance, while a one-third drop in income reduces happiness by 2 points, being widowed, divorced, or separated reduces happiness by 4, 5, and 8 points, respectively (Layard, 2006).

From this perspective, decreasing the quality or quantity of social relationships in exchange for higher income levels may not be good policy. People may get better-paid jobs and be able to afford more goods and services, but this may not compensate the adverse effects of losing contact with their family and friends. Of course, this is a trade-off, but policy makers should be aware of the critical importance of social relationships. As Diener and Seligman note, for instance, "the military and corporations should relocate employees and their families only when it is absolutely essential to do so, or when an employee requests it. Automatic moves every few years leave individuals without strong community ties, and with fewer close friends in times of crisis" (Diener & Seligman, 2004, p. 20). More generally, the potential effects of forcing people to move around the country and the world for the sake of job opportunities should be considered from this perspective whenever possible. People might be better off earning much less money near their family than being expatriates, and hence stranded at a great distance from their sustaining social network.

Social support is not the only human preference that is sacrificed by exclusively GDP-centered policies. Psychological studies have also shown that security is a very important component of well-being (for a review, see Layard, 2006). Living in an unpredictable environment, not knowing whether one will be able to keep one's job, for instance, is very stressful. From a psychological perspective, it might be better to have a job that pays less but is more secure than the contrary. In the same way, autonomy is a very important component of well-being, because it is very stressful for individuals to feel that they have no control over their lives. Working in a small company or a shop might be much better for an individual's well-being, even if it is less well paid, than working in a big company where individuals have less responsibility for their success and less control over their job.

CONCLUSION

The standard economic approach to human development assumes that most problems result from institutional failures. This is sometimes the case. But many other problems result from that fact that human behavior is often at odds with the goals of development policies: People fail to save for their retirement, they keep eating in an unhealthy way despite medical campaigns, they do not trust each other and refuse to cooperate, and so on. This is why people sometimes need a nudge from public policy.

But *when* do people need a nudge? In standard behavioral approaches, people are often said to need a nudge when the problem they face is complex, when it offers poor feedback, or when the costs must be paid now but the benefits will only come later (Thaler & Sunstein, 2008). But from a psychological point of view, this view doesn't stand up. Walking on two legs or learning thousands of words in the first 2 years of life is pretty complex, and the chief benefits are often quite far off. Yet, humans do it easily and effortlessly. Deciding which foods are toxic for the fetus is quite impossible, because individuals do not have the means to establish the causal link between one food and its effects—and yet women have very efficient and well-informed intuitions about which foods they should eat when pregnant. Finally, raising children costs a huge amount of resources, and the full benefit can only be enjoyed years later. Humans have no problem, however, when it comes to sacrificing their leisure time or their energy to take care of their offspring.

So when do people *really* need a nudge? The response that psychology offers is that they need to be nudged when their interests are not aligned their evolved psychology: when there is a gap between the ancestral environment and their current environment. These are the kinds of situations where people need public policies. And what is a good nudge? A good nudge is one that takes human psychology as a constraint, acknowledges its limits, and does not entertain grand expectations about human nature. But it is also a nudge that takes advantage of how human psychology works and uses its mechanisms as levers to increase the impact of public policies.

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CHAPTER 50

Evolution and Consumer Psychology

GAD SAAD

INTRODUCTION

Consumer behavior is an ideal context from which to study evolutionary principles as applied to humans (Colarelli & Dettman, 2003; Griskevicius & Kenrick, 2013; G. Miller, 2009; Saad, 2006a, 2007a, 2008a, 2011, 2013; Saad & Gill, 2000). We prefer foods that correspond to our evolved taste buds. The spaces where we live, work, or play feel more welcoming when they conform to our biophilic instinct. We purchase products that serve as sexual signals in the mating market (e.g., luxury sports cars and cosmetics for men and women, respectively). We offer gifts as means of forging, maintaining, and strengthening bonds of kinship as well as nonkin friendships and alliances. The romance novels, movie themes, song lyrics, religious narratives, and other cultural products that move us do so because they capture fundamental aspects of our universal human nature. Briefly put, to study consumer behavior is to put a magnifying lens on our evolved preferences, choices, and behaviors.

Given that consumers are biological beings whose minds and bodies have been shaped by the forces of evolution, it is perhaps surprising that the application of evolutionary psychology in consumer behavior is a very recent endeavor. A search on Google Scholar on December 25, 2013, using the conjunction of two search terms "evolutionary psychology" and "consumer behavior" for each year from 1988 through 2013 yielded the following results: 1988–1999: 22 hits; 2000–2005: 133 hits; 2006–2010: 347 hits; 2011–2013: 394 hits. A search through the *Handbook of Consumer Psychology* (Haugtvedt, Herr, & Kardes, 2008), a 1,273-page edited tome covering the key theories and topics of interest in consumer psychology, revealed that "evolutionary psychology" did not arise once. An analysis of consumer behavior textbooks offers an equally telling demonstration of the lack of evolutionary theorizing within the field. The content is usually quite standardized and includes chapters on perception, learning and memory, attitude formation and attitude change, decision making and information processing, motivation and emotions, personality, and culture. The theoretical frameworks for each of these areas of interest are largely disjointed from one another, yielding an otherwise incoherent view of consumers' minds. Furthermore, there is a (typically implicit) assumption that the human mind is composed of content-independent, domain-general computational systems (e.g., classical and operant conditioning; elaboration likelihood model; theory of reasoned action; rational choice theory).

The idea to Darwinize the field of consumer behavior came to me in fall 1990 during my first semester as a doctoral student at Cornell University when I read *Homicide* by Martin Daly and Margo Wilson. For approximately the first 10 years of my grand project, I was the sole marketing professor working at the nexus of evolutionary psychology and consumer behavior. Over the past few years, though, a growing number of marketing scholars, many of whom were trained by David M. Buss and Douglas T. Kenrick (two of the leading pioneers of evolutionary psychology), have entered this field and are amassing an impressive body of works. Notwithstanding this growing critical mass of highly talented evolutionary consumer psychologists, the great majority of marketing scholars remain reticent if not hostile to evolutionary theorizing, in part because of their allegiance to a tabula rasa view of the human mind.

Most marketing scholars construe consumer choices as largely driven by socialization. Toy preferences constitute the prototypical example of such a social constructivist viewpoint. The argument is that gender roles are arbitrarily imposed by an otherwise sexist society, the process of which starts early via parentally imposed toy preferences. Little Bob learns to roughhouse by interacting with blue trucks and military action figures while little Bernadette is taught to be demur and nurturing by playing with pink-dressed dolls. With that view in mind, some "new age" parents commit to raising their children with so-called gender-neutral toys, so as to avoid the shackles of "sexist" gender ascriptions. Several independent research streams suggest that this pervasive premise does not bode too well when held up to empirical scrutiny. For example, infants who have yet to reach the cognitive developmental stage to be socialized display the traditional sex-specific toy preferences (Alexander, Wilcox, & Woods, 2009; Jadva, Hines, & Golombok, 2010). Infant vervet and rhesus monkeys have comparable sex-specific toy preferences to those of their human counterparts (Alexander & Hines, 2002; Hassett, Siebert, & Wallen, 2008). Little girls who are affected with congenital adrenal hyperplasia, an endocrine disorder that results in the masculinization of morphological features and behavioral patterns, exhibit toy preferences that are more typical of boys as compared to little girls who do not suffer from the disorder (Berenbaum & Hines, 1992). On a related hormonal note, Lamminmäki et al. (2012) measured infants' testosterone levels (via urine samples) for the first 6 months of their lives, and correlated these with the Pre-School Activities Inventory (PSAI; measures sex-typed behavior) as well as with sex-typed toy choices (train versus baby doll). For boys, testosterone was positively correlated with PSAI scores and negatively with playing with the doll. For girls, testosterone was positively correlated with the amount of time played with the train. Similar correlations have been obtained using proxy measures of androgen exposure. For example, boys with more masculinized left-hand digit ratios (an indicator of androgen exposure in utero) engage in more masculinized play behaviors as measured by the PSAI (Hönekopp & Thierfelder, 2009). Finally, specific design features of toys have been analyzed via an evolutionary lens. Take, for example, the inborn favorable disposition toward baby features. This innate preference has been documented for several products, including car fronts (Miesler, Leder, & Herrmann, 2011) as well as teddy bears. Specifically, a majority of 6-year-old and 8-year-old children prefer teddy bears that possess baby features (Morris, Reddy, & Bunting, 1995). For a review of toy preferences from an evolutionary perspective, see Alexander (2003).

While not all consumer preferences and choices are rooted in evolutionary realities, many could be classified onto one of four key Darwinian clusters: survival, reproduction, kin selection, or reciprocal altruism (Saad, 2006a, 2007a, 2011, 2013; Saad & Gill, 2003). See Garcia and Saad (2008) and Crouch (2013) for applications of these four clusters in neuromarketing and tourism research, respectively. Ultimately, numerous consumer phenomena are rooted in one of these basal evolutionary drivers. In the remainder of this chapter, I offer examples that speak to this reality, within each of the four Darwinian clusters. I conclude with a discussion of some advantages that are reaped via an incorporation of evolutionary theorizing within the field of consumer research.

SURVIVAL

Food is central to many of the most fundamental survival challenges, and these include ensuring that one consumes the necessary minimal daily caloric requirements (food foraging) and avoiding becoming part of someone else's caloric count (predator avoidance). These basic drives manifest themselves in myriad of ways within the consumer realm. Humans have evolved gustatory preferences that speak to an ancestral environment in which caloric scarcity was a frequent reality. As such, it is not surprising that consumers exhibit a universal preference for highly caloric and tasty foods (Drewnowski, 1997; Drewnowski & Almiron-Roig, 2010). How do these preferences manifest themselves in terms of actual consumer choices? Whether one ranks the leading restaurant chains in the United States alone or expands the analysis globally, the same set of companies appear on any such list and includes McDonald's, KFC, Wendy's, Pizza Hut, and Burger King. These companies are globally successful because they offer products that are in line with our evolved gustatory preferences. The menus might be tweaked to fit culture-specific requirements (e.g., McDonald's adheres to Hindu beef restrictions in India), but the universal commonality is that the food items are highly caloric and fatty.

Marketing academics wrongly presume that evolutionary psychologists are singularly focused on identifying cross-cultural similarities (human universals). They posit that actionable marketing strategies typically seek to understand consumer heterogeneity, be it at the individual or cultural level. Of course, this is a false premise in that evolutionary theory fully recognizes that many cross-cultural differences are rooted in adaptive processes, and as such are well within the meta-framework's purview (e.g., Gangestad, Haselton, & Buss, 2006). Take cross-cultural differences in culinary practices. Why are some cuisines more meat-based while others are nearly bereft of meat? Why do some gastronomical traditions make greater use of spices, pickling, or smoking than others? How does salt consumption vary across cultural settings? Several researchers have demonstrated that culinary traditions serve as adaptations to a very real biological problem, namely, the density of pathogens within a local niche, which is correlated to the ambient temperature in that local climate (antimicrobial hypothesis). Hotter climates (due to geography and/or seasonality) are likely to contain greater food pathogens, and as such, one would expect the adoption of culinary practices (e.g., more pronounced use of spices) that quell that threat (Billing & Sherman, 1998; Ohtsubo, 2009; Sherman & Billing, 1999; Sherman & Hash, 2001). Of note, Zhu et al. (2013) demonstrated that culinary traditions across regions of China adhere to a copy-and-mutate mechanism based on geographical proximity.

Culturally and religiously sanctioned food taboos have also been explored from an evolutionary perspective. While most cultural anthropologists are satisfied at merely documenting varied food restrictions across cultures, evolutionary-minded scholars examine whether these might be rooted in biological realities. For example, Henrich and Henrich (2010) showed that Fijian food taboos serve as shields against otherwise harmful marine toxins. Saad (2011) argued along similar adaptive lines regarding the kosher prohibition against the consumption of shellfish. Other environmental contingencies could also alter one's food-related behaviors. Using a life-history perspective, Laran and Salerno (2013) exposed participants to cues of environmental harshness and found that their food choices were more likely to converge on alternatives that were perceived as being highly caloric and filling. In other words, priming people about harsh settings triggers a caloric hoarding mechanism.

There are countless other food-related items of relevance to consumer scholars that speak to evolved biological mechanisms. These include how food preferences are passed from mother to child in utero or during breastfeeding (Beauchamp & Mennella, 2009; Mennella, Jagnow, & Beauchamp, 2001); women's food cravings and aversions during gestation (cf. Sherman & Flaxman, 2001); the link between women's food-related behaviors and preferences and their menstrual cycles (Fessler, 2001; Saad & Stenstrom, 2012); the evolved penchant for food variety, even in instances when objectively speaking, the varied offerings are identical in terms of their taste or smell (e.g., manipulating the number of colors of M&M candies or the number of distinct pasta shapes; Kahn & Wansink, 2004; Rolls, Rowe, & Rolls, 1982); the positive relationship between situational hunger and food-related attitudes and purchases (Lozano, Crites, & Aikman, 1999; Nisbett & Kanouse, 1969); and the adaptive ways by which people recall the location of high-calorie food items (Allan & Allan, 2013; New, Krasnow, Truxaw, & Gaulin, 2007).

While it is clear that food is central to survival, it also plays an important role in various mating-related rituals across a wide range of species, including humans. In some instances, nuptial gifts amount to offerings of food, in which case there is a clear implicit contract: food for sex. Nowhere is this economics of sex exchange more explicit than in species that engage in sexual cannibalism (e.g., some spider and praying mantis species; Buskirk, Frohlich, & Ross, 1984). In the human context, many courtship rituals revolve around food (e.g., a first date, Valentine's dinner, wedding banquet), and couple intimacy is in part signaled by the extent to which the two individuals share food with one another (Alley, Brubaker, & Fox, 2013; L. Miller, Rozin, & Fiske, 1998). People are more jealous when they have to imagine their current romantic partners sharing a lunch or dinner date with an ex-lover as compared to imagining similar encounters not involving food (Kniffin & Wansink, 2012).

Beyond food, there are other consumer-related phenomena that map onto the survival cluster including individuals' inborn preferences for particular environments (e.g., natural landscapes; man-made spaces). Many marketing scholars have explored how commercial atmospherics (e.g., background music in a mall; ambient smell in a retail store) affect consumer outcomes, albeit these works have not been rooted within an evolutionary framework (for relevant reviews, see Krishna, 2012; Turley & Milliman, 2000). There are at least two evolutionary-based frameworks that could contribute to this literature: prospect-refuge theory (Orians & Heerwagen, 1992) and the biophilia hypothesis (Wilson, 1984). The former proposes that humans have an innate preference for natural landscapes that permit for a wide visual prospect whilst affording refuge (Falk & Balling, 2010) precisely because this protects against predators and other environmental menaces (e.g., hostile outgroup members). These instinctual spatial preferences can inform how one designs a multitude of man-made environments, including retail stores (Joye, Poels, & Willems, 2011) and interior spaces (Scott, 1993). The biophilic instinct refers to our innate desire to seek communion with nature, as evidenced by the fact that there are countless psychological, emotional, and physical benefits that are reaped by interacting with the natural world (Maller, Townsend, Pryor, Brown, & St Leger, 2006). Optimal architectural, urban, and interior designs are in part defined by the extent to which they cater to our biophilic instinct. The few studies that have applied these evolutionary principles within a consumer/business setting include the benefits of incorporating scenes of nature in green advertising (Hartmann & Apaolaza-Ibáñez, 2010), the use of trees in designing optimal business districts (Wolf, 2005), the preference for shiny items and products as an instantiation of humans' inborn need for fresh water (Meert, Pandelaere, & Patrick, 2013), and individuals' reduction of future discounting (i.e., greater willingness to delay gratification) subsequent to viewing photos of natural landscapes or strolling in a forest (van der Wal, Schade, Krabbendam, & van Vugt, 2013).

MATING

There are many ways by which mating-related issues manifest themselves within the consumer setting. First, the contents of cultural products (e.g., pornographic films, advertising) could be analyzed to highlight evolved aspects of human nature in general and human sexuality in particular (Saad, 2004, 2012). Pound (2002) conducted a content analysis of pornographic materials (films and photos) that were produced for the viewing pleasures of men, and found that polyandrous depictions were much more frequent than their polygynous counterparts. He theorized that this was driven by the excitatory visual cues associated with sperm competition. Kilgallon and Simmons (2005) obtained support for Pound's premise by having men either masturbate to pornographic photos containing polyandrous depictions (one woman with two men) or not (three women together). They found that samples stemming from the polyandrous image possessed a greater percentage of motile sperm (motility is positively correlated with fertility). The sales rank of pornographic DVDs is correlated to the frequency of polyandrous images on the DVD covers (McKibbin, Pham, & Shackelford, 2013). In addition to having a direct impact on sales, evolutionarily relevant stimuli affect an advertisement's efficacy. Vyncke (2011) examined whether the manipulation of an endorser's evolutionarily relevant features (e.g., facial symmetry, waist-to-hip ratio, or skin quality) might enhance an ad's likability. Participants were shown 80 pairs of advertisements (neutral and manipulated versions) to gauge the effects of incorporating fitness-enhancing advertising cues. Sixty-nine out of the 80 pairs of ads yielded results in line with the evolutionary predictions; 7 produced findings that were contrary to the evolutionary expectations; and 4 bore no effects. In other words, successful advertisements are precisely those that cater to our evolved preferences.

Beyond analyzing cultural products for their mating-related content, one could investigate how consumers utilize products as sexual signals, the classic example of which is conspicuous consumption. Most marketing scholars who have studied conspicuous consumption have done so without recognizing that it is a form of sexual signaling (Saad, 2007a). That said, several recent studies have situated ostentatious consumer displays within the biological realm. Using a within-subjects field experiment, Saad and Vongas (2009) examined the effects of conspicuous consumption on men's testosterone levels. Participants drove a 2006 Porsche and an old decrepit 1990 Toyota sedan both in a highly public environment (downtown Montreal) and in a less public setting (semi-deserted highway). Salivary assays were collected after each of the four driving conditions, and these were compared to baseline measures to gauge how cues of social status would alter men's testosterone levels. Driving a high-status car yielded an increase in men's T levels (in both the public and private settings), as this serves as a powerful signal to a man's social standing. Of note, viewing photos of sports cars also increase men's salivation, but only when they are primed about mating (Gal, 2012).

