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Evolutionary Biology, Cognitive Adaptations, and Human Culture

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An evolutionary understanding of human behavior and cognition has progressed considerably in the past 30 years. In the early years of "sociobiology," researchers, following behavioral biologists, proposed that human behaviors had evolved to maximize inclusive fitness (e.g., Alexander, 1979; Chagnon & Irons, 1979; Wilson, 1978), based on the assumption that behavioral mechanisms evolved in a way that generates fitness-maximizing behavior on average and in most contexts. Rarely did the early human sociobiologists contemplate the cognitive mechanisms that would be required to produce this outcome.

The sociobiological view (later subsumed into "behavioral/evolutionary ecology") was criticized by the founders of evolutionary psychology in the late 1980s (e.g., Barkow, Cosmides, & Tooby, 1992; Tooby & Cosmides, 1989). Specifically, evolutionary psychologists proposed that "fitness-maximizing" cognitive mechanisms were impossible to design (or evolve) and that, instead, the brain was organized into a series of domain-specific modules designed to solve particular adaptive problems efficiently and produce favorable outcomes only in the currency of the relevant proximate goal. This

idea was illustrated with examples of a few likely domain-specific psychological mechanisms (ones for mate choice, extracting resources, detecting social cheaters, learning language, etc.) and rapidly expanded to include "mental modules" for almost every cognitive task that humans were observed to perform efficiently. The modular view was supported by persuasive logical arguments, but meanwhile, empirical studies of animal behavior increasingly demonstrated that specific goals in very different domains were regularly traded off to produce fitness maximizing outcomes (e.g., Lima & Dill, 1990).

TRADE-OFFS AND CONTEXT-SPECIFIC BEHAVIOR

Behavioral ecologists have continued to harbor reservations about the extreme modular view of cognition and the improbability of multiple disconnected domain-specific mechanisms producing anything remotely close to adaptive (i.e., fitness-maximizing) behavior. If animals such as fish and snails could evolve fitness-maximizing compromises between disparate goals such as foraging, mating, and predation avoidance, surely human cognition was designed in a similar fashion. Only with higher-level cognitive integration could domain-specific cognitive abilities truly be adaptive. And the closer that the weighting of proximate goals resulted in fitness-maximizing actions, the more likely that the trade-off cognitive mechanism would be favored by natural selection. The Swiss army knife analogy of the mind advocated by early evolutionary psychologists presents an obvious example of this problem. For the knife to be useful (i.e., adaptive), it must have an intelligent actor choosing which blade to employ and when to improvise when there is no appropriate blade for the job at hand (Smith, Borgerhoff Mulder, & Hill, 2001). The fitness-driven integrated view of cognition is supported by hundreds of studies in behavioral ecology showing trade-offs maximizing fitness at the foundation of all successful evolutionary theory about animal behavior (see Parker, 2006, for a review). Thus, even though evolutionary psychology has contributed a more sophisticated view of the way that cognition must be hierarchically organized, its emphasis on extreme domain specificity provides an incomplete understanding of adaptive cognitive organization. Not surprisingly, skepticism of extreme domain specificity theory is shared by other cognitive specialists as well (e.g., Fodor, 2001; Uttal, 2003).

A second weakness of early evolutionary psychology is rooted in the deduction that complex cognitive mechanisms underlying behavior should

be universal in our species. Although undoubtedly true given the time necessary for the evolution of any complex mechanism, this fact has been misread to imply nearly invariant human behavioral patterns (i.e., universal behaviors rather than universal mechanisms) adapted to Pleistocene hunter-gatherer environments. Both the idea of invariant behavioral tendencies and the belief that they produce behaviors that make adaptive sense only in remote past environments are problematic. Although some proponents of evolutionary psychology were clearly aware that universal adaptations could produce substantial behavioral variation in different ecological–environmental contexts, early studies in evolutionary psychology almost always sought out universal behavioral patterns (poor treatment of stepchildren, male preference for younger mates, etc.). Evolutionary anthropologists, on the other hand, focused on explaining the variation in observed behavioral patterns (e.g., why treatment of stepchildren might be nearly identical to that of biological children in some circumstances, and why men might favor much younger mates in some societies but not in others). The anthropological interest in observed behavior rather than mechanisms led to a methodological emphasis on modeling of behavioral variation based on assumptions of phenotypic plasticity, contingency, and evolved reaction norms rather than invariant patterns.

