
COMMENTARIES

Parasites, Behavioral Defenses, and the Social Psychological Mechanisms Through Which Cultures Are Evoked

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Let's talk first about parasites. Given the persistent influence that bacteria, viruses, and other parasites have had on human evolution (Van Blerkom, 2003), it's astonishing that so little scientific attention has been devoted to their impact on human psychology and human culture. There are extensive bodies of research documenting the role of parasites on evolved patterns of animal cognition and behavior. Many studies reveal that mammals are sensitive to signs of parasitic infection in potential mates and avoid mating with individuals who show those signs (e.g., Kavaliers, Colwell, Braun, & Choleris, 2003). These kinds of effects are not restricted to mating contexts either. Bullfrog tadpoles selectively prefer to swim near healthy tadpoles, while avoiding tadpoles that carry parasitic infections (Kiesecker, Skelly, Beard, & Preisser, 1999). Closer to home (phylogenetically speaking), chimpanzees react with unusual violence toward other chimpanzees that show the physical symptoms of debilitating diseases (Goodall, 1986). It is likely that the human mind too is characterized by mechanisms designed to recognize and respond negatively to individuals who show signs of parasite infections—and to do so especially under conditions in which the risk of parasitic infection is especially high (Kurzban & Leary, 2001; Schaller, Park, & Faulkner, 2003).

In recent years, empirical studies have documented the presence of just such mechanisms and their consequences on social cognition and behavior. Some of these consequences are straightforward: We stigmatize and avoid sick people, especially when we perceive their sickness to be contagious (Crandall & Moriarty, 1995). Additional consequences are more subtle. We not only stigmatize people who really are sick; we also stigmatize people who may be perfectly healthy but who—on the basis of some superficial feature—appear to pose a risk of parasite transmission. And we do so especially under conditions in which we feel especially vulnerable to parasitic infection. Xenophobic reactions to foreigners are stronger

among folks who feel personally vulnerable to germs and disease (Faulkner, Schaller, Park, & Duncan, 2004). Individuals with deviant or nonprototypical morphological features—people who are disfigured or disabled, or who are grossly obese—are similarly stigmatized, and, again, this stigmatization seems to occur especially strongly among people who are personally concerned about their own vulnerability to disease (Park, 2005; Park, Faulkner, & Schaller, 2003). The preference for physically attractive mates might also be understood within this context. Physical *unattractiveness* is based substantially on perceived deviations from a population prototype (Langlois & Roggman, 1990). Consequently, the subjective assessment of unattractiveness may serve as a cue indicating the potential presence of a parasitic infection at the moment, as well as a cue indicating potential susceptibility to parasitic infections in the future. Within this conceptual context, it is no surprise that people care about the physical attractiveness of someone with whom they are destined to spend a lot of time with and that they care especially within populations that have historically been more vulnerable to debilitating parasitic infections (Gangestad & Buss, 1993). Now, in the results reported by Gangestad, Haselton, and Buss (this issue), we encounter even more impressive evidence that parasite-prevalence influences mate-selection preferences, and this influence occurs across an even broader set of preferences.

The Behavioral Immune System

It is because of results such as these that I am increasingly convinced that there evolved a sort of behavioral immune system that serves as an organism's first crude line of defense against potentially harmful parasites and pathogens. (It would probably be more apt to refer to this as the "psychological immune sys-

tem,” because the system involves emotions and cognitions as well as behavior, but that term has appeared already in the psychological literature, referring metaphorically to a different set of processes that have nothing to do with parasite defense; see Gilbert, Pinel, Wilson, Blumberg, & Wheatley, 1998.) The behavioral immune system is triggered by the perception of specific kinds of stimuli (e.g., morphologically unusual appearance). When such stimuli are perceived, there ensues the automatic activation of the specific emotions and cognitions (e.g., disgust; automatic inferences about disease-connoting traits) that facilitate functional behavioral reactions (e.g., avoidance, social exclusion).

Of course, there are costs as well as benefits associated with the activation of this suite of reactions, and so the behavioral immune system is functionally flexible, responsive to information bearing on these costs and benefits. Relevant information may lie in temporary features of the immediate situation, and so these discriminatory reactions may be triggered in some situations more strongly than in others. Relevant information may also lie in chronic individual differences, and so these reactions may be triggered among some people more strongly than among others. Finally, relevant information may also lie in chronic aspects of the ecological context, and so these reactions may be triggered in some populations more strongly than in others.

That last remark—about the effect of ecological contexts and differences across populations—provides a point of transition into a bigger, broader point about universal evolutionary mechanisms and cross-cultural differences. I devote the rest of my remarks to this issue. The question I want to grapple with more fully is this: Just how are different cultural norms “evoked” under different ecological circumstances?