While the use of biological substrates in the study of conspicuous consumption is quite rare, experimental priming remains the most frequent paradigm within this area of research. Griskevicius and colleagues (2007) primed men with mating-related stimuli (e.g., photos of desirable women), and this increased their stated proclivity to engage in conspicuous consumption. Sundie and colleagues (2011) built on this work by demonstrating that conspicuous consumption is more likely to be used by men pursuing short-term mating opportunities. Furthermore, women are attracted to men who engage in such showy behaviors, but only as prospective short-term partners (and not as marriage suitors). On a related note, Janssens and colleagues (2011) demonstrated that single men who were primed with a photo of a scantily clad woman were more likely to recall status products than their counterparts who were shown the same woman but in plain clothes. So when men are primed with mating cues, they appear to differentially focus on products that might be used as sexual signals to woo women. While most research has explored conspicuous consumption as a male-based form of sexual signaling, Wang and Griskevicius (2014) recently examined how women utilize this strategy as a means of warding off same-sex rivals.

There are numerous benefits that accrue to men who engage in conspicuous consumption. Guéguen and Lamy (2012) recently established the links between the status of the car that a man is driving and his likely success in the mating market. They demonstrated that women's likelihood of accepting a request for their phone numbers was contingent on the status of the car in which the soliciting man was seated. The compliance rates across the high-, middle-, and low-status cars were 23.3%, 12.8%, and 7.8%, respectively. Dunn and Searle (2010) asked men and women to rate the physical attractiveness of opposite-sex targets who were either seated in a pricey Bentley or in an inexpensive Ford Fiesta. While men's ratings of the female target were unaffected by the car that she was seated in, women's evaluations of the same man were higher when he was associated with the Bentley. So the Bentley's "status glow" seeps its way onto a man's morphological features. Dunn and Hill (2014) obtained similar findings using photos of male or female targets that were shown in one of two apartments that varied in terms of their luxury levels. Participants were asked to rate the physical attractiveness of opposite-sex targets. The apartment's luxury level did not affect men's ratings, while women's evaluations were very much dependent on which of the two apartments the same man was shown in: Greater luxury yielded higher attractiveness scores. Saad and Gill (2014a) created two versions of a man's online dating profile, one element of which was for the individual to show his favorite possession (photo of the product was included). The product was manipulated to be either a luxury brand or its inexpensive counterpart across two categories (Porsche versus Kia; Rolex versus Casio). The objective was to gauge participants' impressions of the individual as a function of which product he was associated with. His comparative height (in relation to the participant) was perceived quite differently depending on whether he was being judged by male or female participants. Intrasexual rivalry led men to reduce his perceived height (*status contraction effect*), while women increased his height (*status elongation effect*). These perceptual biases are rooted in the evolutionary calculus that regulates same-sex derogation and intersexual wooing.

The status of a man's clothes constitutes another crucial determinant to his perceived attractiveness on the mating market. Townsend and Levy (1990) manipulated a target's status via the clothes that he/she wore (Burger King uniform, off-white shirt, or fancier clothes and Rolex watch), and asked opposite-sex participants to rate the target's physical attractiveness as well as their willingness to engage in one of six types of relationships with the target: *coffee and conversation*; *date*; *sex only*; *serious involvement, marriage potential*; *sexual and serious, marriage potential*; and *marriage*. The effect of costume status was greater for female participants across all six relationships, and only the physical attractiveness of the male target was affected by his costume status. In other words, in the mating market, the status of an individual's clothes carries much greater weight for women (when judging men) than it does for men (when judging women). When facing a choice between immediate versus delayed monetary rewards (intertemporal choice), both sexes are influenced by clothes-based sexual primes albeit different senses are operative. For men, the sexual prime has to be elicited visually, namely, exposure to scantily clad women (e.g., wearing bikinis or lingerie) results in a greater desire for immediate rewards (van den Bergh, Dewitte, & Warlop, 2008). For women, tactile cues appear to be the operative modality such that subsequent to touching men's boxer shorts they exhibit a greater penchant for immediate rewards (Festjens, Bruyneel, & Dewitte, 2013). Beyond clothes, other beautification-related issues that have been explored from an evolutionary perspective include high heels (Morris, White, Morrison, & Fisher, 2013), cosmetics (Etcoff, Stock, Haley, Vickery, & House, 2011), perfumes (Milinski & Wedekind, 2001; Roberts & Havlicek, 2012), hairstyles (Hinsz, Matz, & Patience, 2001; Mesko & Bereczkei, 2004), hair color preferences (Hinsz, Stoesser, & Matz, 2013), and men's facial hair (Dixson & Brooks, 2013). Generally speaking, such studies demonstrate how a given product or service caters to an evolved sex-specific preference (e.g., high heels lift a woman's buttocks by at least 20 degrees and as such create a more youthful figure—see Smith, 1999, and relevant references therein; cosmetics accentuate a facial contrast sexual dimorphism—Russell, 2009).

While some beautification elements are universally operative (e.g., preference for facial symmetry), others are influenced by evolutionarily relevant situational factors. Several evolutionary-minded scholars have established that both women's fashion styles (e.g., hemlines) as well as their spending on beautification products are affected by environmental contingencies such as economic conditions and sex ratios (Barber, 1999; R. A. Hill, Donovan, & Koyama, 2005; S. E. Hill, Rodeheffer, Griskevicius, Durante, & White, 2012). So in the same way that culinary traditions are cultural adaptations to local niches (e.g., extent of spice use as a function of the density of pathogens), fashion cycles and beautification spending are manifestations of adaptive behavioral plasticity. These studies dispel the common misconception that evolutionary psychology posits rigid and nonmalleable deterministic processes (Confer et al., 2010). Of all situational variables that operate within the mating domain, the menstrual cycle is perhaps the most frequently studied. In their theoretical treatise of how evolutionary psychology could inform the field of marketing, Saad and Gill

(2000) argued that menstrual cycle effects should be prevalent within the consumer setting. Numerous researchers have since explored this exact link. Faraji-Rad, Moeini-Jazani, and Warlop (2013) found that women exhibited greater variety seeking in rewards during the fertile phase both in the food and mating domains. Pine and Fletcher (2011) examined women's scores on the Recent Spending and Saving Scale (RSSS) across three time periods of the menstrual cycle. RSSS scores were higher in the luteal as compared to the follicular phase, namely, women's spending behaviors were more impulsive and less controlled in the premenstrual phase (lesser ability to self-regulate). Perhaps the most documented phenomenon, though, has been that women are more likely to engage in signaling (e.g., wearing sexy clothes) when maximally fertile (cf. Durante, Griskevicius, Hill, Perilloux, & Li, 2011; Saad & Stenstrom, 2012). In a context where a woman's capacity to sexually entice is linked to her livelihood, G. Miller, Tybur, and Jordan (2007) found that exotic dancers received larger tips when in the ovulatory phase of their menstrual cycles. The color red has been shown to augment a woman's perceived attractiveness and sexual desirability as judged by men (Elliot & Niesta, 2008), and this red effect applies to women of reproductive age only (Schwarz & Singer, 2013) and appears to be a universal excitatory cue, as it has been demonstrated in numerous cultures, including in an isolated society of Burkina Faso (Elliot, Tracy, Pazda, & Beall, 2012). It is perhaps not surprising, then, that women are more likely to wear red and pink hues when they are in the maximally fertile phase of their menstrual cycles (Beall & Tracy, 2013).

Beyond an increase in their own sexual signaling when maximally fertile, women exhibit a perceptual bias toward male-based sexual signals when ovulating. Subsequent to being shown both status and functional products, women recalled a greater number of the former (conspicuous and expensive products) and did so earlier in the recalled lists when in the fertile phase of their cycles (Lens, Driesmans, Pandelaere, & Janssens, 2012). Although most menstrual effects focus on intersexual signaling, some are shaped by intrasexual rivalry. For example, women's economic decisions (e.g., the offers they make when playing the dictator game) are driven by same-sex competition but only so during the ovulatory phase of their menstrual cycles (Durante, Griskevicius, Cantú, & Simpson, 2014).

GIFT GIVING: MATING, KIN ALTRUISM, AND RECIPROCAL ALTRUISM

Kin selection (Hamilton, 1964) and reciprocal altruism (Trivers, 1971) are two of the basal Darwinian mechanisms that shape human sociality, both of which manifest themselves within the universal ritual of gift giving. Perhaps no gift is more profound than the proverbial gift of life as instantiated by living organ donations. Not surprisingly, though, such gifts are almost always made to kin and very rarely to close nonkin (e.g., friends), let alone to strangers (for relevant references, see Saad, 2011, p. 311, footnotes 17–19). The practice of gifting one's kidney to a total stranger (known as a Samaritan donation) is so counterintuitive and rare that in most instances it has been frowned upon, as this might serve as a signal to the altruist's mental instability (Kranenburg et al., 2008). Clearly, then, gifts are meted out according to an evolutionary calculus that is in part driven by genetic relatedness. In the consumer setting, the exchange of gifts is a wonderful venue from which to explore a wide range of evolutionary motives. Saad and Gill (2003) asked men and women about the reasons that drive them to offer gifts to their romantic partners. These were classified as tactical (displaying financial resources; creating a good impression; as a means of seduction; showing affection; displaying long-term interest; and displaying generosity) or situational (occasion demanded it; reconciliation after a fight; to reciprocate). As expected from an evolutionary perspective, men scored higher on five of the six tactical motives (the only one that did not yield a sex difference was "displaying generosity"), while the two sexes did not differ on any of the three situation motives. Men utilize romantic gift giving as an integral and tactical element of the courtship ritual. Cronk and Dunham (2007) examined perhaps the grandest of all mating-related gift giving rituals: a man's offering of an engagement ring to his prospective bride. The cost of the ring was negatively correlated to a bride's age (young female age being linked with high reproductive value).

Using the same set of six tactical and three situational motives, Saad and Gill also collected participants' perceptions as to why they thought their partners offered them gifts. The goal was to see whether men and women are equally calibrated in understanding how their own motives might be different from those of their partners when it comes to romantic gift giving. While no differences were found along situational motives for either sex, tactical motives yielded profound sex differences. On all but one of the tactical motives, men thought that their motives and those of women are the same. On the other hand, on all but one of the six tactical motives, women recognized that men were much more likely to be driven by such motives than they were. In other words, women are very accurate and men grossly inaccurate in understanding the signals inherent to romantic gift giving. From an evolutionary perspective, this makes perfect sense in that the costs of misreading such gift-giving signals loom much larger for women, not unlike the sex difference in the ascription of sexual intent stemming from, say, a smile, as outlined according to error management theory logic (Haselton & Buss, 2000).

Gift giving does not solely manifest itself in the mating arena. It is also a ritual that is universally used to forge, strengthen, and deepen bonds of affiliation among kin and nonkin alike. One would also expect that the cost of a gift would be in part determined by the strength of the relationship between giver and recipient. Saad and Gill (2003) documented a correlation between the genetic relatedness of gift givers and gift recipients and the amount of money to be spent on a gift. Furthermore, of all possible recipients, individuals planned to spend the most on their mates ($106.43), followed by closely genetically linked individuals ($r = 0.50$; $73.12), close friends ($46.34), moderately close kin ($r = 0.25$; $19.03), and more distant kin ($r = 0.125$; $18.56). Stepfamilies and others had mean gift sizes of $19.37 and $27.03, respectively.

While Saad and Gill collected data on the estimated amounts to be spent on future gifts, Tifferet, Saad, Meiri, and Ido (2014) investigated actual monetary gifts at Israeli weddings. The genetic relatedness effect was replicated in that guests who were close kin ($r = 0.50$ and $r = 0.25$) gave larger sums to the brides and grooms than gifts of more distant kin ($r = 0.125$ and $r = 0.0625$). Furthermore, genetically related guests offered larger monetary gifts than their nonkin counterparts. Note though that kin-based investments are not solely driven by genetic relatedness but are also affected by genetic assuredness (i.e., the certainty of the genetic link). While matrilineal relationships are genetically assured (e.g., the link of a maternal grandmother to her grandchildren), patrilineal ones are fraught with paternity uncertainty (e.g., the paternal grandfather-to-grandchild relationship has two sources of potential cuckoldry). Several evolutionary-minded scholars have shown that investments are affected by this genetic assuredness effect across grandparents, uncles, and cousins (Euler, 2011;

Euler & Weitzel, 1996; Jeon & Buss, 2007; Júnior, Dunbar, & Brito, 2014; Pashos & McBurney, 2008). Using this evolutionary principle, Tifferet et al. (2014) showed that the matrilineal side of the newlyweds gave larger monetary gifts than their patrilineal counterparts. This finding would have been difficult to predict, let alone uncover, void of the requisite evolutionary lens.

HOMO CONSUMERICUS: THEORETICAL, EPISTEMOLOGICAL, AND METHODOLOGICAL BENEFITS

In an editorial published in one of the premier journals of consumer research, Michel Pham, the recent president of the Society for Consumer Psychology, identified seven problems of the field, including "(1) a narrow conception of the scope of consumer behavior research; (2) adoption of a narrow set of theoretical lenses; (3) adherence to a narrow epistemology of consumer research" (Pham, 2013, p. 411). I contend that each of the seven problems would be attenuated if evolutionary psychology were adopted as the meta-framework for understanding consumer behavior (see also Kenrick, Saad, & Griskevicius, 2013). In two of my books (Saad, 2007a, 2011), I offer an all-encompassing evolutionary-inspired definition of consumer behavior that goes well beyond the standard scope covered by consumer scholars. Evolutionary psychology offers a meta-theoretical framework that encompasses broad middle-level theoretical approaches (Buss, 1995; Ketelaar & Ellis, 2000), all of which are organized into a coherent tree of knowledge. Furthermore, it expands greatly the epistemological realm of consumer research by recognizing the import of both proximate as well as ultimate explanations for any given phenomenon involving biological beings. In their editorial in the *Journal of Consumer Research*, Deighton, MacInnis, McGill, and Shiv (2010) ask of consumer scholars to broaden the scope of their investigations in one of several ways, including "providing new ways of thinking about an important aspect of consumer behavior" or working to "develop an elegant higher-order parsimonious perspective that both accommodates past findings and accounts for anomalous ones." (p. vi). Evolutionary psychology caters to both objectives in that it provides the epistemological footing to explore consumer phenomena in new ways (e.g., at the ultimate level), and it is the integrative framework par excellence that can engender consilience (Wilson, 1998) to a discipline that is otherwise disjointed and largely incoherent (November, 2004; Saad, 2007a, Ch. 7; Saad, 2008a; Saad, 2011, Ch. 11; Saad, 2013).

By virtue of their methodological focus (Sternberg & Grigorenko, 2001) on conducting "clean" laboratory studies, many consumer psychologists suffer from what I refer to as *epistemological dichotomania*. In sum, they subscribe to the notion that countless cognitive processes exist in binary and typically mutually exclusive forms (e.g., heuristic versus systematic processing; implicit versus explicit categorization; central versus peripheral routes of persuasion; prevention versus promotion self-regulatory focus). Even within a particular subfield of marketing such as advertising copy, the world is viewed through the prism of binary realities: one-sided versus two-sided messages; rational versus emotional appeals; simple versus complex messages; cosmetic versus substantive executional ad changes. This epistemological penchant shackles consumer researchers into viewing the natural world through the rarified and limiting world of 2×2 factorial designs. Given the methodological pluralism inherent to the evolutionary behavioral sciences, this narrow focus is much less likely to occur among evolutionarily informed consumer psychologists. Take, for example, men's near-universal preference for women to possess a waist-to-hip ratio of 0.70.

Evolutionary psychologists have utilized a bewildering number of methodological approaches and dependent measures to establish the veracity of this premise, including cross-cultural preferences, via the use of line drawings as well as actual photos of women's bodies pre- and postoperative cosmetic surgeries (see Singh, Dixson, Jessop, Morgan, & Dixson, 2010 and relevant references therein); content analyses of Indian, African, Greek, and Egyptian art spanning several millennia (Singh, 2002); content analyses of online advertisements of female escorts across 48 countries (Saad, 2008b); brain imaging and eye-tracking studies (Dixson, Grimshaw, Linklater, & Dixson, 2011; Platek & Singh, 2010); and the preferences of congenitally blind men as elicited by touch (Karremans, Frankenhuis, & Arons, 2010). Not only does this serve as a telling demonstration of the methodological pluralism that evolutionary psychology engenders, but also it belies a common, but typically erroneous, attack on evolutionary psychology, namely that the field consists of hand-waving just-so story-telling (Confer et al., 2010). Evolutionary behavioral scientists test their theories using an evidentiary threshold that is typically set astoundingly higher than that typical of the social sciences.

In their analysis of the disciplinary status of the field of consumer behavior, MacInnis and Folkes (2010) concluded that it is neither an independent field of inquiry (but rather is subsumed within the marketing discipline) nor an interdisciplinary one. Scholars who publish in the leading consumer journals (e.g., *Journal of Consumer Research*, *Journal of Consumer Psychology*, *Journal of Marketing Research*) are overwhelmingly housed in marketing departments. Furthermore, members of the premier society of consumer researchers (Association for Consumer Research) are nearly fully composed of marketing scholars. This is in stark contrast with the members who belong to the leading evolutionary psychology society (Human Behavior and Evolution Society), which has representatives from more than 30 disciplines across the natural sciences, social sciences, and humanities. Garcia and colleagues (2011) compared first authors' departmental affiliations of articles published in two of the leading evolutionary psychology journals (*Evolution and Human Behavior* and *Evolutionary Psychology*) to those published in eight other leading psychology journals (two each from the general categories of neuroscience, cognitive psychology, learning/behaviorism, and psychodynamic psychology). A total of 1,000 articles were analyzed (100 articles for each of the 10 journals). The evolutionary psychology journals contained a greater proportion of first authors who were housed in departments other than psychology and they originated from a broader number of fields. The reason for this interdisciplinary is quite simple: Evolutionary psychology is a meta-framework that serves as an epistemological key that can be applied seamlessly across intellectual landscapes. This is precisely the reason that in my own career I have published evolutionary-based works spanning highly disparate and heterogeneous topics including the effects of birth order in understanding consumer conformity and adoption of innovations (Saad, Gill, & Nataraajan, 2005), sun tanning (Saad & Peng, 2006), the framing effect when evaluating prospective mates (Saad & Gill, 2014b), sex differences in sequential mate choice (Saad, Eba, & Sejean, 2009), sex differences when playing the ultimatum and dictator games (Saad & Gill, 2001a, 2001b), financial risk taking and pathological gambling (Stenstrom & Saad, 2011), and a slew of psychiatric conditions, including obsessive-compulsive disorder (Saad, 2006b), suicide (Saad, 2007b), and Munchausen syndrome by proxy (Saad, 2010).