Formal modeling leads behavioral scientists to focus on the relevant characteristics of the environment that elicit adaptive behavioral variation. And it is not obvious that the *relevant inputs* to the cognitive mechanisms that have evolved in the past are necessarily absent in modern environments. Whether the relevant characters of the environment have changed in ways that would lead to maladaptive behavior is an empirical question (Irons, 1998; Smith, 1998). Some of the most important breakthroughs in recent behavioral studies come from researchers who avoid assuming that all puzzling results are simply due to environmental mismatches with evolved psychological mechanisms (e.g., Fehr & Henrich, 2003). Finally, although cognitive mechanisms might be complex and evolve slowly, the tastes, preferences, and tendencies that determine the behaviors generated from such mechanisms can probably be altered by single genes; thus, they may be adapted to fairly recent conditions. For example, an increased tendency to cooperate with nonkin, to provide extensive paternal investment, to engage in negotiation rather than violence, or to prefer a particular body shape might have evolved during the time of Holocene farmers and city dwellers rather than that of remote Pleistocene Africa. There is no reason to assume that natural selection has stopped tweaking evolved preferences, and mutations that adjust behavioral tendencies should emerge at an in-

creasingly more rapid rate through time, because of population growth, given that production of new mutations is a direct function of population size.

The emphasis on extreme domain specificity and the misinterpretation that complex mechanisms must result in universal behavioral patterns adapted to the Pleistocene have been reflected in methodology. Evolutionary psychologists have failed to develop explicit theoretical models of how cognitive mechanisms might handle trade-offs and result in adaptive behavior (optimality models), and to verify proposed evolutionary scenarios with rigorous data on the fitness outcomes associated with different behavioral patterns (Smith et al., 2001). Sociobiologists and behavioral ecologists, on the other hand, have been naive about the importance of cognitive design for understanding behaviors that do not always maximize fitness or are not appropriate for modern contexts. The shortcomings of both evolutionary fields have been partially corrected in the past few years, and I believe that the two fields will become increasingly indistinguishable as they incorporate each other's strengths.

Given the recent convergence of evolutionary psychology and human behavioral ecology–sociobiology, one might expect that the next generation of researchers will rapidly untangle all the major mysteries of human behavior and cognition. Unfortunately, I do not think that this will happen quickly. The main reason is that no branch of the evolutionary social sciences has an adequate understanding of human culture. Culture is a product of evolved cognitive mechanisms, but its existence may significantly alter behavioral patterns from those normally expected (from noncultural organisms), and its emergence has probably uniquely shaped evolved human cognition and emotion. Because of culture, evolutionary researchers will need to develop some special theoretical models to predict adequately and understand human behavior.

CULTURE

For most animals, the factors that determine the payoffs to alternative behavioral options are straightforward—the physical characteristics of the environment, the behavior of predators, prey and competitor species, the location and behavior of potential mates, offspring survival with different levels of investment, and so forth. However, it is unclear how well unmodified models borrowed directly from behavioral ecology can predict human behavioral variation. Cross-cultural research suggests that to test ecological

models on humans, cultural similarity must often be controlled (e.g., Borgerhoff Mulder, 2001). The fact that nearby populations belonging to the same ethnographic "culture" are often not considered independent data points in comparative studies even when they live in different habitats (e.g., grassland vs. woodland Selk Nam, coastal vs. inland Eskimos) illustrates the potential importance of culture in determining behavior. Ethnolinguistic affinity (implying shared cultural history) and geographic proximity (implying cultural diffusion) are contributing predictors of variation for a large number of behaviors that also respond to ecological payoffs, from economic patterns to mating arrangements, social structure, and even demographic trends. This is because socially transmitted information partially determines available options or alters their relative payoffs. Moreover, the punishments and rewards for adhering to specific social norms often override the cost–benefit rewards structure expected from noncultural constraints. In short, socially transmitted information and enforced rules often determine optimal behavior.

Few evolutionary researchers explicitly incorporate culture into an evolutionary perspective of human behavior (for notable exceptions, see Boyd & Richerson, 1985, 2005; Cronk, 1999; Richerson & Boyd, 2004). In the past 2 years, only 8% of the articles in the flagship journal *Evolution and Human Behavior* have considered the development or influence of culture on behavior as their main topic of study. Although anthropologists have grappled with the essence of culture and its effects for more than a century, they have produced a plethora of different definitions and a Panglossian view that culture explains all human behavior. Because most anthropological definitions include behaviors and material products as part of culture (see Cronk, 1999), they cannot provide a theoretical basis for modeling how culture influences behavior (given that behavior cannot determine itself). Evolutionary scientists working on culture have also failed to influence the social sciences to the extent that they should have, perhaps because evolutionary definitions of culture are too general, emphasizing socially transmitted information and not specifying the special types of information that humans transmit. Nearly every species transmits some information by social learning, but an overly broad evolutionary definition of "culture" (as socially transmitted information) had led many behavioral biologists to equate socially learned and locally variable traditions in a variety of nonhuman animals with human culture (Byrne et al., 2004). Indeed, some scholars now refer to animal groupings with different local traditions as "cultures." This view is probably misleading and undermines our ability to understand why *Homo sapiens* is a special species with special cognitive

abilities. Instead, productive research will require evolutionary social scientists to recognize explicitly that human culture has several components that must be accounted for independently, that have independent properties, and that produce independent effects on behavior. Some of these components may be absent from other species (Hill, 2006).