Questions Lurking Within the Concept of Evoked Culture

The notion of evoked culture is easily extrapolated from what we know already about evolved plasticity and environmental contingency. Those concepts are so well accepted within the biological sciences that, as concepts, they are almost boring. Not boring at all, of course, are the discoveries that result from the recognition that these concepts matter.

Consider the many wonderful examples that illustrate the operation of evolved plasticity and environmental contingency. Gangestad et al. (this issue) mention several (e.g., contingent mating strategies among collared flycatchers). I have a few other favorite examples. The tendency for cannibalistic spiders to selectively avoid eating their own kin is contingent on the extent to which alternative sources of food are

available (Bilde & Lubin, 2001). Genetically-identical butterflies may take on entirely different appearances depending on local climatic conditions during the larval stage of development (Beldade & Brakefield, 2002). And, among several families of tropical fishes, changes in local sex ratio and social density may lead individuals to actually change from male to female or vice-versa (Godwin, Luckenbach, & Borski, 2003). Not only are these examples fascinating and fun in their own right, they offer a sort of standard against which we can judge the plausibility of evoked differences in human populations. If ecological variables can trigger such profound phenotypic variability in spiders and butterflies and fishes, it is hardly surprising that powerful ecological forces posed by parasites might evoke somewhat different mating preferences in a species as famously flexible as *Homo sapiens*.

The other thing that is definitely not boring about any environmental contingency in the biological sciences is the process through which it occurs. Interesting scientific stories lie not only in the observation that phenotypic differences are evoked under different ecological contexts; they lie also in the sophisticated programs of research that attempt to answer the question of exactly how this actually happens. These answers take us beyond the observations of zoology and behavioral ecology and deep into the realms of functional genomics and developmental biology (e.g., Hofman, 2003; Godwin et al., 2003; for a discussion of applications to human cognition, see Marcus, 2004). The documentation of an evolved environmental contingency is not a conclusion; it is an introduction. It opens the door to an enormous world of scientific exploration.

The same is true when the concept of evoked culture is introduced into conversations among psychologists and other social scientists. Evoked culture is not really an explanation for cultural variation. It is an observation that seeks explanation and offers logical clues to the sorts of theories that might be generated to provide those explanations. If indeed certain kinds of cultural norms are evoked by certain kinds of ecological circumstances, how does this actually happen? What are the actual psychological mechanisms involved? And what are the evolutionary roots of those mechanisms?

We are still a long way from having satisfactory answers to those questions. There is neither surprise nor shame in that. It is difficult enough to arrive at convincing answers to questions that address just the psychological level of analysis. It is even more difficult when connecting the psychological with either an evolutionary or a cultural level of analysis. And to connect all three levels of analysis together, coherently and convincingly—well, that is going to take some time and serious collective effort.

The Importance of Social Transmission Processes

As one step toward that goal, it will be valuable to sidestep the rhetorical baggage that sometimes accompanies the concept of evoked culture and explicitly integrate it with the concept of transmitted culture.

The baggage to which I refer is an ideology-tinged tendency to view evoked and transmitted culture as alternative theoretical approaches to the emergence of cultural differences. The presence of this baggage may help explain why some folks mistakenly believe that evidence of cultural transmission argues against the plausibility of evoked culture, and other folks mistakenly believe that evidence of evoked culture argues against the importance of social learning, interpersonal communication, and other modes of cultural transmission. This baggage might be traced, in part, to the manifesto-like tone of the chapter in which Tooby and Cosmides (1992) introduced the concept of evoked culture and contrasted their evolutionary perspective against the so-called standard social science perspectives that focused merely on domain-general learning and transmission processes. I have nothing against manifestos (in fact I rather like them), and that rhetorical approach probably made sense at the time. But it doesn't anymore. No longer is it necessary to argue that the principles of evolutionary psychology can be applied usefully to questions about culture. The intervening years have supplied plenty of evidence establishing that point. (Gangestad et al.'s, this issue, article offers one nice example. For other examples, see Atran & Norenzayan, 2004; Henrich & Boyd, 1998; Kameda, Takezawa, & Hastie, 2003; Kenrick, Li, & Butner, 2003; Krebs & Janicki, 2004; Norenzayan, Schaller, & Heine, 2006). What is necessary now is to document more exactly the mechanisms through which evolved psychological processes actually do influence culture.