Radical scientific innovations arise in one of several ways. At times, novel research streams remain hidden until the appropriate methodological tools have been developed (e.g., the electronic microscope, the telescope, brain imaging, genotyping). In other instances, a new epistemological lens is needed to open new lines of discovery. Evolutionary psychology offers a powerful epistemological key to unlock unchartered territories. In recognizing the epistemological benefits of ultimate-level explanations and the associated adaptive proximate mechanisms, consumer scholars are bound to identify novel research questions and generate findings that would have remained otherwise concealed (Saad & Gill, 2000; Saad, 2007a). Take, for example, the finding that women are more likely to purchase beauty-related products when primed to think about economic recessions (S. E. Hill et al., 2012). At first glance, this appears counterintuitive, as one might expect that hard economic times would yield a decrease in such sales (since less disposable income is likely available). However, using an evolutionary lens, Hill and her colleagues reasoned that during economic hardships, fewer men with resources are to be found thus causing women to engage in more vigorous sexual signaling (instantiated via greater beautification). This example and countless others discussed in this chapter demonstrate the distinct explanatory power afforded by an evolutionary lens. Consumer scholars should not construe evolutionary psychology as a threatening framework bent on taking over their existing research programs. Rather, in most areas of interest to consumer scholars, the evolutionary perspective offers a complementary toolbox of organizing principles that only enriches the depth and richness of existing explanations.

CONCLUDING REMARKS

In the 15-plus years that I have been Darwinizing the field of consumer behavior, I have been exposed to a wide range of criticisms and attacks, some of which are applicable to evolutionary psychology in general, while others are unique to the consumer behavior field (cf. Saad, 2008a; Saad, 2011, pp. 22–32). Some believe that findings stemming from the field of evolutionary consumer psychology are dangerous in that they can be "misused" to justify reprehensible realities. This is what a librarian from the University of Toronto wrote me subsequent to having read about the results reported in Saad and Stenstrom (2012) regarding women dressing more provocatively during the fertile phase of their menstrual cycle: "Perhaps you have not noticed that this is a highly problematic contention, not least as it is still used as a defense for rapists." Others dislike the fact that the same evolutionary mechanisms that explain animal behavior could be operative in elucidating consumer behavior. Here is what one clinical psychologist thought of my drawing behavioral homologies and analogies between consumers and our animal cousins (from http://modernpsychologist.ca/delusions-of-a-consuming-instinct/):

> For our purposes, we might simply note that right from the start Saad is looking to compare us with monkeys, and that he is emphasizing our innate animal nature, believing it holds the ultimate causal explanation for many of our everyday human behaviors . . .
>
> Saad claims that we have a similar "instinct" for "hoarding and gorging," but since we do not have the same metabolic rate, as say a hummingbird, we are left with the current American obesity crisis and other "dreadful diseases." Note how quickly Saad went from comparing us to monkeys (and monkeys to us) and now to hummingbirds. I am less comfortable in making such comparisons, but let us set that point aside for the moment—we will pick it up again later.

His quotes are emblematic of the reaction of many consumer psychologists. For example, subsequent to my 2007 academic book being published (Saad, 2007a), I had been invited to discuss my evolutionary consumption work at one of the leading marketing departments in the world. I faced an endless litany of hostile interruptions, including one of relevance to the current issue: "Are you suggesting that we [consumers] are animals?" asked with an air of loathing, if not outright disgust. The tide is changing, though, as evidenced by the fact that Vicky Morwitz, the 2011 president of the Society of Consumer Psychology conference, recently published a paper highlighting how an exploration of animal cognition could be used to better understand consumers' minds (Morwitz, 2014).

Despite some continued resistance to the notion that consumers are biological beings whose bodies and minds were designed by evolution, such detracting voices are on the losing end of the grand Darwinian debate. Consumer behavior exists within the biological realm and not in some parallel universe where evolution ceases to matter. Notwithstanding the myriad of ethnic, cultural, religious, linguistic, and racial differences that enrich the human tapestry, *Homo consumericus* unites us via our shared biological heritage.

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CHAPTER 51

Evolution and Organizational Leadership

NIGEL NICHOLSON

More ink has been spilled on leadership than any other topic in the business literature, and yet it seems that knowledge has failed to accumulate in a way that provides a unified consensus on what leadership is, what leaders do, why they emerge, what determines their success and failure, and what impacts they have (Bennis, 2007; Drath et al., 2008).

I shall argue that evolutionary theory has the capacity to provide the framework for such a unified view, though one that will require scholars to take a step back from their many articles of faith and sacred cows in this highly evocative and emotive field.

Why the field has this hyperactive character is itself a consequence of our evolved identity as a species, for any way you look at it, leadership is "special" for humans.

This is one of several key questions I shall seek to answer in this chapter, as follows:

- What is leadership? What relationship does human leadership have with equivalent functions elsewhere in the natural world? What does the history of our species teach us about the essence of leadership?
- What can we glean from the academic literature on leadership? What are the gaps that an evolutionary approach might fill? How can an evolutionary approach shed light on the key processes of leadership emergence, effectiveness, and failure?
- How is leadership changing? What are some key issues in contemporary contexts, such as gender issues and new models of leadership?

Let me start this chapter with what an evolutionary view of leadership connotes. It conceives of leadership as a set of functions that coordinate and direct the effort of conspecifics—other species members (van Vugt, Hogan, & Kaiser, 2008). It occurs in various forms among social mammals but among humans reaches an unparalleled level of refinement and diversity. Multilevel selection modeling is needed to explain these forms. That is, leadership serves the interests of those who would lead and those who would follow, and in so doing increases the fitness of the group. Group fitness is context dependent (Sober & Wilson, 1998). The forms that leadership takes—for example, shared versus top-down—are selected according to how adaptive they are for the constitution of the group (e.g., mature vs. dependent members), and the environmental challenges it faces (e.g., peace vs. war).

Scholars have searched for a genotype that encodes the qualities of willing and capable leaders, but with very limited success to date (Judge & Long, 2012). The reason is that selection in all its forms (natural, sexual, and kin) operates at the level of the phenotype, whose fitness-relevant qualities are defined by the ecology of the group and the wider context. Multilevel selection directs us to analyss interactive dynamics to understand the emergence, performance, and consequences of leadership in the human group.

ADAPTIVE SYSTEMS AND LEADERSHIP

Consider the simplest automaton, say a robot vacuum cleaner. It moves around, sucking as it goes, and changes direction when it encounters an obstacle or a cliff, programmed to move in systematic sweeps of whatever area it is placed within. The instructions are in-built along with sensors to detect bumps and cliffs, plus all the machinery necessary for locomotion and directional changes. Biological organisms are little different—such as simple photophobic bugs that walk into dark corners, eating whatever detritus they find on the way—directed by a comparator that tells them about the gap between current and target states of existence. Figure 51.1 shows the basic model of this adaptive system, input, and output elements, linked to create an adaptive system.

The routine that drives such a system has been characterized in psychology as the TOTE routine: Test-Operate-Test-Exit (Miller, Galanter, & Pribram, 1980), where the organism seeks to reduce discrepancies between goals states and experienced states by testing for these gaps and executing behaviors to reduce them, until it can exit, that is, reach equilibrium and come to rest. The TOTE model was conceived as a way of characterizing purposeful systems, and it works well as a framework in an evolutionary context, where plans serve the goals of organisms. Figure 51.2 shows how this may be represented in the adaptive challenge facing individuals (2a) and indeed social groups (2b), both of which can be described in terms of an adaptive cycling between seeing (sensors), being (goals and capabilities), and doing (action repertoire and outputs).

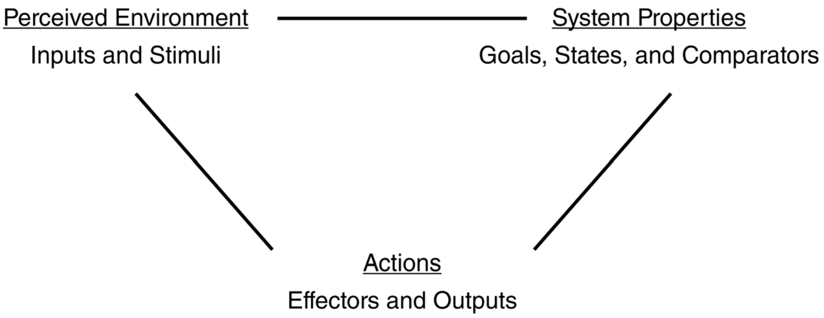

Figure 51.1 Adaptive Control Systems: The Basic Elements.

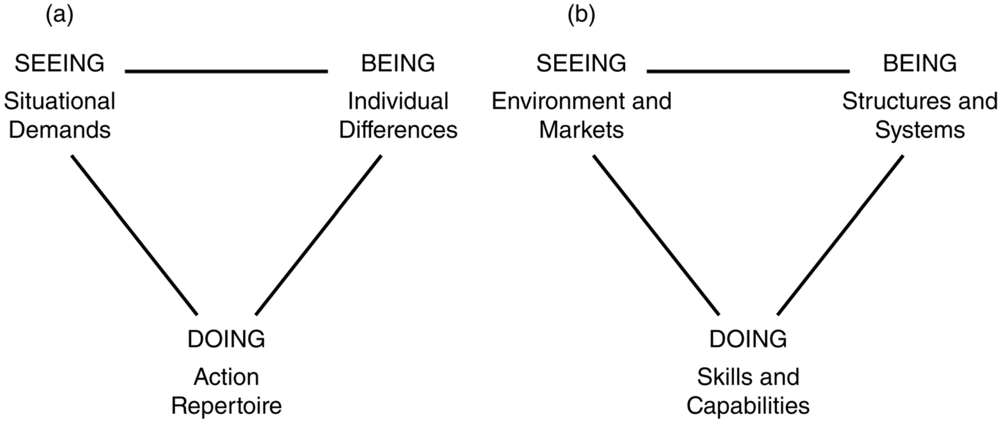

Figure 51.2 (a) Individual and (b) Organizational Models.

Expanded analyses of this challenge have been developed elsewhere (Nicholson, 2011, 2013) to the effect that adaptation, especially for humans, is not solely a reactive process. When an entity—institution or individual—selects behaviors from its repertoire to meet the new demands of the altered situation, this may prove costly, impractical, or impossible. Two other adaptive strategies are possible. One is to abandon the over-demanding environment and seek a fresh context that has similar features to the environment as it was formerly so the familiar equilibrium can be recreated without behavior change—what has been called "habitat tracking" (Eldredge, 1995). A more radical adaptive strategy, one that is of growing interest to evolutionary theorists, is "niche construction" (Laland, Odling-Smee, & Feldman, 2001)—the active shaping of the environment to enhance the fitness relevance of a species' repertoire. Beavers, leaf-cutter ants, and chimpanzees and other social species all modify their local ecology the better to harvest its benefits; in the case of chimps, this has notable regional variation—what are in effect material subcultures that are adaptive to the local ecology (McGrue, 1992).

Humans have taken subculture niche construction to unprecedented levels of sophistication and variety, most profoundly in the "invention" of agriculture, and since then a proliferation of social and cultural forms have populated the globe. Multilevel selection theory shows how cultures evolve to mediate between human nature and environmental forces, each cultural niche resetting many of the criteria for the fitness of individuals, groups, and institutions (McElreath & Henrich, 2007). It is the central argument of this chapter that leaders are critical agents in these coevolutionary processes, especially the adaptive strategy of niche construction (Spisak, O'Brien, Nicholson, & van Vugt, 2015).

Leaders emerge and are successful to the degree to which they can fulfill what I have called "the Leadership Formula"—to be the right person, at the right time and place, doing the right thing (Nicholson, 2013). "Right," of course, is an indeterminate value denoting what is adaptive to circumstances, which implies that there is no single right way of leading. Different types of leaders are selected to enact the behaviors that are required to meet the needs of local circumstances. This view triangulates situations, processes, and qualities (SPQ), connoting, respectively, leadership contexts (and how they are perceived), leadership strategies and behaviors, and leader attributes

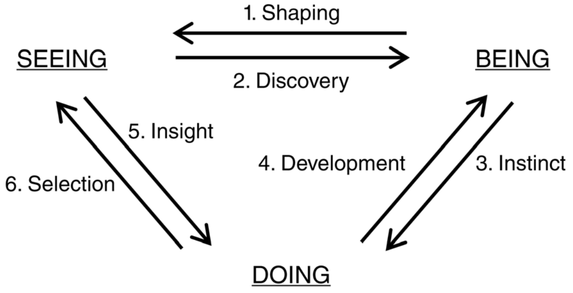

Figure 51.3 The Six Adaptive Paths.

(including shared leadership). This simple framework has many ramifications and helps us to comprehend the variations we see in leadership in the natural world and across human history. The logic of the model is that there are six paths to adaptation, which I shall use to analyze the themes in the remainder of the chapter (as shown in Figure 51.3).

The first path (path 1: shaping) underlies niche construction—leaders who by force of will and purpose shape the leadership situation and how it is perceived. The second path (path 2: discovery) is the process by which immersion in a situation exposes or awakens the latent qualities of a leader. The third path (path 3: instinct) is the determining force of dispositions—how the qualities of leaders, if unrestrained by self-control, translate into the exercise of their preferred behaviors, routines, and habits. Powerful leaders are often rewarded for exercising their instincts, that is, until they fail. Failure avoidance requires learning—insight into oneself (the discovery path, 2), but also the logic of adaptive responses to change, which lie in the remaining three paths. Leaders can grow and develop through experience, but only if they practice and embed novel routines and behaviors (path 4: development). The prerequisite for such discipline is awareness that the world has changed or that one has attained a new and deeper understanding of it (path 5: insight). This is the key to the holy grail of adaptive leadership, the recognition that new behaviors have to be selected and enacted to meet the demands of the situation as newly appraised (path 6: selection).

One final note to this model is to reemphasize that it is the *perceived* world that matters: what an organism's sense organs are attuned to (Powers, 1973). In the human case, this perceptual world is also a conceptual world. Leaders' adaptive strategies must encompass the realm of ideologies and beliefs, what some call socially constructed reality. To analyze these, we must first review more basic models.

Leadership in the Natural World

The concept of leadership only makes sense in relation to social systems (van Vugt et al., 2008). In the leadership literature definitions abound, but most center upon contemporary human purposes (e.g., influencing towards an outcome) (Northouse, 2012). I wish to avoid these presumptions by adopting a more naturalistic perspective. The evolutionary functional view says that leadership can take a variety of forms, from personal to impersonal, shared to singular. This treatment also allows a continuum of strategies from directive or controlling at one end to facilitative or coordinating at the other. Hence, a working definition to guide us will be that leadership is the direction or coordination of the members of a social group towards a goal.

The natural world contains many social species: insects, birds, some reptiles, and many mammals among them. The most intensely coordinated are the "eusocial" insect colonies—subservience of all to the colony, with rigid divisions of labor and sexual function and a high degree of genetic identity (more than 50% shared genes for offspring). The group acts, in effect, as a "superorganism" (Wilson, 1971). "Leadership" here resides in the encoded instincts the support collective action. The presence of a "queen" could hardly be called monarchical rule so much as a central entity around which automatized leadership functions revolve, to ensure she serves her allotted role in the reproductive fitness of the hive.

Birds and many ungulates have more solitary habits but flock and herd together for safety, shared food supply, and breeding. Without the imperative of genetic identity as in eusocial species, social organization is around family groupings (parents + offspring), commonly in haremic groups—dominant male plus females and their offspring. Leadership equates with parenting here, punctuated by contests among competing males for dominance and the breeding opportunities, but when the herd moves collectively, leadership is governed more by shared instincts than "leaders" (Gueron, Levin, & Rubenstein, 1996). Typically in social species, contests for superordinacy are based on physical fitness markers—large antlers, weighty tail feathers, fighting strength, and quality of song. Note that the first two of these are the classic "handicapping" markers of fitness—the burden to be carried by an individual for no other purpose than to mark his fitness to bear it (Zahavi, 1975).

More complex social organization is found in pack animals and higher mammals—dogs, marine mammals, and primates, where more complex status hierarchies allow dominance to be based on criteria other than physicality, such as ability to conciliate within the group, trust, and intelligence.

In humans, all these forms of coordination are visible. Those that have negligible recourse to the singular personification of a leader include:

- Impersonal coordination: People acting in parallel will spontaneously self-organize, such a queuing behavior.
- Crowd behavior: People will coact like herds at sporting events, in street protests, and in financial markets, where their behavior is motivated by imitation and observation of others.
- Coordinating mechanisms: Most of the time, people are not waiting for leaders to tell them what to do but are following routines, decision rules, and operating procedures (Tooby, Cosmides, & Price, 2006).

Self-organization: There are numerous circumstances under which humans (and other highly intelligent social mammals) will act together, informally sharing responsibility for directing their collective action, thought, and feeling, as in business organizations where self-managing teams operate (Purser & Cabaner, 1998). Leadership is thus a systemic function that can be shared (Pearce & Conger, 2003). However, this functional view is not what characterizes many writings on leadership, where more personalized and indeed "romantic" conceptions, often with heroic overtones, prevail (Meindl, Ehrlich, & Dukerich, 1985).

So persistent is this imagery that we must recognize that it is part of human nature to adopt personological conceptions. Even when we have recourse to "substitutes for leadership" (Kerr & Jermier, 1978), we seem to opt for forms where we are led by personal rather than impersonal processes (such as rules and procedures). It seems that this preference is rooted in the sense of purposive agency that accompanies human self-consciousness, an evolved capability that enables everyday "mind reading" and intersubjective awareness (Leary & Buttermore, 2003; Nicholson, 2011).

It seems that leadership is special and iconic for humans, and a source of many of the themes that have predominated, not just in the popular media but in the academic study of leadership, as we shall see.

THE LESSONS OF HISTORY

A first observation to make is that human leadership has been highly instrumental at all the major junctures of cultural, economic, and social change. Leaders make a difference (Kaiser, Hogan & Craig, 2008), history also teaches us that leadership can take a vast array of very different forms.