I propose that human culture consists of three types of socially transmitted information: (1) information about the world; (2) norms (i.e., rules of behavior) reinforced by punishments and rewards; and (3) signaling designed to perpetrate the rules and communicate adherence to a particular rule system. Other evolutionary theorists have discussed each of these components, but none have explicitly stated that their combination forms the essence of what we call "culture" in humans.

The first component of culture consists of socially learned information about techniques and technology, as well as facts of nature, and causal understandings of natural and supernatural phenomena. Because the information learned may be correct or incorrect, some scholars refer to such information as "beliefs." This component of culture is present in some primates and other nonhuman animals, but it does not appear to generate cumulative change, as it does in humans (Boyd & Richerson, 1996). The second component of culture defines the morality of a social group and can result in behaviors not predicted by acultural models of human behavior. Enforced rules are internalized to form values when individual actors deduce that a specific rule system serves their interests. The third component of culture consists of communication in the form of rituals (religious practices) and ethnic markers, which exist in conjunction with the rules component. It is unclear (and doubtful) whether any nonhuman species exhibit the second and third components of culture. Until this is established, I believe that it is inappropriate to talk about animal culture.

Research into the development and implications of culture should be a top priority for future studies in human cognition and behavior. The rules of any cultural group probably arise through a social bargaining process that often maximizes the mean utility of all participants in the negotiation process. At other times, norms are imposed to serve only the fitness interests of a small group. Social rules of behavior are often explicitly developed to solve potential intragroup conflicts in the most efficient way and to facilitate group-beneficial cooperation in the face of public goods problems. The most common cultural rules in hunter-gatherer societies, for example, are about dividing up "resources," such as potential mates (marriage rules), acquired food resources (sharing rules), access to food resources (territoriality), and regulating conflict (rules for ritual combat, warfare, settling disputes).

The ability to stabilize group norms may require language to negotiate what constitutes a breach of contract and to determine the appropriate penalties. Perhaps this is why humans uniquely develop enforced moral systems. Although we know that costly punishment of noncooperators is commonly expressed in humans (e.g., Fehr & Gachter, 2002), how this tendency evolved is still a fascinating problem (Boyd, Gintis, Bowles, & Richerson, 2003; O'Gorman, Wilson, & Miller, 2005). The same theoretical dilemma is confronted when we consider how rewarding those who diligently abide by the rules could evolve. Regardless of the explanation for evolved reinforcement of social rules, the production of beneficial social norms was probably favored by some type of cultural group selection, whereby groups that failed to develop norms were outcompeted and replaced by groups that did (Soltis, Boyd, & Richerson, 1995). Cultural group selection does not face the difficulties of genetic group selection, because inmigration of selfish variants is eliminated due to punishment of deviant types.

Once social norms are adopted, they must be transmitted to become stable. This often takes place during formal signaling sessions (rituals) that exist primarily to remind members of the social rules and to ensure that they are adopted by the next generation. These rituals are public, emotionally charged, and utilize nonverbal signals in a highly effective fashion to reinforce the status quo, often implying that norms are linked to supernatural rewards and punishments, as well as reinforcement by a large majority of peers. Because "rule abiders" generally prefer to interact with others who will "play by the same set of rules," ethnic marking in the form of adornments, dialects, and ritual participation emerges as a way to obtain social partners, allies, and mates (McElreath, Boyd, & Richerson, 2003). Importantly, this aspect of human culture is readily detectable in the archeological record and probably indicates when complex rule systems first emerged in hominin history.

Understanding culture is critical for future research in human cognitive evolution. Increasingly, evidence and theory suggest that the evolution of intelligence in humans and primates was mainly driven by social complexity (Whiten & Byrne, 1997; Dunbar, 2003; Kamil, 2004). However, social complexity in humans is unique. At some point in time, the main adaptive challenges that shaped human cognition came from utilizing socially learned information and competition–cooperation *in the context of making, breaking, modifying, and changing the enforced rules mentioned earlier.* Thus, human social competition consists of both direct interaction and political strategizing to influence the rule–enforcement system to one's ad-

vantage. This higher level of social complexity may explain unique human cognitive abilities. Likewise, unique social environments probably provided the context for the biological evolution of unique cognitive propensities found only in our species (e.g., Orbell, Morikawa, Hartwig, Hanley, & Allen, 2004; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Because of culture, humans alone may have evolved the emotional underpinnings of anger, fairness, justice, and indignation that lead humans to judge those who violate norms in moral terms (jerks, sleazeballs, criminals) and react to certain behaviors as "disgusting," "revolting," "repulsive," and "deranged." In short, our unique humanity rests on the cultural components produced by and acting on the evolution of the human brain.

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