Here is where we need to take seriously an important point that Gangestad et al. (this issue) make toward the end of their article: that the mechanisms of evoked and transmitted culture are unlikely to be completely independent. I would hit that point even harder: The mechanisms of transmitted culture are integral to the process through which different cultures are evoked under different ecological circumstances. Just as biologists cannot fully understand environmentally contingent differences in the morphology of fishes without attending to the developmental mechanisms through which these differences emerge, we cannot fully understand the process of evoked culture without attending to the mechanisms of social transmission. Let me try to explain why.

A Few Thoughts on Social Learning

If I had a bit more space (and a lot more expertise), I might go into detail on ways in which social learning mechanisms are implicated in the process through which cultures are evoked. Instead, I just make a few quick points that suggest the need for closer attention and future elaboration. Basic mechanisms of social learning—mimicry, imitation, conformity—have deep evolutionary roots, operate automatically, and are ubiquitous aspects of the contemporary social landscape (Lakin & Chartrand, 2003; Moore, 2004; Henrich & Boyd, 1998). Many other evolved psychological systems employ basic learning mechanisms as a necessary means of facilitating adaptive behavior. One example is found in the set of mechanisms that comprise a sort of “fear module,” endowing individuals with the adaptive tendency to respond fearfully toward potentially dangerous things. A fundamental part of that fear module is an evolved capacity to learn specific stimuli that signal danger, and it appears that there may be an innate preparedness to learn certain fears—such as a fear of snakes—especially quickly (Öhman & Mineka, 2001). These fears can be learned through entirely nonsocial associative mechanisms, but social learning is implicated as well. Rhesus monkeys, for instance, learn to fear snakes simply from observing other monkeys' fearful reactions to snakes (Cook & Mineka, 1990; see also Whiten, 2000). Just as social learning mechanisms are implicated in the process through which individuals acquire the capacity to react fearfully to potentially dangerous stimuli, it is also likely that social learning mechanisms are implicated in the process through which the behavioral immune system acquires the capacity to respond aversively to deviant morphological features and the process through which individuals acquire the capacity to distinguish desirable mates from less desirable ones.

Finally, just as other evolved psychological mechanisms (such as those that comprise the behavioral immune system) are triggered more strongly under specific kinds of circumstances, these learning mechanisms may be functionally flexible as well. Under conditions of high parasite prevalence, one might display an especially strong expression of disgust on encountering some stranger who is disfigured or otherwise unattractive. Under these same conditions, another person might be especially vigilant to those expressions of disgust and might be especially quick to form a learned association linking physical unattractiveness with social disapproval. Under conditions of low parasite prevalence, these associations may be learned more weakly.

The Causes and Consequences of Communication

Now let's talk about communication. The basic mechanisms that underlie interpersonal communication are activated and applied across every imaginable domain of social life. Over time, simple acts of communication exert a dynamic cascade of consequences that result, inevitably, in the emergence of different cultures defined by different norms (Harton & Bourgeois, 2004; Latané, 1996).

If we just left it at that, it might appear that communication processes create cultural differences independent of the sorts of evolutionary pressures described by Gangestad et al. (this issue). But we cannot leave it at that. People do not just talk; they talk about specific things, and the specific contents of communication have cultural consequences (Schaller, 2001). Plus, people make strategic decisions (not always consciously) to talk about some things and not others. Those decisions may reflect the role of functionally flexible psychological adaptations: In ancestral populations, strategic acts of interpersonal communication are likely to have had consequences on the communicator's reproductive fitness.

To appreciate this last point, it is helpful to bear in mind the important evolutionary concept of inclusive fitness, whereby any individual's fitness is affected not merely by his or her own individual outcomes, but also by the outcomes of others who share the same genes. Assume, for a moment, that you and I are living in some ancestral environment. To the extent that you and I are related, my inclusive fitness can be influenced by my decisions to tell you about some things, rather than others. If you are my sibling, for instance, my own inclusive fitness (or, if you prefer, the fitness of my genes) may be influenced by my decision to alert you to the danger posed by a poisonous berry or by the appearance of a stranger with peculiar-looking pustules on his face. If you are my child, my own inclusive fitness may be influenced by my decision to advise you to choose a symmetrical man for your mate, rather than some goofy-looking guy with a goopy eye.

Furthermore, within any highly social species, an individual's fitness may be influenced by the outcomes of other members of a coalitional ingroup, even if those members are not immediate kin. My own well-being, and thus my reproductive fitness, is likely to be adversely affected if you—a fellow group member with whom I expect regular social contact—become infected with a contagious parasite that I might then catch from you. Thus it would not only be in your best interests, but also in the best interest of my genes, for me to warn you against interactions with anyone who might already be infected. And, of course, it would be adaptive to err on the side of caution (Haselton & Nettle, 2006; Nesse, 2005), encouraging you to seek inter-

actions with folks who appear to be healthy (e.g., attractive people) rather than with those who might not be.