The prototypical form that characterized our way of life for the first 95% of our history was that of semi-nomadic hunter-gatherers in a clan-dwelling existence. Contemporary anthropological and historical paleontological evidence suggests that the prevailing model of organization and leadership throughout this period exhibited a high degree of fluidity, a morphing process of continually adjusting social roles to cope with the flow of a mobile existence and variable environment (Boehm, 1999; Erdal & Whiten, 1996). Leadership in the hunter-gatherer world is a function that is passed from hand to hand according to local conditions and demands. Boehm's detailed study of tribal peoples reveals this model prevails where there is little or no nonperishable wealth—that is, where power and status through resources cannot be stored or transmitted, resulting in egalitarian, communal, and fluid power relationships. Tribal members deploy a variety of informal sanctions to prevent what Boehm calls "upstartism," leaders who exceed the temporary and provisional basis of their authority.

Radical climate change created population pressure, which triggered the invention of agriculture and domestication of animals around 10,000 years ago, leading rapidly to organized settlements of relatively large fixed populations (Diamond, 1997). In this new world, for the first time wealth could be accumulated and social status transmitted between generations, leading to the accretion of power, kingship, slave states, and extreme forms of authoritarian leadership (Betzig, 1993; Padilla, Hogan, & Kaiser, 2007), along with a supporting range of designated positions of authority and servitude. This model coexisted alongside yet another model of governance adopted by tribes of semi-nomadic pastoralists, consisting of a social structure highly segregated by gender and rank, with ultimate authority in shared and consensual decision making among council elders. Comparative study of tribes suggests their leadership is governed by three principal situational challenges: decisions about where to hunt and camp, food sharing, and the control of aggressive males (Nicholson, 2005).

A predominant model in tribal societies has been that of the Big Man (van Vugt et al., 2008), whereby the best hunter or fisherman shares his surplus with his people in a way that is conspicuously self-denying, reserving a modest share for himself. In this way, the Big Man acts out the role of the chief servant to his people (Coon, 1979; Harris, 1979), demonstrating his ability to meet the needs in the situation, a patron trusted to acquire resources and distribute them fairly. The Big Man model seems to recur in a quite perverted form in the political leadership of many developing economies, where leaders oppose any kind of democratic opposition, accumulate vast wealth, and then distribute them selectively among followers in ways that ensure control, usually via the military, economic, and political institutions (van Vugt & Ahuja, 2010). The contingency that facilitates its success is the existence of a poor, uneducated follower group whose culture incorporates a historic faith in patronage, plus a clan mentality that incorporates a tradition of dependence on the largesse of chieftains.

Recent history—that is, the past few hundred years—has witnessed the development of what we might call a consensual model of leadership on the contingency of followers who have the education, resources, and power to restrain or remove the leader.

As we have noted, multilevel selection explains the coevolution of culture and leadership.

Leaders stand at the center of this coevolutionary logic as both the causes and effects of cultural change—potentially innovators through institution building, but also the products of cultural arrangements having been selected and socialized to fill specific purposes. Applying the control loop SPQ guiding this chapter helps us appraise this adaptive dynamic, to the effect that dictates the lessons of history are these:

- Leaders succeed until they fail! They have to be the right person, at the right place and time, doing the right things, that is, in an adaptive equilibrium of persons in leading roles who have the characteristics that enable them to deliver what circumstances demand. Leaders fail because their control cycle moves from congruence to incongruence, typically through failing to adapt to changing contexts (Hogan, Hogan, & Kaiser, 2010).
- There is no one right model of leadership. Different kinds of responses are needed to meet the demands of the times, and this generally causes different kinds of leaders to emerge to meet them. Van Vugt and Spisak (2008), for example, have noted how masculine and feminine leaders' attributes are favored, respectively, in times of war and peace.
- Leaders can succeed to the degree that they can dictate the circumstances to be congruent to their style, goals, and image—a variety of niche construction—which, of course, is possible to the degree that leaders can shape the social construction of their followers' reality (Conger & Kanungo, 1988; Nicholson, 2013). But the lesson of history, especially of powerful despots such as Stalin and Hitler, is that social constructions may prove to be unsustainable if they deviate from followers' experienced reality (Lord & Maher, 1991).

THEORIES OF LEADERSHIP: AN EVOLUTIONARY CRITIQUE

We have reflected that the huge volume of research and publication around leadership is motivated by a search for formulaic solutions to our desire to stimulate the supply of leaders worthy of our regard. Much of the genre is in adulatory thrall of heroic life stories (Meindl et al., 1985).

An evolutionary overview of the literature enables us to see how its themes and foci have shifted to reflect and serve, in a coevolutionary loop (i.e. as both a cause and effect), the conditions and needs of the times. This is also resource-based, for leadership theory and research has mainly emanated from U.S.-based consultancies and business schools. The center of gravity for the field has been located close to the issues confronting the 20th-century American multidivisional corporation, rather than such as the family, not-for-profit, or governmental organizations, for models from other parts of world.

FROM ANCIENT TO MODERN CONCEPTIONS OF LEADERSHIP

The classical political philosophers from Aristotle to Cicero were concerned with creating a rational-moral order through the institutions of the state, with leaders embodying moral rectitude commensurate with a virtuous state, conscious all the while of the fortitude required to master base impulses. The idea of leaders as exemplars of self-sacrificial nobility was overtaken in the Middle Ages by the ideas of Nicolai Machiavelli, who entertained a much less sanguine view of the realpolitik of leadership, though based upon an appraisal of the contextual challenge facing the leader.

The 20th century has witnessed the advent of individualism and "psychologism," with a shift from the close identification of people with social roles toward recognizing that individual differences shape role performance. This saw the flowering of the field of personality psychology in an era of increased mobility and flexibility in social roles, where people are guided less by dutiful subservience to authority than the exercise of discretionary responsibility. This spawned a new literature seeking to identify the enduring, central, and common factors in "great" leaders. The search for the profile of the great man ultimately failed, as the lists of qualities lengthened and came to reflect more the values of cultural stereotypes than empirical predictors of leadership success (Northouse, 2012).

These predictive failures shifted attention back to the situation, with two key ideas. One was the recognition that leaders may have limited scope to act or determine outcomes—they may only make a difference when situational constraints are weak (Mischel & Shoda, 1995). The second was the idea that followers matter—in particular their willingness and ability to perform (Hollander, 1992). Early contingency theory tracked the relative importance leaders need to place upon goal achievement versus human relations at work (sometimes called task vs. consideration), a balance that depends upon the characteristics of followers and the leader's attributes (Fiedler, 1978; Hersey & Blanchard, 1969). These conceptions focused on the concept of leadership "style," with the assumption that leaders should be able to respond adaptively to changing demands. An evolutionary approach would support the idea that people can alter their behaviors to meet changing demands, but note that it is more likely that different types of leaders will self-select and be selected for differing sets of circumstances—one of the "lessons of history."

Trait approaches have become much more sophisticated with the revival of the field through enhanced measurement and more sophisticated predictive modeling. The consensus that emerged around the Five Factor Model (FFM) of personality proved a major stimulus in leadership research (Judge, Bono, Ilies, & Gerhardt, 2002). Although the FFM was conceived and constructed entirely on empirical grounds, ex-post, evolutionary theorists have advanced plausible theoretical arguments for the fitness relevance of its categories (MacDonald, 1994).

This raises the question of why, if personality types have fitness relevance, there is variation at all. The answer, variously, has included frequency dependent selection (the comparative advantage of having a profile different to others) and the likelihood that personality is encoded in non-additive gene combinations, which may vary randomly or by association with other biological markers (Jang, Livesley, & Vernon, 2006; Nettle, 2006). Certainly, behavior genetics has shown us that although highly heritable, personality does not run in families (because it encoded via unique genetic combinations) (Lykken, McGue, Tellegen, & Bouchard, 1992). Research also shows that leadership emergence has a lower limit of 17% heritability, though this is more likely to be due to generalized drive for dominance and prominence than because there are specific universal leadership traits (De Neve, Mikhaylov, Dawes, Christakis, & Fowler, 2013; Henrich & Gil-White, 2001; Ilies, Gerhardt, & Lee, 2004).

Research does indicate that traits are distinctively implicated in leadership emergence and effectiveness, but not independent of context (Judge & Long, 2012). As we argue later, the universals of leadership are around trust and influence in relation to followers, whereas specific traits are invoked to a greater or lesser degree according to the condition of the followers and the challenges facing them. Perhaps closest to a universal trait on this reasoning is the desire to lead, which itself does seem to have a degree of heritability (Chan & Drasgow, 2001; Ilies et al., 2004).

Research focusing on the contingencies of style heralded a move into much more behavioral approaches to leadership, identifying suites of specific behaviors (Yukl, Gordon, & Taber, 2002). The coevolutionary driver underlying this emphasis is the growing professionalization of management, stimulated by a dearth of well-trained managers, and the rise of consultancies and business schools offering tool kits for would-be leaders.

Social exchange theory and the growing power of social psychology as a discipline moved the behavioral orientation of leadership research further into the microscopy of leader-follower interactions, via the advent of leader-member-exchange (LMX) research, which views the interactive process as an entity distinct from its participants yet under their control (Graen & Uhl-Bien, 1995). The practice-based accompaniment to this has been the growth of the coaching movement—recognizing the levels of support leaders need to bear the increasing weight of role demands, parallel to the emphasis in the practitioner literature on the "leader as coach" (Ely et al., 2010).

Transformational Leadership and the Return of Charisma

Around the 1980s, the management literature divided into two strands. One was a return to the heroic conceptions of leadership, the other to a more sociological critique of the phenomenology of leadership. The first was initiated by an outsider to the management disciplines—James McGregor Burns (1978), a political scientist and presidential biographer who wrote a treatise on leadership that seemed to fire a starting pistol to reengage the heroic individualism of earlier "great man" conceptions of leadership, but this time in terms of it as transformative process. Burns, and the writers who pursued this line (Bass & Avolio, 1994; Hunt, 1999), contrasted transformational leadership, where leaders mobilize followers in a process of enhancement, engagement, and idealization that raises their aspirations and achievements to a higher level, with transactional leadership, the instrumental, task-focused direction of activity, based upon a calculative exchange of obligations for inducements. Again, one can smell the late 20th-century zeitgeist in these constructs. The construction of "transactional" leader is ambiguous—denigrating perhaps in its view of management

(Hamel, 2008). Yet the model overall can be seen as an internal contingency model for corporate leadership, amounting to a recognition that in a corporate hierarchy the nature of "leadership" changes markedly by level (Katz & Kahn, 1978).

At the upper strata of organizations, where leaders exercise greater discretion, inducements are less material than around the alignment of values, the sharing of power, and the delivery of strategic goals. At lower levels, the psychological contract is less moral than an instrumental, and the required skills, personality, and goals of leaders are quite different—to do with error reduction, reward and control, and efficiency of execution (Etzioni, 1975).

In the same climate of visionary zeal, there was a resurgence of a more ancient and controversial topic "charisma." It was the sociologist Max Weber who noted the hazardous nature of this "gift of the gods" in proposing that bureaucracy was a safer structural alternative to the capricious risks of personal leadership, where high-power models can prey on the weak and induce states of dependency. Charisma was rescued by psychologists and management scholars by inverting this dark conception of charisma to one where the visionary leader enhances the self-concept of followers—inspiring rather than disempowering them (Conger & Kanungo, 1988; House, 1977). At this point, scholars start to talk about transformational and charismatic leaders as interchangeable concepts (House, Shamir, 1993) and reify their existence through the traditional route of psychologists: psychometrics. Scales measuring these attributes have become probably the most common and attractive tools in the field, serving to validate and reinforce its persistence (Avolio, Bass, & Jung, 1995).

It is worth taking a step back and viewing this again in cultural context. There is more than a whiff of what McAdams calls the persistent "redemptive" stream in American culture, from a born-anew frontier people seeking hope (McAdams, 2013), especially from leaders who will come to awaken and inspire followers to collective acts of transformation and renewal. One can discern the primitive yearnings housed in this romantic view, which bears the cultural imprint of the parental model (Keller, 1999). However, it is perhaps in recognition of a growing mistrust and disillusionment with leaders that has led to increasing attention to the "dark side" of charismatic leaders, such as their narcissism, disempowering relationships, and tendency to leave a successor vacuum in their wake (Padilla et al., 2007).

The most recent incarnations of leadership theory around the imagery and social construction of leadership have taken their lead from Meindl's critique of the "romance of leadership" (Meindl et al., 1985) in the form of what is called "implicit leadership theory" (Ayman & Korabik, 2010; Lord & Maher, 1991)—developing the idea that the projections of expectations onto leaders influence their emergence, selection, and evaluation. This is entirely consistent with our coevolutionary argument that leadership is conceptualized in ways that reflect people's needs—those that are proximate and locally enculturated drawing on the distal, deeper, and more timeless themes in the human story.

THE UNIVERSAL LEADER—AN EVOLUTIONARY PERSPECTIVE

As van Vugt and colleagues point out (van Vugt et al., 2008), leadership exists to solve the adaptive challenges members of species have to face repeatedly. In the world of our primate cousins, as careful observers have noted, these involve a mix of brute force, coalitional politics, nurturance, and acts of reciprocation, in order to advance such goals as security of food supply, mating opportunities, child rearing, and conflict resolution (de Waal, 1989). Not much different than humans, really! Yet, if there are to be universal leadership qualities, then we need a closer specification. For van Vugt and Ahuja (2010) these are (a) finding resources, (b) conflict management, (c) warfare, (d) building alliances, (e) resource distribution, and (f) teaching.

Returning to our theme of adaptive leadership models, as we have seen over human history, the emphasis on these varies greatly. Thus, we devote many more resources today to teaching than to warfare, but the reverse was true not long ago in human history (Pinker, 2011). Our coevolutionary view is that these challenges as highly contingent. Drath and colleagues (2008) essayed one of the most comprehensive recent reviews of the field, concluding that the essential tasks of leadership can be resolved into three areas: direction, alignment, and commitment. This corresponds with the three points of our control model: situations-seeing-direction; qualities-being-alignment; and processes-doing-commitment.

Direction

Whether embodied in the person of a single designated leader, a committee, a team, or a set of operating rules, leadership has to achieve this most central of need: to make decisions about goals—what kind of strategic intent will satisfy the most important challenges facing the collective. As we observed earlier, this involves the duality of adapting responses to meet changed circumstances, or seeking to control and shape the circumstances (the roots of niche construction). Political history is replete with such cases, which are also visible in business. Notable examples include Henry Ford, who set the agenda for an entire industry, and more recently Steve Jobs, who defined the parameters of the digital world for the industry and the market it inhabited. Both are clear examples of one person acting as the channel for coevolutionary processes that persist beyond their lifetimes. Although we can enumerate the talents we might look for in someone able to do these things, universal qualities to match them remain elusive.

It is easy to conceive of leadership scenarios where the leading group has relatively little need to set out vision, direction, or purpose, such as tribal groups who are servants of tradition, or are following the implacable ambient events, such as might be dicated by externalities such as the weather or hostile neighbors.

The other way to go in the search for universals is to specify the recurrent challenges faced by human groups, much as van Vugt and others have done, and then define what they require of leaders. However, niche construction and ecological change shift the balance of demands and responses required (Spisak et al., 2015). One element that continually recurs in the leadership literature is "vision," but not clearly associated with any specific trait (House, Dorfman, Javidan, & Hanges, 2013).

In the adaptive framework offered here, the "vision" element is the critical role of the leader, or the leading group, in apprehending the environment, creating images of the challenges it confronts, and offering a strategic approach to dealing with them (Conger & Kanungo, 1988). It is conceivable, for example, that it could be concluded that someone different from the incumbent would be better equipped to deliver the strategy. The wise leader may even conclude this him- or herself.

The universal quality this invokes is therefore an adaptive shift in "seeing," as the SPQ model characterizes it, which involves disseminating a construction of reality that promotes the people and processes that can mobilize the required responses. It is a prime function of leadership to see beyond the vision of others, gathering data from new or disregarded sources, challenging assumptions, and critically evaluating capabilities and delivery systems. Indeed many companies and their leaders fail because of deficiencies in "seeing"—unawareness of existing or nascent shifts in the environment—rather than deficiencies in "being" (core competences) or "doing" (capabilities).

ALIGNMENT

What is the identity of the "follower" group? What are their skills, capabilities, beliefs, values, strengths, and weaknesses? How are they organized? What cultural imperatives or technological constraints compel them to relate to each other in particular ways? Again, it requires a dialectical perspective that conceives of humans both as responsive adaptors and as proactive agents. There are clearly aspects of identity—both personal and organizational—that can be shaped to purpose, and others that are nonnegotiable biogenetic givens to be navigated or aligned. Evidence for the former comes from research in job design showing how incumbents shape the roles they are in and in the field of transitions where job shifters alter the roles they take (Nicholson, 2010). Sociologists have coined the term "structuration" to denote the agentic capacity of leaders and others in relation in the creation of institutional structures (Jarzabowski, 2008), and clearly "niche construction" is a tool of transformational leadership (Spisak et al., 2015).

At the level of personal identity, this can be seen as the leader's ability to navigate the traits of his or her personality and to construct a "style" that will work. In the leadership literature, this is treated either, on the one hand, as if style were a matter of choice, or on the other, as if leaders are the helpless victims of their traits. The truth lies between these extremes, in the domain of self-regulation (Karoly, 1993). This is the active construction agents put upon their own mental states and impulses, and how they conceive of the environment and its risks, awareness, and then exercise some degree of self-control over these elements and the actions that follow from them, often via personal narratives (Nicholson, 2011; Van Knippenberg, de Cremer, Hogg, & Van Knippenberg, 2005).

This is alignment at a personal level. For example, we know that certain physical attributes, such as height, are favored in the selective processes that advance leaders (Judge & Cable, 2004), yet many diminutive leaders override any selective disadvantage through their strong narratives, driven by their motivation to lead.

It is harder to alter one's personal identity than it is to change an institution's. Yet corporate identity change may be a central component of a firm's adaptive strategy, when it purchases new technologies, revises its structures, or merges with other entities. Leaders play a central role in such transformations (Kaiser et al., 2008).

However, organizational design is not always purely a matter of rational-economic choice; creating structures that are fit for purpose, that is, the configuration of environmental demands. The evolutionary perspective urges us to look deeper at whether humans have innately preferred ways of organizing, though, as discussed earlier, the human journey has traversed a great variety of social forms, each an experiment in how to align human effort to meet environmental challenges and pressures.

Three principles govern organizing: hierarchical stratification, grouping, and centralization. Hierarchy enables control from top to bottom, grouping promotes facilitates efficient division of labor, and centralization promotes integration. So far, so rational. But consider: Strong features of the human tool kit include dominance and reputational ranking (Henrich & Gil-White, 2001), which may lead organizations to be more hierarchical than they need to be to accomplish their work. Tribal instincts—human "groupishness" may subvert efficient divisions of into "clannish" self-serving networks within the compass of so-called Dunbar's number of 150. Leaders may also over-centralize organizations in their desire to build and secure their power base.

Commitment

The function of leaders to engage, mobilize, inspire, and influence followers, as we have seen, has dominated the literature, and the search for a universal skill set has largely failed, or at best produced long lists. The coevolutionary reasoning here suggests that almost any specific behavior—even inaction—may be an adaptive response to a given circumstance. Yet one can also reason that our species does have a common platform of psychological needs and interests, and that when in groups responding to a leader, exhibit common tendencies.

Following the logic of our argument, the first step in adaptive leadership is to apprehend what Mary Parker Follett, an early writer on management, called "The Law of the Situation" (Urwick, 1987). This involves both the skills of awareness—such behaviors as exploring, investigating, and questioning—and those of shaping reality, or challenging, defining, and building. Conversely, many leadership failures emanate from what has been called "bounded awareness" (Bazerman, 2014) coupled with a lack of courage to confront challenging truths. The recent emphasis on the need for emotional intelligence in leadership captures the need to have self-awareness and exercise self-control, in tandem with the need to read and manage the emotions of others (Goleman, Boyatzis, & McKee, 2002). Leader-member exchange research also implicates the importance of interpersonal reciprocation in how leaders achieve impact (Graen & Uhl Bein, 1995). As we have noted, influencing behaviors, in one form or another, seem to be an indispensable part of the repertoire of leadership, whilst reminding ourselves that no methods of mobilizing followers are independent of the state of mind of the followers and other contingencies (Hollander, 1992; Tjosvold, Andrews, & Struthers, 1993). For people in a state of disorganization, acute need, or threat, leaders will mobilize using some combination of willpower, vision of future states, and self-conviction—what is called charisma in the literature. For leaders under conditions of social complexity, political diversity, and conceptual challenge, a more facilitative model of influence will be required.

The most persuasive universals in this domain are not trait based. This is perhaps the most startling conclusion of the vast multinational GLOBE project, led by Robert House (House, Hanges, Javidan, Dorfman & Gupta, 2004). Rather, traits and styles are culture specific, whilst the universals include vision—seeing, as we have characterized it—and relational qualities, such as trust and integrity, reminding us that leadership is a social contract that engages the moral sensibilities that are present in all human communities (Brown & Trevino, 2006).

THE FUTURE OF LEADERSHIP: AN EVOLUTIONARY PERSPECTIVE

The enormous and diverse literature offers a host of possible ideas for cultivating states of mind and competencies for leaders, plus a huge array of human resources management methods to measure, develop, and support leaders, their teams, and their decision making. Yet this ship is rudderless without some guiding goals. What kind of world are we seeking to choose and prepare leaders for? The options seem limitless, though two growing trends are the challenge of leading dispersed diverse and virtual global teams, and the challenge of integrating ever more complex technologies and processes. Much that used to need leaders is now automated. The improving education and capability of knowledge workers is shifting towards new models of leadership and away from traditional control functions. Leadership in many areas of the economy becomes more facilitative around innovation, intelligence, implementing strategy, connecting networks, and managing change, against a background of rising expectations, increased regulation, and public scrutiny. This makes leaders more accountable, pressured, and in need of support.

These trends hold three important implications for how we develop and resource leaders.

SHARED LEADERSHIP

It is essential that the burden of leadership should not become so onerous as to demean and destroy those who might aspire to the role, or that its demands select out the people we most need to step up to the role. It is well to remember that how leadership roles are constructed is in our hands through institutional design. It is particularly pertinent that to manage the speed, complexity, and volatility of today's markets and technologies, more than one set of eyes, hands, and brains might be required, that is, for leadership to be less identified with the "lonely leader" model (O'Toole, Galbraith, & Lawler, 2002; Pearce & Conger, 2003). True shared leadership is rarely achieved overtly in formal paired leader roles, though informal sharing is a present feature of many leaders' partnerships with specific individuals, such as finance directors, COOs, and external trusted advisers (Hambrick & Cannella, 2004). These can be called "Critical Leader Relationships" (Nicholson, 2013).

In terms of the control model, the value of such partnerships is towards all three points of the model. Seeing: Leaders need insights beyond the charmed circle of acolytes and supporters that power always attracts, and for contrarian perspectives to the status quo to be entertained—especially important where adaptive demands are fast changing. Doing: To meet the demands of increased complexity and uncertainty, leaders need the advice and help of people with complementary skill sets. One pair of hands will not do. Being: Leaders need reflective disciplines, aided by constructive feedback and emotional support to navigate demands and expectations with confidence and courage (Alvarez & Svejenova, 2005).

For these relationships to flourish requires supportive structures and cultures that deemphasize intercolleague competition and an openness to the kinds of co-coaching practice that would enable these very substantial benefits to be realized (Nicholson, 2013). As we shall see in the next section, the feminization of leadership should help move in this direction.

WOMEN IN LEADERSHIP

Some feminists argue that gender biases in the social construction of leadership implicitly discriminate against women who might aspire to leadership roles. This seems at odds with scientific knowledge about sex differences in capability and preference (Buss, 1995; Geary, 1998); there is a case for saying that the multiplex world that is emerging in our times is highly amenable to the more collaborative egalitarian orientation of women. Such characterizations can be seen as stereotypical (Carli & Eagly, 2012), which raises the question about whether biological differences might underlie sex-typed attributions. It is also odd that such supervening power should be accorded to these beliefs, to the point of debarring women from leadership positions.

According to some writers, the effects are a deep and pervasive "gendering of the organization" through the infusion of discriminatory assumptions and expectations (Acker, 1990; Britton, 2000). But what if at root men and women have, for evolutionary reasons, preferences for different kinds of social order: men for agonic hierarchies where they can engage in competitive displays, and women for networks of inclusion and collaboration? The alternative reasoning here is that male dominance hierarchies, tournaments for dominance, feed the evolved need for reliable signals of fitness. Female exogamy (leaving the natal home to seek status through mating outside the family), on the other hand, favors the attributes such as interpersonal and collaborative skills that will enable a female to achieve and retain acceptance in a foreign clan (Ridley, 1993).

This would lead to an alternative explanation for the paucity of women in leadership roles, namely, that they do not like the games that have to be played in conventional hierarchical career progression and may be less skilled in playing them. An unpublished partial test strongly points in the direction of this hypothesis (Nicholson & Lee, 2014). The data show that the gendered organization does exist insofar as women strongly prefer to participate in, lead, and be led by women in decentralized nonhierarchical collaborative organizational designs, while men strongly prefer to join, lead, and be led by men in traditional hierarchies.

Such data suggest that the gendered organization exists as a structural phenomenon. The classic corporate hierarchy persists as a form preferred by men, rather than for its rational-economic benefits. That is, it satisfied needs and skills of the people who hold command over it, and who have prospered under it: dominant males. The scarcity of few women leaders is thus partly because the construction of leadership and paths to it are unattractive, unamenable, and unavailable to many women.

It is also part of our evolutionary heritage that the generally higher male desire to succeed in competitive environments—to provide enhanced reproductive fitness—means that men will endure more stress, risk, and degraded experience for the sake of getting ahead in hierarchies (G. F. Miller, 2000). This has the consequence that even in "feminized" environments, a disproportionate number of males are found in the more senior roles.

Can we be hopeful that there we can anticipate a causal sequence as follows? The business environment requires flatter, more collaborative structures to deliver innovation, service, and quality; these structures attract more women and advance them faster to positions of leadership because they possess the requisite skills. Possibly, but the evolutionary argument suggests that so long as leadership roles are highly rewarded positions, even the in the flattest structures, men will strive unequally for them, and indeed may be motivated to reproduce hierarchical forms where possible.

The Self-Regulated Leader

The implication of the analysis I have presented here points in two directions for the future development of leaders. The first is Follett's "Law of the Situation"

(Urwick, 1987), and the idea that attention should shift from "being" to "seeing." Rather than seeking and selecting "universal" leaders, we would do better to equip the men and women who would lead with the tools for visionary inquiry. These are those that take the leader beyond the charmed circles of local culture, power, informants, and stakeholders. The challenge of "being" that this arouses is how leaders can be helped to retune perceptions, beliefs, and intentions to meet the challenge of insight.

This then leads to the second strand for development, what in the literature is called self-regulation (Karoly, 1993). In much of the psychological literature, this is reduced to simple dichotomies of information processing, such as promotion and prevention focus (Higgins, 2002) and mood self-management (John & Gross, 2004), but the challenge is much wider, as William James first observed over a century ago (James, 1890/1950). He saw the self as an adaptive organ, with the supreme attribute of reflexive control. This is not the same as free will, though it feels very much like it, for alone among species we seem to have extraordinary powers of self-control, mediated by a consciousness of ourselves and of others as willed agents with the ability to control and plan future outcomes (Bandura, 2008).

Reflexive self-consciousness presents a profound challenge to evolutionary thought. Some have dismissed the self as epiphenomenal or a delusion (Dennett, 1995; Kurzban, 2010), though others recognize that complete accounts of human behavior are impossible without it (Leary & Buttermore, 2003; Nicholson, 2011). Autobiographical narratives are an important part of the leadership process and the niche construction. Evolutionary science does not have to be a detached bystander in the observation of leadership and its consequences. It can play an active role in helping us conceive of workable arrangements of power and response and provide us with new tools for insight into the kinds of institutions, management systems, and subcultures that can bring out the best in society and its members.

Rather than continuing the search for leadership laws and universals, which turn out to be locally bounded and driven by the covert needs of our primitive "romantic" yearnings, we can embrace more systemic and contextualized perspectives. As an adaptive function, leadership is prone to failure, often due to the idealized and stereotypical simplification attributions it attracts. The future of scholarship lies in understanding how this function operates differently according to the needs of time, place, and occupants and how we can ensure we reap the benefits by managing the adaptive capabilities of leaders and their institutions.

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CHAPTER 52

Evolutionary Psychology and the Law

OWEN D. JONES

FORGET CRIMINAL TRIALS, speeding tickets, and plaintiffs' attorneys looking for big wins on small injuries. Forget divorce lawyers, robed judges, and antidrug legislation. These are among the many distractors for the unwary, who often miss the most important thing to understand about law. It is a tool for moving human animals to behave in ways they would not otherwise behave if left solely to their own devices. Put starkly, legal systems modify features of the human environment in order to modify human behavior. Viewed this way, law's need for evolutionary perspectives on behavior, including those from evolutionary biology and evolutionary psychology, becomes obvious. A better understanding of behavior can aid society's efforts to change behavior.

Legal systems encourage people to act in ways that further public goals. These goals obviously vary. For example, they range from controlling pollution to ensuring a minimum income for society's poorest, from facilitating a thriving economy to protecting property from theft, and from ensuring that foods and drugs are safe and effective to ensuring that important disputes are resolved without violence in fair and principled ways.

Of course, it is the rare public goal that would, if achieved, benefit all individuals in a society equally. The interests of individuals are rarely identical—and in democratic societies public goals are typically those goals that a sufficient number of individuals representing yet other individuals designate as public goals. In the end, however, legal policy makers are among the key players in soliciting, framing, articulating, and ultimately defining these varied public goals. Policy makers not only influence which goals will become top priorities, they also help to choose among possible methods for pursuing these goals.

Although methods vary considerably, they typically sort into two general categories. One category includes methods that physically force people to behave (or not to behave) in a given way. For example, incarceration, among other things, physically prevents offenders from reoffending. The other category includes methods that influence behavior less directly, by changing incentives through things such as taxes, fines, rewards, and threats of various sorts.

In general, efforts to effect a behavioral change by changing incentives rely on numerous assumptions, comprising explicit or implicit behavioral models, about where human behavior comes from, what affects it, and how. Yet, to date, with some notable exceptions, legal policy makers are either surprisingly unaware of the extent of their dependence on behavioral models or, instead, complacent in their belief that they already deploy good ones.

In either case, integrating evolutionary perspectives on human behavior can help (Jones & Goldsmith, 2005). This chapter (originally written for the previous edition of this book, but now including an update at the end, about developments over the last decade) consequently explores and illustrates a number of specific contexts in which "evolutionary analysis in law" (Jones, 1997) can prove useful.

INCREASING EFFICIENCY

At the most general level, evolutionary analysis in law can help to increase efficiency. The efficiency of legal methods in achieving legal goals by inspiring changes in human behavior depends on a robust behavioral model. In this way, and as Figure 52.1 illustrates, the efficiency of law depends on an accurate behavioral model in the same way that the efficiency of a lever depends on the solidity of its fulcrum.

Soft fulcra are poor fulcra. Inaccurate behavioral models therefore serve as inefficient fulcra for the lever of law. Moreover, behavioral models that omit evolutionary perspectives are often materially inaccurate. Thus, to the extent that evolutionary processes influence human behavioral predispositions, a robust behavioral model should incorporate evolutionary perspectives. More specifically, if improving behavioral models can yield more effective legal tools, and if human behavior is influenced by evolutionary processes, then greater knowledge of how evolutionary processes influence human behavior may improve law's ability to regulate it.

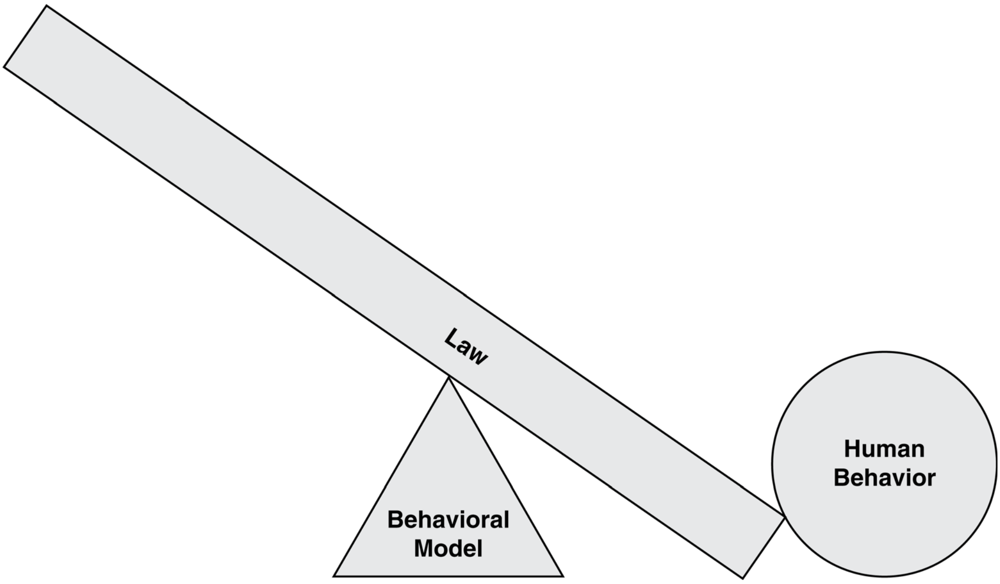

Figure 52.1 The Dependence of Law on Sound Behavioral Models.

DISCOVERING USEFUL PATTERNS IN REGULABLE BEHAVIOR

Because data neither self-collect nor self-organize, discovering patterns in data often requires some theory that suggests what data to collect and what aspects of the data to cross-correlate. Evolutionary analysis can often serve as one source of theories to help us collect and collate data in pattern-revealing ways relevant to law.

For example, there is a vast literature in animal behavior on infanticide (Hausfater & Hrdy, 1984; Jones, 1997, includes an overview). Natural selection appears to have favored, in many species, the selective elimination of unweaned infants by unrelated males in a position to mate with the mother. Nursing has a contraceptive effect (which apparently functions to adaptively regulate the interbirth interval), and the death of the infant speeds the mother's return to an impregnable state. This affords material advantage to the selectively infanticidal male, and the great risk to unweaned infants drops off commensurately at weaning age, when the juvenile impinges less directly on its mother's impregnability.

The evolutionary analysis of this pattern in other species suggested to psychologists Daly and Wilson (1988) that a similar pattern may occur in human populations. It does. Although the contraceptive effect of nursing is somewhat less pronounced in humans, Daly and Wilson found an extremely elevated risk of death to an unweaned infant (roughly a 100-fold increase) in the presence of unrelated males, and a similarly precipitous drop in risk at weaning age. It is important that, although there was some general assumption of increased risk, neither the magnitude of the risk nor the sudden change in risk at weaning age was previously appreciated, largely because data on relevant variables (e.g., the presence or absence of genetic relatedness) were often uncollected.

The point here is not that stepparents of dead infants should be considered guilty until proven innocent. The point is that through political processes, the legal system is presently tasked, in part, with helping to improve ways for investigating and preventing child abuse and infanticide. And it could do this, in part, by directing limited resources toward child protective services agencies, helping to fund data collection efforts, helping to specify variables on which data should be collected, and aiding in the creation of effective protocols for prioritizing and investigating rumors of abuse that may precede serious injuries.

Consequently, a theory that could influence data collection in ways leading to the discovery that stepparents are roughly 100 times more likely to kill an infant than genetic parents would seem extremely useful in achieving maximum prevention. And there are probably many other law-relevant patterns that evolutionary analysis can help reveal. These might arise from contexts pertinent to spousal abuse, homicide, marriage patterns, family size and composition patterns, deviations from rational choice predictions, and the like, to name a few.

UNCOVERING POLICY CONFLICTS

Evolutionary perspectives cannot by themselves justify what law should do. For instance, the fact that stepparents not only kill but also abuse their stepchildren at far higher rates per capita than do parents says precisely nothing about whether the law *should* take stepparentage into account in any way (as it might do, for example, in specifying investigation protocols for child protective services agencies having limited investigative resources).

Nonetheless, one use for evolutionary analysis is to identify previously under-recognized policy conflicts. Consider, for example, the seemingly unrelated goals of destigmatizing stepparentage, on one hand, and reducing infant deaths, on the other. Evolutionary analysis, by itself, has no bearing on which of these two goals should be deemed the higher priority. But it can suggest that success in pursuing either goal may importantly trade against success in pursuing the other. Revealing such trade-offs in law may aid our efforts to lessen them—because seeing a potential policy conflict is the first step in resolving it.

SHARPENING COST-BENEFIT ANALYSES

We know that when a legislature allocates funds to build a tunnel or fails to prohibit its governed from driving cars, people will die. But we consider the benefits worth the costs. Although there is much legitimate debate about the contexts in which cost-benefit analysis may be useful, one thing is clear. Whenever it is used, inaccurate tallies will improperly skew results.