A couple of interesting implications emerge from this line of reasoning. First, it suggests that our behavioral immune system may be designed not merely to protect ourselves but to protect the broader population of individuals whose outcomes have implications for the reproductive fitness of our genes. Second, to accomplish that goal, the behavioral immune system is designed to produce specific kinds of communicative signals that alert those people.

This line of reasoning is not specific to the behavioral immune system. It can be applied to many other domains of social life and the psychological adaptations that apply to them. And so, generally speaking, the contents of communication are likely to follow the same principles that we commonly see in the operation of evolved cognitive processes. Just as we observe the selective activation of emotions and cognitions that are instrumental in guiding adaptive patterns of behavior (e.g., the tendency for morphologically unusual people to elicit disease-relevant cognitions), we are likely to observe that people selectively communicate fitness-relevant information to kin and other coalitional ingroup members. And just as the selective activation of emotions and cognitions occurs more strongly under some circumstances (e.g., morphologically unusual people elicit more disease-relevant cognitions under circumstances in which the perceived risk of contagion seems especially high), the selective communication of fitness-relevant information is likely to be exaggerated under the same circumstances.

These general points are perhaps illustrated by recent findings reported by Bangerter and Heath (2004) on the prevalence of media reports about the so-called Mozart effect—the alleged, but actually nonexistent, effect whereby children who listen to classical music become more intelligent. These results showed that the prevalence of these transmissions was especially high within populations in which there was greater collective anxiety about the quality of early childhood education. The prevalence of these transmissions may reflect an overgeneralization of the presumably adaptive tendency to provide kin with information that is instrumental in raising children with qualities, such as intelligence, that might enhance their fitness. If so, it follows that this tendency would be exaggerated under conditions in which there is greater reason to worry about their acquisition of such qualities. I am speculating, of course. But if there is any merit to this speculation, then these results document a sort of evoked cultural difference, and communication mechanisms play an essential role in the process through which these cultural differences are evoked.

We can apply the same logic to help understand how interpersonal communication may be an essential

mechanism through which parasite prevalence evokes different cultural norms. People are more likely to communicate about others' traits and characteristics that more clearly connote potential threat or lack of threat (Schaller, Faulkner, Park, Neuberg, & Kenrick, 2004). People are also especially likely to transmit urban legends—which often serve as cautionary tales—that most strongly elicit disgust, the emotion that serves as a cue for potential contagion (Heath, Bell, & Sternberg, 2001). Although it has not yet been documented, I bet that the latter effect would be especially strong under conditions in which parasite prevalence, and thus the potential risk of contagion, was especially high. Similarly, under conditions of high parasite prevalence, people may be especially likely to advise their family and friends to selectively interact with healthy or healthy-looking (i.e., attractive) individuals and to avoid interactions, especially in mating relationships, with sickly or unattractive folks.

Advice on interpersonal relationships is not merely communicated through private conversations among family and friends; it is also embedded in the folk tales, fairy stories, and other narratives that comprise the oral traditions of any culture. The handsome knights, beautiful maidens, and loathsome trolls that populate these tales are not merely stock characters. They also serve as prototypes, instructing children (and other individuals whose outcomes influence our own fitness) about what sorts of folks to avoid, what sorts of folks to spend time with, and what sorts of folks are suitable mates. Some narratives are more likely than others to be told and retold. This selectivity is influenced, in part, by memory mechanisms (Norenzayan, Atran, Faulkner, & Schaller, 2006). In addition, I suspect that some of this selectivity is a function of the extent to which a narrative offers implicit lessons about the features that discriminate between the healthy and the ill, the fit and the unfit, the desirable mate and the mate that just won't do. And this selectivity is likely to be even more pronounced under conditions in which parasites are especially prevalent.

The point is clear, I hope: Different ecological circumstances are likely to evoke different decision rules that have direct consequences on the contents of interpersonal communication. It is through deeper inquiry into this mechanism of transmission that we can more fully understand what's going on when we talk about evoked culture.