When evolutionary analysis reveals hidden policy contexts, it also offers collateral benefits, in that it helps to clarify and quantify the trade-offs involved in simultaneously pursuing two different legal goals that conflict. For example, evolutionary analysis suggests that one cost of moving aggressively to reduce infanticide and child abuse may be the collateral stigmatization of all stepparents due to the actions of only a fraction. Correspondingly, the cost protecting stepparents from such stigmatization may include some number of otherwise preventable infant deaths or child injuries.

CLARIFYING CAUSAL LINKS

Because causality cannot be inferred from data alone, we are typically hesitant to base legal policies on mere correlations lacking explanations. Consequently, one role for evolutionary analysis in law concerns the development and support of causal theories that trace an understandable pathway between correlated phenomena.

For example, even if we strongly suspected that stepparents were more likely per capita to abuse stepchildren than were genetic parents, we would have good reason not to act on that suspicion. Our observations may be skewed as a function of prejudice. Our righteous zeal to aid children might lead to scapegoating vulnerable targets. And our collective history in oversimplifying complex phenomena should give us proper pause. There may be complicating confounds.

But consider how evolutionary analysis offers two things. First, it details a pathway by which natural selection can favor condition-dependent male behavioral predispositions that can yield fatal abuse of unweaned offspring of potential mates. Second, it connects empirical data on infanticide in humans and nonhumans. In such cases, and even when evolutionary analysis might not itself lead to discoveries of new patterns, its frequent ability to provide robust explanations for correlations can make an important difference in legal policy. It can help to provide the logical foundation that serves as an important prerequisite to establishing legal policies that are both efficacious and reasonable.

PROVIDING THEORETICAL FOUNDATION AND POTENTIAL PREDICTIVE POWER

Evolutionary analysis can sometimes provide theoretical foundation for known behavioral data lacking coherence, and thus serve to help predict undiscovered patterns in human behavior (Jones, 2001d). Consider, for example, that large body of literature known as *behavioral law and economics* (BLE). Eschewing traditional law and economics approaches, scholars of BLE seek to incorporate insights from cognitive psychology (of the Tversky and Kahneman heuristics and biases kind; Tversky & Kahneman, 1982). Their efforts are aimed at understanding apparent deviations of human behavior from neoclassical economic rationality predictions. Examples follow, but the key point is that humans often behave in ways that seem substantively irrational, and BLE scholars would like law to take account of these deviations. The law generally assumes—particularly when estimating the efficiency properties of rules—that people will not make routine errors in their attempts to maximize their utility. And if that assumption is wrong, then laws based on it may be flawed.

On one hand, the BLE movement usefully draws attention to the ways in which real people behave differently from theoretical people. And this is obviously useful for policy makers. On the other hand, the BLE scholars are presently far better at detailing *that* people behave in manners inconsistent with various rational choice predictions than they are at explaining *why* they do so (Jones, in press). And that *why* is the key to a theoretical foundation sufficiently robust to aid predictions about undiscovered patterns. By way of illustration, consider three seemingly irrational biases, and the problems they pose for law.

Rational choice theorists assume that people deploy rationally appropriate "discount rates" when evaluating the future. For example, a dollar to be received 5 years from now should be discounted, compared to a dollar received today, at a rate that reflects reasonable expectations for inflation. Yet people often employ absurdly high discount rates. For example, they often underinsulate their homes, even though the cost of adding insulation will be earned back in energy savings within a very short time (Ulen, 1994). That is, they act as if inflation will be enormously high over the next few years (between 45% and 300%, by some estimates, when energy-saving appliances are at issue; Ulen, 1994) such that the large money they save in energy efficiency in the future will be worth less than the small amount they save today in purchasing less insulation. The existence of seemingly oversteep discounting has important legal implications. These include, for example, matters as diverse as discouraging needless pollution and encouraging appropriate savings for retirement.

Rational choice theorists also assume that people will base their choices on realistic assessments of probabilities. But people routinely make gross errors in assessing probability. For example, they often fail to recognize that an activity posing a .7 risk of death is more dangerous than an activity in which 6 out of 10 people participating will die (Slovic, Fischhoff, & Lichtenstein, 1982). This error has important consequences for legal policies concerning risk regulation.

Rational choice theorists assume that people will value property sensibly and consistently. For example, the difference between an individual's maximum willingness to pay for a good or legal right and the minimum compensation that individual would demand to willingly sell it should be negligible. But often it is not. Experiments indicate that people often value something they have just received at a higher amount than they would have been willing to pay for it (E. Hoffman & Spitzer, 1993). This phenomenon, often referred to as an *endowment effect*, has important consequences for the legal distribution of entitlements. For example, and as with goods, the end distribution of various legal rights should be insensitive to the initial distribution (at least when information and transaction costs are low) because the party who values the right more will simply purchase the right from the party who values it less (Jones & Brosnan, 2008), leaving the end result economically efficient, regardless of to whom the legal system initially gives the right. But the existence of endowment effects suggests that, in sharp contrast, the initial distribution of rights will be "sticky," because those who receive them first will suddenly value those rights more than they would have been willing to pay for them in the first place, which may leave the end result inefficient.

These legally relevant irrationalities, and others like them, are presently thought to arise from some peculiar combination of *bounded rationality* and (in these oft-used terms) cognitive fallibilities, frailties, flaws, errors, defects, quirks, limitations, and imperfections (Jones, 2001d). Bounded rationality describes deviations from rational choice predictions as the result of (a) constraints on time and energy for gathering perfect information and (b) constraints on the brain's information capacities, wiring, and computing speed (Simon, 1990).

But even a moment's reflection makes clear that this approach is unsatisfactory. There is no theoretical framework that explains the patterns of irrationalities, connects them together, and points in new directions. For example, why do people apparently tend to overdiscount the future, rather than to underdiscount it or to discount it randomly? Why do people apparently tend to overendow goods, rather than to underendow goods or to endow goods randomly?

A number of people have independently explored these and related phenomena from evolutionary angles. There are at least three approaches. Gigerenzer (1991, 1998; Gigerenzer, Todd, & The ABC Research Group, 1999) developed the idea of "ecological rationality," which considers some seeming irrationalities as artifacts of experimental designs. For instance, mistaken probability assessments may follow from information about risk being presented in the format of modern statistics, rather than the more natural format of frequency distributions. Haselton and Buss (2000, 2003) developed "error management theory," which suggests that biases leading to error can evolve from the effects of evolutionary processes responsive to the asymmetric costs of false positives and false negatives, when attempting to infer the intentions of others. For instance, asymmetries between the sexes in minimum investment in offspring and maximum lifetime number of offspring can ultimately lead to male overperception of female sexual interest and female underperception of male commitment. My own work (Jones, 1999a, 2001b, 2001d) develops the concept of "time-shifted rationality," which considers much of what gets lumped under the umbrellas of *bounded rationality* and *cognitive quirks* to reflect finely tuned cognitive adaptations to environments lacking the modern features (such as highly abstract notions of legally enforceable rights to resources) that render them irrational in the present era. For instance, viewed in the context of ancestral environments, endowment effects may reflect an adaptive bias to keeping a less preferred but certain resource already possessed, instead of risking uncertain performance of an offered exchange for a more valued item.

These three evolutionary approaches—focusing on ecological rationality, error management, and time-shifted rationality—emphasize different aspects of various cognitive puzzles but are nonetheless compatible. Whether joined or used separately, the perspectives on human irrationalities that these three approaches offer hold some significant promise, in the legal arena, of providing theoretical foundation to patterns in existing anomalies and helping to predict undiscovered patterns.

ASSESSING COMPARATIVE EFFECTIVENESS OF LEGAL STRATEGIES

Time-shifted rationality—the propensity toward behavior that was adaptive in ancestral environments, even if it is irrational or counterproductive in novel current environments—also has a role to play in helping us compare probable effectiveness of differing legal approaches to changing people's behaviors.

We know that, with some exceptions, the demand for a given good will tend to go down as the price for that good goes up. The general relationship between changing price and changing demand is commonly represented graphically by a "demand curve" (often portrayed for simplicity by a straight line, with price on the vertical axis; see Figure 52.2).

We also know that behaviors have their own demand curves. Increase the "price" of engaging in a behavior, by increasing the associated fine or the prison term, for example, and generally the incidence of that behavior will decrease (holding constant the probabilities that an offender will be detected, apprehended, and subjected to penalty).

The problem is that we know very little about the precise *relationship* between increased prices and decreased incidence of behavior, except from trial, error, and intuition. Because sanctions are themselves costly to administer, we would benefit from having some sense, ahead of time, of the likely return on our investment in sanctions. Specifically, we would like some sense of *how much* of a decrease in undesirable behavior are we buying with each increment of increased penalty?

Figure 52.3 makes the point more graphically. At one extreme, a behavior may be very responsive to increases in sanctions, so that a relatively small increase in price yields a big decrease in behavior. The demand curve for such a behavior may look like the more horizontal curve A. Or, at the other extreme, a behavior may be relatively

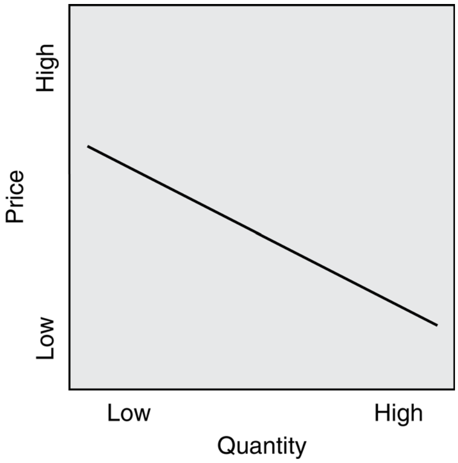

Figure 52.2 General Assumption in Law About the Relationship Between the Incidence of a Behavior and the Cost of That Behavior.

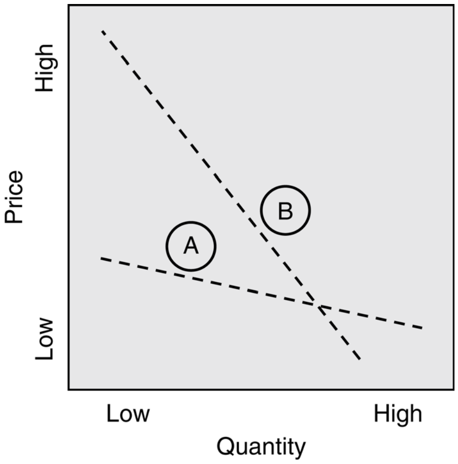

Figure 52.3 Variations in Responsiveness of Behavior to Increasing Cost.

insensitive to increases in sanctions, so that a very large increase in sanctions is necessary to achieve even a modest decrease in behavior. The demand curve for such a behavior may look like the more vertical curve B.[1] Holding the probabilities of detection, apprehension, and penalty constant, the curve for some behaviors, such as jaywalking, will more closely resemble curve A. And the curve for some behaviors, such as becoming violent when coming upon a spouse engaged in adulterous sex, will more closely resemble curve B.

Evolutionary perspectives enable us to derive a principle that can help legal thinkers anticipate in general terms the comparative sensitivities of various human behaviors to changes in incentives effected with legal tools. That principle helps not only to explain but also to predict differences in the relative steepness of demand curves for, and hence the comparative sensitivities of, different behaviors.

I call that principle the *law of law's leverage* (Jones 1999a, 2000, 2001b, 2001d). It predicts that

> The magnitude of legal intervention necessary to reduce or to increase the incidence of any human behavior will correlate positively or negatively, respectively, with the extent to which a predisposition contributing to that behavior was adaptive for its bearers, on average, in past environments.

Here is what the terms mean.

"Magnitude of legal intervention" refers, in most instances, to costliness. Greater resistance to change will increase the cost of effecting change. "The extent to which" a predisposition contributing to the behavior was adaptive to its bearers underscores the fact that while members of a species share a variety of different adaptations, some

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[1] This discussion adopts the common convention of using variations in slope to capture the idea of variations in what, technically, are "elasticities" (by, for example, describing inelastic demand with a steeply sloped demand curve). The slope of a demand curve is the rate of change of price with demand. Elasticity is the percentage change in price divided by the percentage change in demand. It can be computed from knowledge of the slope at a given point on the curve. In comparing nonlinear demand curves for different activities, comparisons of slope must refer to comparable regions of curves.

(such as hunger) are comparatively more important than others (such as the capacity for empathy). "A predisposition" refers to a psychological trait that is a heritable and behavior-biasing algorithm manifested in the brain's neural architecture. For a behavioral predisposition to be "adaptive," it must have conferred greater fitness benefits on individuals that bore it than did any other contemporaneously existing alternatives exhibited by other individuals within the population, and thus have been maintained by natural selection. Genetic fitness is measured in terms of inclusive fitness (rather than simply offspring) taking into account degrees of consanguinity. The term "on average" in the law of law's leverage refers to whether the cumulated effects of the adaptation, across all the organisms that bore it, yielded increases in inclusive fitness that outweighed any decreases. That is, on average the trait increased the reproductive success of organisms that bore it. "Past environments" refers to the environment of evolutionary adaptedness (EEA). The relevant EEA varies from feature to feature.

Consequently, a more detailed and accurate (if also more cumbersome) rephrasing is this: The law of law's leverage states that the magnitude of legal intervention necessary to reduce or to increase the incidence of any human behavior will correlate positively or negatively, respectively, with the extent to which a behavior-biasing, information-processing predisposition underlying that behavior (a) increased the inclusive fitness of those bearing the predisposition, on average, more than it decreased it, across all those bearing the predisposition, in the environment in which it evolved and (b) increased the inclusive fitness of those bearing the predisposition more, on average, than did any other alternative predisposition that happened to appear in the environment during the same period.

This law of law's leverage predicts that, typically, it will be less costly to shift a behavior in ways that tended to increase reproductive success in ancestral environments (measured in inclusive fitness) than it will be to shift behavior in ways that tended to decrease reproductive success in ancestral environments. In other words, the slope of the demand curve for historically adaptive behavior that is now deemed undesirable will be far steeper (reflecting less sensitivity to price) than the corresponding slope for behavior that was comparatively less adaptive in ancestral environments. This rule will tend to hold, even when the costs that an individual actually and foreseeably incurs in behaving in a historically adaptive way vastly exceed the presently foreseeable benefits of such behavior.

Consequently, the law of law's leverage predicts that in criminal law, family law, torts, property, and the like, behaviors involving the following things will prove more difficult to modify than the behavior of median difficulty: mating, fairness, homicide, child rearing, status seeking, property and territory, resource accumulation, sexuality (including infidelity and jealousy), speech, privacy, empathy, crimes of passion, moralistic aggression, risk valuation and risk taking, cooperative/altruistic behavior, male mate-guarding, and the like.

Here (largely from Jones, 2001d) are several examples:

- Evolutionary analysis predicts that, and explains why, the slope of the demand curve for adulterous behavior (like most sexual behavior) is likely to be comparatively steep (Buss 1999a, 1999b, 2000) and thus comparatively insensitive to the imposition of legal prohibitions.
- Evolutionary analysis also predicts that, and may help explain why, marriage, separation, divorce, and remarriage behavior will be less sensitive to legal

changes than will be many other forms of behavior (Ellman & Lohr, 1998; Fisher, 1994).

- Because, as we know, natural selection disfavors inbreeding among close relatives (Goldsmith, 1994; Goldsmith & Zimmerman, 2000), evolutionary analysis predicts that it will be far less costly to achieve a given low rate of incest per capita between a parent and his or her natural children, and among siblings reared together, than to achieve the same low rate of incest per capita between stepparents and stepchildren, and among stepchildren.
- Because we know that natural selection favors discriminative parental solicitude rather than indiscriminate parental solicitude (i.e., it generally favors psychological mechanisms that bias resources toward offspring over nonoffspring; Daly & Wilson, 1995), we can predict that men under court order to provide child support payments for a child they know or suspect they did not father will be less likely to comply, on average, than will biological fathers (Wilson, 1987).
- Because we know that threats to status within a social group impose particularly large costs across evolutionary time (Daly & Wilson, 1988; Buss & Shackelford, 1997), we can predict that the slope of the demand curve for violence consequent to status threats will be steeper than that for most other proscribable behavior, and will be particularly steep in public.
- Because we know that the asymmetries for males and females of internally fertilizing species in the consequences of a partner having sex with a third party favored sexual proprietariness in males more strongly than in females (because only males can be uncertain of their genetic relationship to their putative children), we can predict that the slope of the demand curve for jealous violence (against rivals, or straying partners) will be steeper, on average, for males than for females (Buss, 2000).

Obviously, the law of law's leverage can neither predict demand curves for law-relevant behaviors with precision, nor can it individualize a curve to a single person. Moreover, statements about relative aggregate costs do not translate neatly into conclusions about cost effectiveness. Nonetheless, the law of law's leverage can offer some broad, novel, and useful insights into the differing ways law and behavior interact, depending on the behavior at issue. Because we understand that the brain tends to process information in ways that tended to yield adaptive solutions to problems encountered in the environment of evolutionary adaptedness, we can expect that behavioral inclinations will tend in turn to vary in their susceptibility to the influence of different legal tools. The principle can afford us more intellectual traction than we now have on predicting the comparative slopes of the demand curves. It can thereby afford additional information useful to estimating the relative costs to society of attempting to move different kinds of behavior. The principle also provides a new and powerful tool for explaining and predicting many of the existing and future architectures of legal systems—which is the subject of the next section.

REVEALING DEEP PATTERNS IN LEGAL ARCHITECTURE

Much has been said over the years about why human cultures generally, including legal cultures specifically, vary from place to place. But we have traditionally lacked comprehensive theories about the contexts in which we might expect legal cultures to be similar (e.g., what is punished or encouraged, and how) and why we might expect similarities. Evolutionary analysis can provide some of the framework for the development of such theories.

The logic proceeds this way. Because humans share an evolved, species-typical neural architecture, they in turn share a species-typical repertoire of emotions and behavioral predispositions (Barkow, Cosmides, & Tooby, 1992; Buss, 1999b; Goldsmith, 1994; Goldsmith & Zimmerman, 2000; Pinker, 2002). To the extent that legal systems are sensitive, in part, to the emotions and behavioral predispositions of a governed population, we may expect and predict that legal systems across time and across the world's cultures will tend to have nonrandom similarities in a variety of their major features. That is, because legal systems are both aspects of human behavior and societal responses to human behavior, and because evolutionary processes influence human behavior, we should expect to see the telltale results of evolutionary processes in legal systems.

There will be differences, of course. But we may expect that the architecture of human legal systems will, despite their differences, reflect the effects of evolutionary processes on the human brain, just as (in an example from Dawkins, 1989) the architecture of beaver dams, despite their differences, reflects the effects of evolutionary process on beaver brains.

Many scholars took intriguing initial steps in this direction (Alexander, 1979, 1987; Beckstrom, 1989; Gruter, 1977; Gruter & Bohannan, 1983; Wilson, 1987). I have attempted to build on that thinking—to describe possible foundations for what I call *biolegal history* (Jones, 2001c). And over the past decade (see the chapter-ending update later) there has been some exciting new work to report. In the meantime, and for general orientation, one way of looking at this is to consider how the main design features of legal systems can be described with four variables: *topics*, *content*, *tools*, and *effort*.

In brief, *topics* are the general subject matters that legal systems address (e.g., sexual behavior or access to resources). *Content* reflects the specific normative preferences people in policy-influencing positions tend to have about those subject matters (e.g., minors should be protected from sex with adults, and one person should not take resources from another without justification). *Tools* is a set that includes all methods potentially available to legal systems to bring reality into line with the normative preferences (e.g., incarceration or fines). *Effort* reflects the potential variation—from trivially easy to insurmountably difficult—in how difficult it may be to effect such change using any particular method.

We can roughly approximate some of the superstructure of legal systems—in ways that allow rough but potentially useful comparisons—by sketching together the specific *topics*, *content*, *tools*, and *effort* of which each system is composed. Evolutionary analysis, including both the ways in which evolutionary processes affect morality (*topics* and *content*; Alexander, 1987; Jones, 1999b, 2000) and the ways in which evolutionary processes affect the comparative difficulties law will have moving some behaviors with some methods compared to others (*tools* and *effort*), strongly suggests that superstructural patterns of legal systems will not vary randomly across cultures.

As in so many other contexts in which human behavior is examined, the very existence of variation can yield initial conclusions that differences outweigh similarities. I suspect much the same will be true as our knowledge of different legal systems across the world's many cultures increases. But legal systems should ideally be compared not just to each other (a technique that frequently highlights difference) but also to the possible legal architectures that the overall design space would allow—were the features of legal systems comparatively randomly distributed.

Evolutionary analysis predicts that, when viewed from this greater distance, legal systems will be rather clumped in one small sector of the overall design space. That is, evolutionary analysis suggests that a given legal architecture will not be—as often assumed—simply an amalgam of culture-specific norms, culture-specific religions, culture-specific morals, culture-specific politics, and general economic efficiencies. An evolutionary perspective provides a far different sense of the prior probabilities that various legal systems will have the structural elements they do.

Although this has recently begun to change, relatively little is known about how the propensities among all the world's many societies to govern selves and others with rules, laws, and other forms of legal behavior compare. Although there are some notable commonalities (e.g., proscriptions against the unjustified taking of human life; Brown, 1991), there has been until recently (see below) little work to systematically compare the legal cultures of large numbers of different human societies. Some cultures obviously have very formal legal structures, with copious and minutely detailed statutes, as well as extensive judiciaries and dedicated academies. In other cultures, behavior is regulated principally by less formal but highly significant social controls—such as ostracism—operating within relatively small groups. But in all cases evolutionists would expect that the need to establish norms for proper behavior and the need for enforcing such norms will tend to reflect the evolved features of the human brain, as will the patterns in which these needs are satisfied. Evolutionary perspectives on legal behavior may therefore help us acquire a richer and more coherent sense of the deep structure of human legal systems shared cross-culturally.

EXPOSING UNWARRANTED ASSUMPTIONS

Evolutionary thinking can often supply, in Dennett's (1995) term, a "universal acid" for dissolving untenable ideas. This is as important a function to perform in law as it is elsewhere. Because if reliance on flawed assumptions about the causes of a given behavior are wrong, and evolutionary analysis can help to reveal this, we can minimize the effects of flawed legal approaches and get on with the business of pursuing more effective ones.

A good example comes from the law's various approaches to curbing sexual aggression. Few things warrant greater efforts. Yet different legal approaches have been based, over time, on very markedly different theories of where sexual aggression comes from. An early psychiatric theory led to legal regimes predicated on the notion that rapists are crazy people. Subsequently, a sociological emphasis led to regimes predicated on the idea that rapists are conditioned into being rapists by their sociocultural milieu. And the influence of later feminist theories led, in part, to anti-sexual-violence statutes reflecting the assumption that a cross-sex rape is simply a crime of gender hatred, just as a cross-race lynching is a crime of racial hatred.

Rape is an important and delicate topic, which I have explored elsewhere at length (e.g., Jones, 1999c). Its very existence is a reminder of how disinhibiting the aggressive exercise of power can foster fear, impede female autonomy, and improperly restrain women's bodies, lives, and opportunities. But clearly our inability to eliminate rape, with the various tools available to law, strongly suggests that our understanding of the phenomenon is imperfect.

No single discipline, probably, can alone supply a complete model of the phenomenon. Yet, a thorough grounding in both general evolutionary studies and in the many studies of patterns of sexual aggression in humans and in the many other species in which sexual aggression occurs (see, e.g., studies cited in Jones, 1999c, Appendix A) suggests that at least one thing is intellectually untenable. It is incorrect to assume—as has been done so often that people now mistakenly confuse preference with fact—that sexual desire is entirely irrelevant to sexual aggression.

Specifically, a thorough and detailed study of hypotheses and evidence concerning sexual aggression in the many other species in which it occurs, and in the many distinct patterns in which it appears, suggests that evolutionary processes have had an important influence on patterns of human sexual aggression, just as they have had important influence on other patterns of conflict. The patterns of sexual aggression in other species are simply too numerous, too consonant, and too distinct. And the near identity of those patterns, in relevant respects, with human data on sexual aggression is striking (Jones, 1999c).

The point here, though, is not that evolutionary analysis alone provides useful perspectives on rape phenomena. The point is that evolutionary analysis is often an essential part of any complete picture of human behavior. While causes of any individual's act of sexual aggression can vary, it is simply illogical to assume that the effects of evolutionary processes on the biology of sexual desire are irrelevant to patterns of human sexual aggression. Even a minimum facility in behavioral biology can help to disclose why such an assumption, as well as many similar assumptions in other legal contexts, no matter how well intentioned, are likely unwarranted and also likely to send legal policies in inefficient directions.

DISENTANGLING MULTIPLE CAUSES

Evolutionary analysis in law highlights the distinction between, and essential complementarity of, different levels (proximate and ultimate) of causation. In the context of sexual aggression, for example, this encourages us to look beyond falsely dichotomous thinking, and to recognize that the clear existence of environmental factors that influence probabilities of sexual aggression in no way diminishes the role of evolutionary processes in associating those environmental factors with the behavioral repertoires specific to sexual aggression.

INCREASING ACCURACY

Generally speaking, accuracy is better than inaccuracy. And incorporating evolutionary perspectives into legal thinking will, on many occasions, help to increase accuracy.

There are two principal ways in which legal thinking may reflect inaccurate assumptions. One is to be flat-out wrong. For example, suppose that those charged with developing a legal approach to reducing the incidence of aggression assumed that aggression in humans is entirely socioculturally determined. That assumption, as best as we can know, is simply wrong. The body of evidence, and the robustness of corresponding theory, supporting the existence of evolutionary effects on patterns of aggression is overwhelming, compared to evidence to the contrary.

The other way to be inaccurate is through incompleteness. Incompleteness often contributes to inaccuracy in the form of misplaced emphasis. For example, suppose those charged with reducing the incidence of aggression were agnostic on whether there were evolutionary influences on patterns of human aggression, but their approach ultimately reflected attention only to sociocultural contributions to patterns of aggression. The overwhelming evidence that aggression is affected both by environmental inputs and by the ways in which corporeal brains have evolved to associate certain patterns of environmental inputs with psychological states tending to increase or decrease aggression renders such a legal approach inaccurate through incompleteness.

To be clear, I am not advocating reflexive deference to the evolutionary sciences. For one thing, no scientific principles are categorically beyond legitimate challenge. And, more importantly, there may be times when what it costs (in time, money, misunderstandings, or misuse) to increase accuracy is far greater than the payoff at the other end (Jones, 2004; Ulen, 2001). For legal systems are not just about a search for truth (though they are often about that). Frequently, legal systems are tasked with getting the most bang, measured in desired human behavioral changes, for the fewest bucks—bucks not being infinite. Consequently, for example, a policy based on assumptions that are 80% accurate, and which is ultimately 70% effective, may be preferable to one that is 98% accurate, 98% effective, and 6 times as costly.

There may therefore be, on occasion, justification for knowingly choosing to accommodate inaccuracy in behavioral models. But the point here is that to knowingly engage in a fiction without an affirmative and justifiable decision to do so is to improperly privilege flawed approaches.

INCREASING LAW-RELEVANT UNDERSTANDING ABOUT PEOPLE

Aside from all the many policy-level benefits of blending evolutionary insights into the legal system's approaches toward influencing human behaviors, evolutionary thinking has street value in a number of practical, frontline contexts. For example, good lawyers understand people. They have a good sense of what motivates people and how those motivations translate into behavior relevant to the legal system, such as obeying or disobeying laws, initiating or settling lawsuits, and the like.

Evolutionary perspectives are often useful in this context. Consider litigation. Traditional economic theory predicts that a plaintiff will pursue litigation as long as the potential recovery, multiplied by the probability of success, exceeds foreseeable litigation costs. But real people often do not behave this way, and much litigation behavior is pursued at some cost in order to impose a greater cost on another.

To those with an evolutionary lens, this behavior is not surprising. Our brains did not evolve solely as temporally narrow cost-benefit maximizing machines. And there are at least two pathways by which such costly but cost-inflicting behavior can have evolved.

First, retributive spitefulness can be a component of a mixed, evolutionarily stable strategy for reaping gains from cooperation and punishing defectors. Even when spiteful behavior is unlikely to yield compensating advantages in future interactions with others, as a function of current reputational effects (Frank, 1988), our evolved behavioral predispositions may incline us toward spiteful behavior because of its adaptive effect on local reputation in ancestral environments. Second, behaviors that impose greater costs on competitors than on selves can evolve straightforwardly, even in the absence of retributive predispositions, because a decrease in absolute status or condition that nonetheless results in an increase in *relative* status or condition yields evolutionary gains.

Just as lawyers ignorant of human emotions are likely to be poor lawyers, lawyers ignorant of the effects of evolutionary processes on human psychology are likely, in many contexts, to be less effective than they might be otherwise. The ability of evolutionary perspectives to offer new and useful insights into human psychology can therefore render those perspectives both important and advantageous.

GENERATING NEW RESEARCH QUESTIONS

Notably, this cross-fertilization of evolutionary and legal disciplines need not be unidirectional. If there are a number of advantages for legal thinking in learning more about evolutionary processes from evolutionists, there are at least three advantages for evolutionists in learning more about law.

The first advantage arises from the ability of law to represent an area of *applied* evolutionary analysis. While knowledge generation is a worthy goal in itself, comparatively little attention has focused on the *utility* of evolutionary perspectives on human behavior. Just as Darwinian medicine (Nesse & Williams, 1996) represents a useful application of evolutionary knowledge in health contexts, so can evolutionary analysis in law offer new opportunities for application in legal contexts. The advantage for evolutionists, then, is that the wide variety of things useful for legal thinkers to know can help to generate important researchable questions and to open up new areas of research for evolutionists in search of new research frontiers.

The second advantage, and one apparently first articulated by Beckstrom (1989), is that legal databases contain more than 10 million reported cases (in full on-line texts with Boolean searching) that together can serve as accumulated observational data for testing evolutionary hypotheses. Moreover, the variation in the legal environments of the 50 states yields virtually untapped data from 50 natural laboratories.

The third advantage is the opportunity to analyze the work of legal actors themselves within evolutionary frameworks. For law not only *deals* in human behavior, it *is* human behavior. And the behaviors of judges, legislators, lawyers, police, and the like have yet to be examined systematically from an evolutionary perspective. For example, the way people with effective influence over law actually wield that influence likely reflects condition-dependent predispositions sensitive to relative power and status, which in turn influence their goals and behaviors.

CONCLUSIONS

Let's take stock. By integrating evolutionary insights into legal thinking, both legal policy makers and evolutionists can help to:

- Increase efficiency.
- Discover useful patterns in regulable behavior.
- Uncover policy conflicts.
- Sharpen cost-benefit analyses.
- Clarify causal links.
- Provide theoretical foundation and potential predictive power.
- Assess comparative effectiveness of legal strategies.
- Reveal deep patterns in legal architecture.
- Expose unwarranted assumptions.

- Disentangle multiple causes.
- Increase accuracy.
- Increase law-relevant understanding about people.
- Generate new research questions.

Each of the preceding examples of the usefulness of evolutionary analysis in law could alone justify focused integration of evolutionary sciences into behavioral models essential to sound legal thinking. Viewed together, they make an even more powerful, geometrically stronger case (Jones & Goldsmith, 2005). What, then, might serve to delay?

There are a number of obstacles. For instance, few legal thinkers have either strong backgrounds or interests in science—so ability and enthusiasm are often lacking. Few understand the distinction between proximate and ultimate causation in biology (particularly since the former term bears a different meaning in biology than it bears in law). Consequently, false dichotomization of social and biological influences is common. Condition dependence, and the evolution of algorithmic predispositions, are widely unrecognized. Consequently, the more subtle, environmentally sensitive dimensions of behavioral biology get overlooked.

All of these factors lead to, among other misperceptions (described in Jones, 1999c, 2001a), ascription of genetically deterministic viewpoints, defense of the supposed categorical boundary between meaningful human behavior and the behavior of all other species, and the assumption that discussion in law of evolved behavioral predispositions could prove useful only in the contexts of genetic defenses in criminal trials. The latter both reflects and then reinforces the fear that proponents of evolutionary analysis in law will try to use explanation as justification.

This assumption is, of course, mostly nonsense. And it stems not merely from healthy skepticism, or even from an appropriate and constructive caution concerning all things biobehavioral that traces to the historical misuses of biology in both politics and in law (e.g., *Buck v. Bell*, 1927). Instead, it stems largely from the cultural gap between scientists and nonscientists, the obsolete overdivision within universities of human and nonhuman species, and the general time lag between the advances in scientific arenas and their recognition and understanding in legal arenas.

Many have argued—albeit in differing ways—for the potential value to law of evolutionary perspectives. A sampling of works spanning the first 25 years includes (in chronological order): Gruter, 1979; Gruter & Bohannan, 1983; Beckstrom,1985; Gruter & Masters, 1986; Stake, 1990; Rodgers, 1993; Fikentscher & McGuire, 1994; Browne, 1995; Frolik, 1996; Ruhl, 1996; Jones, 1997; Grady & McGuire, 1997; McGinnis, 1997; Coletta, 1998; Monahan, 2000; Goodenough, 2001; Gruter & Morhenn, 2001; Elliott, 2001; O'Hara & Yarn, 2002; Jones & Goldsmith, 2005. More recent works are discussed in the next section. Together, these illustrate broad interests that have manifested in a wide variety of programs, conferences, initiatives, courses, publications, and organizations.

For example, the Gruter Institute for Law and Behavioral Research (www.gruterinstitute.org) has a long history in educating legal and evolutionary thinkers, through conferences and publications, about prospects for important work at the intersection of their disciplines. And the Society for Evolutionary Analysis in Law (SEAL; www.sealsite.org) has helped to generate engagement and scholarship through its network of several hundred interdisciplinary members spanning more than 30 countries. The prospects for integrating evolutionary insights into law consequently look bright, despite a number of significant but surmountable impediments.

The scope of law is vast. The flow of resources, the protection of the citizenry, the regulation of risks, the funding of scientific research, the protection of ideas, the regulation of sexual, mating, and reproductive behavior, the provisioning of the poor, the enforcement of promises, the allocation of rights and duties, the resolution of disputes, the expenditure of collected taxes, and many, many other things are all inextricably intertwined in the extensive networks of legal systems.

Throughout these networks, however, the underrecognized but fundamental relationship between law and behavior remains constant: Society uses law as a tool for moving human behavior in directions it would not otherwise go on its own. And it is embedded in that pragmatic use that law's frequent need for evolutionary analysis is most clear. A competent model of human behavior is essential to wringing maximum effectiveness from legal systems. And evolutionary perspectives, in turn, can frequently strengthen law's models of human behavior. The many examples this chapter has explored doubtlessly represent but a fraction of the many possible applications of evolutionary analysis in law.

THE PAST DECADE: AN UPDATE

Commensurate with the rapid growth of empirical and conceptual work in evolutionary psychology, the last decade witnessed not only the extension of evolutionary analysis in law by scholars already in the field, but also the addition of many new scholars, with many important new ideas.

The new empirical work both strengthened foundations of, and added support to, conceptual advances at the law/evolution intersection. In addition, scholars developed and deployed evolutionary analyses in a number of new legal domains. Although it is not possible in the supplemental space afforded here to mention every new work (for more, see the bibliography I've compiled at www.sealsite.org), I provide below an overview, some observations about patterns in the field, and brief comments on future directions.

Much recent work has centered on the evolutionary underpinnings of law, which goes variously by the names of "biolegal history" (Jones, 2001d; Jones & Goldsmith, 2005), "law instincts" (Stake, 2004; Guttentag, 2009), "deep structure of law" (Kar, 2006), "moral grammar" (Mikhail, 2007), "universal moralities" (Kuklin, 2009), and "the origins of justice" (Robinson, Kurzban, & Jones, 2007), among others (Arruñada, 2008). The core idea is that legal systems reflect evolved features of the distinctly human brain. Kar, for example, uses evolutionary insights to identify complex but subtle categories of law-relevant social behavior, such as the source of the sense of obligation, how legal systems emerge and stabilize, and how a more universal sense of respect for human rights and international law might be promoted (2006, 2012a, 2012b, 2012c, 2013). Guttentag (2009) argues that the propensity to create law-like structures is itself an evolved adaptation, such that reliance on legal systems to organize social activity is an integral part of human nature. Mikhail (2011) draws on philosophy, linguistics, and cognitive science to discover and explain law's patterns. And a number of scholars have explored implications for the field of Comparative Law (De Coninck, 2010; Du Laing, 2011; Du Laing & De Coninck, 2011; Gommer, 2011a; Goodenough, 2011; Mikhail, 2009; Wangenheim, 2010).