Envoi

The biological sciences can be great sources of inspiration to people who study human psychology, culture, and other social sciences. (The spark of inspiration travels in the reciprocal direction as well; let's not forget that Darwin's evolutionary insights were influ-

enced, in part, by his reading of Malthus; see Hull, 1988). Behind the concept of evoked culture lurk many wonderful findings from research on evolutionary theory and behavioral ecology. Those findings themselves pose deeper questions, which are addressed in other domains of biological inquiry (e.g., functional genomics) that focus on underlying mechanisms. It is probably premature to turn to genomics for answers to questions about evoked culture. But it is not premature to follow an analogous path and to dig more deeply into the actual mechanisms through which culture is evoked. When we do this digging, we discover that interpersonal transmission processes (social learning, interpersonal communication) are not alternative routes to culture; they are important links in the coherent causal chain through which evolutionary processes create culture. Then, by trying to figure out the specific details, we discover whole new realms within which to develop theories and conduct empirical research at the intersection of the biological and social sciences. I reckon that'll keep us busy for a while.

Notes

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Evolutionary Psychology: Resistance Is Futile

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The Borg is an imaginary federation of Star Trek creatures who conquer other beings not by annihilation but by incorporating them into a larger collective. Thus, the strengths of former foes become assets for an ever-enlarging and ever-strengthening network. When a member of the Borg alliance encounters opposition, he responds with a simple declaration: "Resistance is futile. You will be assimilated."

For several decades, a Borg-like federation of researchers in several disciplines has been working toward a fully integrated perspective for the behavioral sciences. This increasingly inclusive perspective melds insights from evolutionary psychology, cognitive science, and dynamical systems theory (Cosmides, Tooby, & Barkow, 1992; Kenrick, Li, & Butner, 2003; Kenrick et al., 2002). Attacking individual proponents of this integrative perspective is akin to attacking individual ants—it may bring a temporary sense of relief, but it will do little to slow the growth of the colony, and it may result in a surprisingly effective counterattack.

Gangestad, Haselton, and Buss's (this issue) article illustrates why years of frequent and persistent attack have not caused evolutionary psychology to crumble. Evolutionary psychologists have used the many attacks to fortify strengths, jettison weaknesses, and borrow the best weapons of their enemies. This is of course nothing more than science-as-usual. Incorporating criticism into newer and stronger theories is what makes scientific approaches resilient in a way that has perennially annoyed proponents of dogmatic belief systems.

Evolutionary Epistemology and Coevolutionary Arms Races

Evolutionary psychology is simply the scientific study of thought, emotion, and behavior, in light of a general adaptationist framework. This framework includes two general assumptions: (a) All organisms living today are descendents of ancestors efficiently designed to survive and (more important) reproduce, and (b) successful survival and reproduction is usually accomplished most efficiently by living systems composed of domain-specific mechanisms. Domain-specific mechanisms are features such as the special breathing apparatus, fins, and sonar communication capacities of whales, each efficiently designed to accomplish a different function. Evolutionary psychologists assume that, like physical traits, cognitive and behavioral mechanisms are most efficient when designed

to deal differently with different problems (such as avoiding poisonous foods vs. learning language vs. choosing mates vs. making economic decisions involving kin).

Adaptationist reasoning can be applied to any aspect of psychology. Much of the early research applying evolutionary models to human behavior focused on sex differences in mating and intrasexual competition. These topics were chosen not randomly, but because they were conceptually low-hanging fruit. Sex differences in mating strategies are ubiquitous in the animal kingdom, and men and women manifest a number of obviously different physical features linked to mating. It follows that men and women should manifest behavioral and psychological characteristics that correlate with those physical differences (see Geary, 1998; Kenrick, Trost, & Sundie, 2004, for reviews).

The process of natural selection itself is partly driven by a coevolutionary arms race between any given species and its enemies (e.g., Dawkins & Krebs, 1979). Animals surviving today inherited complex defenses designed to respond not only to particular threats but also to flexibly redesign new defenses for new attacks. At the phylogenetic level, sexual reproduction may have evolved to reshuffle physiological structures to keep one step ahead of cell-sized enemies (such as viruses and bacteria; Hamilton, Axelrod, & Tanese, 1990; Ridley, 1993). At the ontogenetic level, the immune system works in this way, flexibly responding to attacks from previously unknown enemies.

Evolutionary epistemologists assume scientific theories are subject to a process analogous to natural selection (e.g., Campbell, 1974). Good theories compete more successfully for intellectual territory, and better theories emerge from a process of variation and selective retention. Some theories are completely eliminated by better alternatives, but even the survivors are continually evolving. Critics sometimes complain that evolutionary psychologists won't stand in one fixed place long enough to let them get in a good shot. But committing to one rigid and immobile posture is not how science works. Instead, evolutionary psychologists, like all working scientists, respond to criticisms with empirical and theoretical attempts to remove weaknesses and to build a stronger and more incorporative intellectual architecture. The foundation of Darwinian adaptationist assumptions has proven itself remarkably capable of supporting an ever-larger and more elaborate empirical edifice.

To the criticism that early research in evolutionary psychology focused too heavily on male psychology,

feminist-inspired evolutionary theorists responded with an increasing consideration of topics such as the role of female choice in mating, female alliance formation, mothering, and grandmothering (e.g., Hawkes, 1999; Hrdy, 1999; Taylor et al., 2000). To the criticism that early work ignored the complexities of ongoing human cognition, there has been increasing research on evolutionary social cognition (Becker, Kenrick, Guerin, & Maner, in press; Haselton & Funder, in press; Krebs & Denton, 1997; Maner et al., 2003; Park & Schaller, 2005). To the criticism that evolutionary psychology has focused too narrowly on sex and aggression, there is an increasing emphasis on a wide range of topics, including racism and stereotyping (e.g., Cottrell & Neuberg, 2005; Schaller, Park, & Faulkner, 2003), positive psychology (Buss, 2000), health psychology (Taylor et al., 2000), social influence (Sundie, Cialdini, Griskevicius, & Kenrick, in press), and social dilemmas (Kenrick & Sundie, in press; Van Vugt & Van Lange, 2006). And to the criticism that evolutionary psychologists ignored the complexities of culture, there has been an increasing integration of cultural and evolutionary psychology (e.g., Norenzayan, Schaller, & Heine, 2006; Tooby & Cosmides, 1992).

Why have researchers in an increasing number of subareas of psychology started investing time in exploring evolutionary hypotheses? A commonly stated reason is broad intellectual appeal: The perspective connects the subdisciplines of psychology and makes our work mutually informative with developments in other fields such as biology and anthropology. But broad ideas do not count for much by themselves. In the economy of scientific ideas, data talks. The general Darwinian or adaptationist framework has been a rich mine of productive hypotheses about a wide range of behavioral and cognitive phenomena. This makes sense given that animals, including *Homo sapiens*, are designed by natural selection to do something, and to do it relatively well. Hypotheses that consider ultimate function stand a better chance of being on the right track than those that presume behavior and cognition stems from arbitrary and random causes (cf. Alcock, 2001).

The increasing exploration of domain specificity has also helped make evolutionary hypotheses more interesting. According to this view, qualitatively different processes apply to different aspects of thought, feeling, and behavior. It bypasses the classic “goldfish problem” that can make domain-general approaches boring. In the apocryphal story, a graduate student proposes a dissertation based on the following reasoning: Researchers had already demonstrated conditioning in rats, mice, humans, cockroaches, and even one-celled organisms, but no one had ever demonstrated it in a goldfish. As psychologists began exploring how conditioning is differentially linked to each organism’s evo-

lutionary history (e.g., Garcia & Koelling, 1966; Wilcoxon, Dragoin, & Kral, 1971), things simply got more interesting.

A less frequently stated aspect of this intellectual breadth is evolutionary psychology’s capacity to embrace the research topics and methods of its critics. Despite the wishful thinking of those who have not yet joined the alliance, evolutionary psychology does not involve a narrow commitment to one set of topics, one set of methods, or one dogmatic way of interpreting data. Evolutionary psychology involves simply a call to consider the adaptive background of whatever behavioral phenomenon one chooses to study. Thinking about adaptation generates a reasonable ratio of empirical hits but of course plenty of misses as well (Alcock, 2001; Kenrick, 1995). Like all good scientific frameworks, the evolutionary perspective is strengthened and expanded by considering phenomena that first appear to be exceptions to the current way of viewing things. Even if all current evolutionary hypotheses are replaced, they will likely be replaced by hypotheses that better correspond to actual evolved mechanisms. The only limiting condition would be if the majority of behavioral phenomena ultimately prove to be governed by mechanisms that operate outside the realm of natural selection. So far, that does not appear to be the way things are looking. Consider the class of phenomena generally known as “cultural influences” on behavior.

The Culture of Evolutionary Psychology

Evolutionary theorists have been considering the interaction between culture and evolution for several decades (e.g., Campbell, 1974; Lumsden & Wilson, 1981). A glance at the literature on coevolution will quickly negate any stereotyped ideas that postulating evolved mechanisms means proposing an “alternative” to cultural influences on behavior (see Janicki & Krebs, 1998, for a review). Perhaps an evolutionary perspective is sometimes misperceived in this way because proponents do, in fact, (a) tend to doubt that culture is something that arises independent of human nature, (b) tend to believe that a number of psychological universals may lie beneath apparent cultural variations in manifest behavior, and (c) take issue with the popular practice of attributing behavioral phenomena to culture without considering any cross-cultural evidence whatsoever. If anyone reads those three points as denying that there is such a thing as culture, or as implying that it is unimportant, he or she should read again. Indeed, an evolutionary perspective inspires more rather than less interest in conducting cross-cultural psychology (e.g., Daly & Wilson, 1988; Kenrick & Keefe, 1992; Norenzayan & Heine, 2005; Schmitt & International Sexuality Description Project, 2003). The cre-

ation of culture is surely one of the more fascinating features of our species, and questions about how cultural variations emerge from, interact with, and shape the development of evolved psychological mechanisms are some of the most important questions in the behavioral sciences.