Much interest in the evolutionary underpinnings of law focuses specifically on the criminal justice domain. For instance, Robinson, Kurzban, and Jones (2007) provided theoretical foundation, rooted in evolved adaptations, for the origins of widely shared intuitions of justice. In a book and series of papers, Hoffman and Goldsmith have provided detailed analyses of the biological roots of punishment and influences on judging (e.g., M. Hoffman, 2011, 2014; M. Hoffman & Goldsmith, 2004). And a burgeoning literature applies evolutionary analyses in contexts of condemnation (DeScioli & Kurzban, 2009, 2013; DeScioli, Gilbert, & Kurzban, 2012), revenge (McCullough, Kurzban, & Tabak, 2013), and reconciliation (McCullough et al., 2013; Petersen, 2013; Petersen, Sell, Tooby, & Cosmides, 2010; Petersen, Sell, Tooby, & Cosmides, 2012).

The past decade has seen increased evolutionary analysis in the four legal fields traditionally considered foundational to others. In the field of Property, for example, Stake (2004, 2009) and Krier (2009) have explored evolutionary underpinnings of the sense of property, in light of the significance of resource acquisition, while Jones, Brosnan, and colleagues have explored the evolutionary origins of law-relevant psychological biases pertaining to ownership, by testing in chimpanzees and orangutans narrow and unique predictions about the so-called "endowment effect" (Brosnan et al., 2007; Jones & Brosnan, 2008; Brosnan, Jones, Gardner, Lambeth, & Schapiro, 2012; Flemming, Jones, Mayo, Stoinski, & Brosnan, 2012). Applications in Criminal Law by Buss and others (Benforado, 2010; Blumoff, 2014; Broussard, 2012; Buss, 2005, 2012; Duntley & Shackelford, 2006, 2008; Goldstein, 2002; Kanazawa, 2008; Thomson, 2008; Walsh, 2006; Wilson, 2005) focus on the effects of evolutionary processes on behaviors that can get one into trouble with the law. In Torts (essentially, noncriminal harms) Bailey Kuklin (2006, 2008) turns to evolutionary psychology to explain common intuitive leaps regarding various legal rules, such as those concerning the rescue of those in peril. And in Contracts, several scholars have recently argued that evolutionary predispositions underlie laws regarding the enforcement of traded obligations (Alces, 2011; Fruehwald, 2009; Robinson et al., 2007; Yelpaala, 2008).

Beyond these four core legal subjects, Family Law continues to be an area of particularly rich activity (overview in Carbone & Cahn, 2009a). For example, David Herring provides evolutionary analyses of child welfare law contexts in a series of important papers (such as 2006, 2007, 2008, 2012, 2014) that raise intriguing questions about how best to avoid child maltreatment, or to improve foster care arrangements, given expected levels of parental investment by different types of kin. And in the vein pioneered by Judge and Hrdy (1992), regarding the effects of evolved sex differences on resource allocations (traceable through testamentary patterns), there has been additional work on the biology of social closeness, resource allocation among relatives, and the like (Segal & Marelich, 2011).

In addition, scholars are actively deploying evolutionary insights in the contexts of Employment Law, such as in the contexts of gender gaps in compensation, occupational segregation, and sexual harassment (Browne, 2008, 2013; Seaman, 2005, 2007; Urias, 2004); Constitutional Law (Almeida, 2014; Dodson, 2008); Corporations (Beecher-Monas, 2007; Geu, 2009; Hill & O'Hara, 2006); Intellectual Property (Gommer, 2011b; Goodenough & Decker, 2009); International Law (Kar, 2013); Environmental Law (Richardson, 2011); Antitrust (Horton, 2012, 2013); and the Law and Emotions arena (Patrick, in press).

With respect to the processes of law, there has been increasing interest in evolutionary perspectives on mediation, reconciliation, negotiation, and settlement (Goldman, 2008; Yarn & Jones, 2009), and in general techniques of persuasion in law (Ridgway, 2011; Vaughn, 2011). And there continue to be frequent invocations of evolutionary processes in law-relevant systemic (e.g., complex adaptive systems) contexts (Arruñada & Andonova, 2008; Cotter, 2005; Ruhl, 2008; Seto, 2005).

With respect to models of human decision-making relevant to law, there has been a great deal of interest in the similarities and differences between evolutionary and economic perspectives on human decision making (Carbone & Cahn, 2009b; Deakin, 2011; Epstein, 2009; Horton, 2011; Jones, in press; Jones, O'Hara O'Connor, & Stake, 2011; Wangenheim, 2010).

And a few critiques, one of them worth reading, appeared during this period. Amy Wax (2004) provides an informed and thoughtful treatment of the field, arguing that a richer understanding of both sexual selection and multi-level selection limits the predictive power of evolutionary analysis in human affairs. She therefore cautions against relying on evolutionary insights for specific legal interventions, and counsels recognition of the complex and subtle ways that evolutionary processes influence human behaviors relevant to law.

Looking at the trends of evolutionary analysis in law, several are emerging. One is the sharp and welcome rise, within the field, of empirical work (e.g., DeScioli et al., 2012; Herring, Shook, Goodkind, & Kim, 2009; Mikhail, 2009; Petersen et al., 2012). For example, Sarah Brosnan, colleagues, and I made and tested several novel and narrow predictions of the "time-shifted rationality" theory of cognitive biases, demonstrating that we could not only predict variation in the endowment effects for two different classes of objects, but we could also turn the effect on and off for the very same objects (Brosnan et al., 2007; Brosnan et al., 2012; Jones, in press; Jones & Brosnan, 2008).

Another trend, concomitant with the rapid growth of neuroimaging techniques, is the increasing overlap of evolutionary analysis in law with neuroscience (Alces, in press; Blumoff, 2010; Chen, 2008; Freeman & Goodenough, 2009; Goodenough & Tucker, 2010; Jones, Marois, Farah, & Greely, 2013; Jones, Schall, & Shen, 2014; O'Hara, 2004; Platek, Keenan, & Shackelford, 2006; Zeki & Goodenough, 2006). For example, numerous studies now illuminate the brain activities underlying punishment decisions (Buckholtz et al., 2008; Krueger , Hoffman, Walter, & Grafman, 2013; Treadway et al., 2014). This parallels the somewhat older and still growing intersection of evolution, law, and genetics (Beecher-Monas & Garcia-Rill, 2006; Jones, 2006).

Other trends include increasing attention to multi-level selection (Almeida, 2014; Wax, 2004), coevolutionary processes (Du Laing, 2011; Richerson & Boyd, 2005), and the evolutionary underpinnings of conscience, cooperation, and trust (Almeida, 2014; Du Laing, 2011; Hill & O'Hara, 2006; Kar, 2006; Parekh, 2004; Stout, 2011; Wax, 2004), as symmetrical pairs to evolved predispositions toward competition, aggression, and the like.

If I could make one prediction—or at least articulate one aspiration for the field—it would be that within a decade or two from now, the methods for studying human behavior relevant to law will have continued much further down the path of disciplinary consilience (an argument I develop more fully in Jones, in press). Because the various phenomena of human behavior do not come in tidy packages addressed to the exclusive attention of one university department or another, we should continue to integrate the disparate streams of research and knowledge until the necessarily complementary perspectives on ultimate and proximate causation—both the historical and the mechanistic processes—combine to provide a more accurate and useful understanding of human behavior.

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Afterword

RICHARD DAWKINS

AT THE END of such a compendium—truly a worthy 23-years-on successor to *The Adapted Mind* (Barkow, Cosmides, & Tooby, 1992) and 10-year successor to the first *Handbook of Evolutionary Psychology* (Buss, 2005)—what is there left for an afterword to say? An attempted summing up of all 52 chapters? Too repetitious. A prophetic "Whither Evolutionary Psychology?" Too presumptuous. An idiosyncratic *jeu d'esprit*, playfully calculated to send the reader diving back into the book to view the whole corpus again but from a different angle of illumination? Rather daunting, but I'll give it a go. Reflective musings of a sympathetic observer of the scene? Well, let me try that too and see what develops.

First, a confession. As a sympathetic observer of the scene, I had not been a very clear-sighted one. I was one of those who mistakenly thought "evolutionary psychology" a euphemistic mutation of "sociobiology," favored (like "behavioral ecology") for its cryptic protection against the yapping ankle-biters from "Science for the People" and their later fellow travelers. I now think that was a travesty, not even a half truth, perhaps at most a quarter truth. For one thing, intellectual heroes of the caliber of Cosmides, Tooby, and other authors of this book need no camouflage. But even that isn't the point. The point is that evolutionary psychology really is different. Psychology it is, and psychology is by no means all, or even mostly, about social life, sex, aggression, or parental relationships. Evolutionary psychology is about the evolution of so much more than that: about perceptual biases, about language, about revealing errors in information processing. Even within the narrower field of social behavior, evolutionary psychology distinguishes itself by emphasizing the psychological and information-processing mediation between natural selection and the behavior itself.

Evolutionary psychology and sociobiology do, however, have one bane in common. Both are subject to a level of implacable hostility that seems far out of proportion to anything sober reason or even common politeness might sanction. E. O. Wilson, struggling to understand the onslaught that engulfed *Sociobiology* at the hands of left-wing ideologues, invoked what Hans Küng in another context had called "the fury of the theologians" (Wilson, 2000). I have known sweetly reasonable philosophers, with whom I could have an amicable and constructive conversation on literally any other topic, descend to the level of intemperate ranting at the mere mention of evolutionary psychology or even the name of one of its leading practitioners. I have no desire to explore this odd phenomenon in detail. It is well discussed by evolutionary psychologists including contributors to this book, and also by Ullica Segerstråle in *Defenders of the Truth* (2000). I do have one additional remark to make about this negativity, and I shall return to it. First, though, in what I intended to be a more positive vein, here is the nearest approach I can make to the *jeu d'esprit* that aspires to shed a little oblique light on the material in this book, from an unfamiliar angle.

Sometimes science proceeds not by experiment or observation but by changing the point of view: seeing familiar facts from an unfamiliar point of view. Two candidates for this role are "The Genetic Book of the Dead," and "Continuously Updated Virtual Reality." I shall briefly summarize them, and then try to bring them together in a way that I hope might provide the oblique light that I rashly promised (for fuller accounts of them, see Chapters 10 and 11, respectively, of Dawkins, 1999, and also my forthcoming autobiography, 2015, *Brief Candle in the Dark*).

The idea of the Genetic Book of the Dead is that an animal, since it is well adapted to its environment, can actually be seen as a *description* of its environment. A knowledgeable and perceptive zoologist, allowed to examine and dissect a specimen of an unknown species, should be able to reconstruct its way of life and habitat. To be strict, the reconstruction is a complicated average of the ancestral habitats and ways of life of the animal's ancestors: its EEA, to use the evolutionary psychology jargon.

This conceit can be phrased in genetic terms. The animal you are looking at has been constructed by a sampling from the gene pool of the species: genes that have successfully come down through a long sequence of generational filters—the filters of natural selection. These are the genes that had what it takes to survive in the EEA. They fit the EEA as a key fits a lock, and, like a key, they are a kind of negative impression of their lock. Genes can therefore be seen as a description of the EEA, written in the language of DNA: hence the phrase Genetic Book of the Dead.

Continuously Updated Virtual Reality is the idea that every brain constructs a virtual reality model of the world through which the animal is moving. The virtual reality software is continuously updated in the sense that, although it might theoretically be capable of simulating scenes of wildest fantasy (as in dreams), it is in practice constrained by data flowing in from the sense organs. What the animal perceives is a virtual reality rendering of objects in the real world.

Visual illusions such as Necker cubes and other alternating figures are best interpreted in these terms. The data sent to the brain by the retina are equally compatible with two virtual models of a cube. Having no basis to choose, the brain alternates.

The virtual world that our brains construct is, no doubt, very different from that of a squirrel, a mole, or a whale. Each species will construct virtual models that are useful for its particular way of life. A swift and a bat both move at high speed through three dimensions, catching insects on the wing. Both therefore need the same kind of virtual model, even though swifts hunt by day using their eyes, and bats hunt by night using their ears. Qualia that swifts associate with color are actually constructions by the virtual reality software. My conjecture could probably never be tested, but I think bats might "hear in color." Their virtual reality software is likely to make use of the same qualia as swifts use for light of different wavelengths, but to signify equally salient features of a bat's auditory world. Surface textures are likely to be as important to bats as color is to swifts, and textures like the hairy pelt of a moth, the sheen of a bluebottle, or the rough stone of a cliff presumably temper echoes in particular ways. So the virtual reality software of bats is, I suggest, likely to adopt the same qualia—red, blue, green, and so on—as internal labels for different acoustic textures. Redness and blueness are constructions of the brain's virtual reality software, and natural selection will have seen to it that such qualia are used as labels for things that really matter to the survival of the respective animals: color for a visual animal like a swift or a person; texture for a bat.

My bat suggestion is just an example of how the idea of Continuously Updated Virtual Reality changes our view of animal psychology. Now I want to unite it with the idea of the Genetic Book of the Dead. If a knowledgeable zoologist can reconstruct a species' EEA using data from its anatomy and physiology, could a knowledgeable psychologist do something similar for mental worlds? Surely the mental world of a squirrel would, if we could peer into it, be a world of forests, a three-dimensional maze of trunks and twigs, branches and leaves. The mental world of a mole is dark, damp and filled with smells, because the genes that built its brain have survived through a long line of similarly dark and damp ancestral places. The virtual reality software of each species would, if we could reverse engineer it, allow us to reconstruct the environments in which natural selection built up that software. By the same reasoning as before, it is tantamount to a description of the EEA.

Nowadays we are accustomed to saying, in a sense that is more literal than metaphorical, that all the genes of a species have survived through a long succession of ancestral worlds, including both physical and social worlds. My suggestion here is that the long succession of ancestral worlds in which our genes have survived include the virtual worlds constructed by our ancestors' brains. Real genes have—again, in something close to a literal sense—been selected to survive in a virtual EEA, constructed by ancestral brains.

That's enough of that. I said I'd return to the hostile reception that evolutionary psychology has received in certain circles. It is a methodological point I am making, and the note I want to strike is one of encouragement.

Skeptical investigators of paranormal claims have a much quoted maxim: Extraordinary claims require extraordinary evidence. All of us would set the bar very high for, say, a claimed demonstration that two men, sealed in separate soundproof rooms, can reliably transmit information to one another telepathically. We should demand multiple replications under ultrarigorous double-blind controlled conditions, with a battery of professional illusionists as skeptical scrutineers, and with a statistical p-value less than one in a billion. On the other hand, an experimental demonstration that, say, alcohol slows down reflexes would be accepted without a second glance.

While nobody would approve poor design or shoddy statistics, we wouldn't go out of our way to scrutinize the alcohol experiment very skeptically before accepting the conclusion. The hurdle in this case would be set so low as almost to escape notice. In the middle, there is a spectrum of scientific claims, of intermediate capacity to arouse *a priori* skepticism. Evolutionary psychology, weirdly, seems to be seen by its critics as way out on the "telepathy" end of the spectrum, a red rag to critical bulls.

Something similar was true of the earlier controversy over sociobiology. Philip Kitcher's *Vaulting Ambition* (1985) is widely touted as a devastating critique of human sociobiology. In reality, it is mostly a catalog of methodological shortcomings of particular studies. The supposed faults range from peccadillo to shoddy, but they are of a type that is in principle remediable by new and improved studies along the same lines. Criticisms like Kitcher's of sociobiology, or like those more recently hurled at evolutionary psychologists such as Daly and Wilson on stepparental abuse, Cosmides and Tooby on social exchange, or Buss on sexual jealousy, are made so strongly only because the critics are treating the hypotheses under test as if they were extraordinary claims that demand extraordinary evidence. Evolutionary psychology is seen by its critics as out at the high hurdle end—the "telepathy" end of the spectrum—while it is simultaneously seen by its practitioners as down at the plausible end of the spectrum with the alcohol and the reflexes. Who is right?

Without a doubt, the evolutionary psychologists are right in this case. The central claim they are making is not an extraordinary one. It amounts to the exceedingly modest claim that minds are on the same footing as bodies, where Darwinian natural selection is concerned. Given that feet, livers, ears, wings, shells, eyes, crests, ligaments, antennae, hearts, and feathers are shaped by natural selection as tools for the survival and reproduction of their possessors in the particular ecological niche of the species, why on earth should the same not be true of brains, minds, and psychologies? Put it like that, and the central thesis of evolutionary psychology moves right along to the plausible end of the spectrum. The alternative is that psychology is uniquely exempt from the Darwinian imperatives that govern the whole of the rest of life. *That* is the extraordinary claim which, if not downright bonkers, at least demands extraordinary evidence before we should take it seriously. Maybe it is right. But given that we are all Darwinians now, the onus of proof is on those who would deny the central thesis of evolutionary psychology. It is the critics who lie closer to the "telepathy" end of the spectrum.

Could it be that the sticking point for critics is that old bugbear, the supposed uniqueness of humans? Is evolutionary psychology permissible for "animals," but not *Homo sapiens?* Once again, such exceptionalism, which Darwin himself fought and popes still hanker after, although conceivably justifiable, bears the heavy burden of proof. There are perhaps 10 million species alive on this planet at the moment, and as many as a billion species have done so in history. It is, of course, *possible* that our species really is the one in a billion species that, with respect to psychology, has emancipated itself from the purview of evolutionary explanation. But if that is what you think, the onus of demonstration is on you. Don't underestimate the magnitude of the surprisingness of that which you purport to believe.

Or could it be "modularity" that sticks in the craw of critics? Maybe. Maybe they are right, and in any case, some evolutionary psychologists are less enamored of modularity than others. But, yet again, modularity is not an extraordinary claim. It is the *alternative* to modularity that bears the burden of coming up with extraordinary evidence in its favor. Modularity is a universally good design principle that pervades engineering, software, and biology, to say nothing of political, military, and social institutions. Division of labor among specialist units (experts, organs, parts, subroutines, cells) is such an obvious way to run any complex operation, we should positively expect that the mind would be modularized unless there is good reason to believe the contrary. Yet again, the detailed arguments are to be found in this book. I merely repeat my point about the onus of proof lying on the opponents of evolutionary psychology.

Of course, some individual evolutionary psychologists need to clean up their methodological act. Maybe many do. But that is true of scientists in all fields. Evolutionary psychologists should not be weighed down by abnormal loads of skepticism and a priori hostility. On the contrary, they should hold their heads high and go to work with confidence, for the enterprise they are engaged upon is flourishing normal science within the neo-Darwinian paradigm. This book shows the way.

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