The notion that some cultural variations are manifestations of flexible adaptations (i.e., evoked culture) is only one of the interesting ideas from the literature on coevolution, and the jukebox-like evocation of a flexible adaptation is only one of several logical coevolutionary relations. Another is the possibility that some cultural norms represent self-amplification of evolved mechanisms in a group context. For example, young men are more physically violent from the early years, a phenomenon that is found not only in humans but also in many other vertebrates. This sex difference seems to be an early life-history manifestation of differential parental investment and sexual selection (e.g., Geary, 1998). The innate differences between male and female found in many other species, however, may be enhanced in human societies by cultural practices such as training in martial arts for boys versus home economics for girls (Kenrick, 1987). Another possibility is that evolved mechanisms exert important influences on the selection of cultural practices. For example, attempts to raise children separately from their biological parents (as practiced in Israeli kibbutzim for some time) would be expected to be less likely to persist than arrangements in which children are kept in close proximity to parents and siblings. Yet another possibility is cultural practices designed to control selfish evolved mechanisms. Laws against nepotism, theft, rape, and gang warfare are examples of such group-designed reactions to universal selfish tendencies (Campbell, 1974; Jones, 2001). Once one begins to consider the diverse ways evolved predispositions can be reflected in, amplified by, and opposed by cultural practices, one is led to question any default assumption that culture regularly operates “independently” of evolved mechanisms.

Jukeboxes and Coloring Books

Tooby and Cosmides’s (1992) jukebox metaphor is useful for describing certain examples of evoked culture. For example, polyandry, though rare, tends to be associated with resource scarcity at the ecological level and to involve brothers at the social structural level. This follows from the differential costs of cuckoldry on men versus women and from the lowered fitness costs associated with investing in a sibling’s offspring. Polygyny, on the other hand, tends to be more pronounced when there is a steep social hierarchy (such that some families control many more resources than others) and when there is occasional famine such that poorer families may occasionally fall below the re-

source threshold needed to provide for children (Crook & Crook, 1988).

Sometimes, however, evolved constraints influence the development of cultural norms in a more flexible and complex manner. For such cases, a coloring book may a slightly more apt metaphor than a jukebox. A coloring book involves not so much a fixed set of outcomes but a flexible possibility space for which biological predispositions provide the predrawn lines and for which local social and physical ecology provides a palette of tints with which to color in the open spaces. The eventual picture drawn on the page of a coloring book is not completely determined, but neither is it completely arbitrary.

Consider for example, the Tiwi of North Australia. According to a classic ethnography on this group, most men did not get married until they were in their twenties or thirties, at which point they married elderly widows (Hart & Pillig, 1960). At first glance, this pattern poses problems for all existing accounts of gender differences in age preferences. To begin with, the practice of young men marrying older women flies in the face of data Keefe and I (Kenrick & Keefe, 1992) collected from a number of societies that suggested a universal mutual attraction between powerful older men and attractive younger women. According to our evolutionary life history perspective, women are attracted to status and material wealth rather than seniority. Men across human societies do not contribute physiological resources directly from their bodies, as women do, but instead contribute indirect resources, such as food and shelter. The ability to provide such resources correlates with a man’s status and material wealth, which in turn tend to increase with age. On the other side, age-linked changes in female fertility are universal, with puberty and menopause forming lower and upper limits on the years of peak fertility in all societies. Data from a large number of societies around the world indeed indicated that men, regardless of their own age, are attracted to women in the years of peak fertility (Kenrick & Keefe, 1992).

The Tiwi pattern of young men marrying older women, however, is directly contrary to this general worldwide pattern and seems to defy the general evolutionary life history model. It also fits poorly with the other models discussed by Gangestad et al. (this issue). Eagly and Wood (1999) reported that the preference for young women was more pronounced in relatively more patriarchal societies and took this to support their social role theory. If this theory applied here, we would expect to find that the usual patriarchal rules found in European societies (which are normally stronger in most third-world cultures) do not apply to Tiwi society. But Tiwi society is actually highly patriarchal. Tiwi men, for example, decide not only who their daughters will marry but even make

such decisions for their widowed mothers. Gangestad and colleagues demonstrate that the simple correlation between patriarchy and age preference disappears when parasite prevalence is considered. Yet the Tiwi do not seem to support their parasite model either. When the classic ethnography was written, the Tiwi lived in something close to a hunter-gatherer lifestyle in a semitropical climate. The best bet is their parasite load is rather unlike modern Europeans living in Sweden, hence the preference for female attractiveness (and youthful characteristics) ought to be especially pronounced rather than reversed.

On closer examination, the Tiwi marriage patterns suggest a dynamic interaction between two sets of sex-differentiated evolved mechanisms—one involving competition for status (which results in the worldwide construction of patriarchies) and the other involving the male preference for relative youth. It turns out that Tiwi men are, like men in other societies, strongly attracted to young women as sexual partners (Hart & Pillig, 1960). If so, why don't young Tiwi men marry younger women, as do men in most of the world's other societies? The answer has to do with the exaggerated patriarchal power over Tiwi mating arrangements. To begin with, Tiwi society is polygynous, and only much older men get to exercise their attraction to younger women. This is because power in Tiwi society is largely monopolized by the older polygynous men. Those older patriarchs tend to betroth their young daughters to other patriarchs, who are in a position to reciprocate. Young men, with no daughters to offer, are thus excluded from obtaining young wives. A young man caught having an affair with a young woman could be punished by expulsion from the group or by being gored with a hunting spear.

The fact that older men use coercive means to monopolize the younger women explains why younger men and women do not marry but not why young men and older widows marry. The explanation for that custom lies in other features of the Tiwi social system. All Tiwi women (but not all men) are required to be married. At birth, an infant girl is betrothed to a powerful older man, and a widow must remarry on her husband's death. But older widows are less desirable to powerful older men once they have acquired young wives. A young man who marries an older widow, though, cements alliances with her relatives and gains some rights in determining who her daughters marry if they become widowed early. As a consequence, a young man takes the first step toward gaining status when he marries an older widow, and, as a further consequence, he is later more likely to acquire desirable younger wives (Hart & Pillig, 1960).

Men from the Mardudjara tribe, another Australian aborigine group, also reportedly prefer younger wives as sexual partners (Tonkinson, 1978). But young wives

are hard to find, as girls are frequently betrothed to powerful older men. Again, a young man may marry a widow as his first wife, thereby increasing his status and social connections and increasing his chance of later attracting younger wives. The pattern is less pronounced than that found among the Tiwi because the Mardudjara do not require all women of all ages to marry.

There is likely a wide range of individual variation among men and women and across societies in attraction toward relatively older versus younger partners. But it would be difficult to imagine a monogamous society in which young men were only attracted to elderly women and in which only older women could find partners. If such a society ever existed, it would have been short lived, given the constraints on reproduction posed by female reproductive life history. Instead, the Tiwi pattern suggests a dynamic interaction between evolved psychological mechanisms (male attraction toward women in the years of peak fertility, female attraction toward men who have acquired status) and local social ecology (a geriatric patriarchy that monopolizes younger women, in combination with a rule that all women must be married).

Dynamical Evolutionary Psychology: Emergence by Domains

To understand how evolved mechanisms and cultural norms interact with one another, the traditional evolutionary approach can incorporate some of the insights of a dynamical systems perspective (Kenrick et al., 2002, 2003). Dynamical systems theory is concerned with complex, multicomponent systems (ranging from the microscopic [e.g., genes within the developing organism or networks of neurons within the brain] to the macroscopic [e.g., animals and plants within a particular ecosystem, or the millions of consumers within an economic market]). A key feature of many dynamical systems is bidirectional causality. In a laboratory, an animal may be given a distinct and unconfounded choice between two carefully controlled types of food. In a natural ecosystem, the food may take steps to avoid being eaten or even bite back. Dynamical systems theorists believe that studying bidirectional causality, though more difficult than studying isolated variables, is essential to understanding many natural phenomena.

Observations of complex dynamic systems have yielded a pair of critical insights. First, great complexity can arise spontaneously from the interaction of just a few simple parameters. Second, self-organization often arises out of initially random interactions of dynamically linked components (Nowak & Vallacher,

1998). Self-organization refers to the spontaneous emergence of new structures and patterns of behavior that were not programmed into the system but that arise from the combined activity of multiple components following simple rules.

Human cultures are complex dynamical systems in which the individual parts often rearrange themselves into something novel. As in all dynamical systems, the rearrangements emerge from the initial decision rules used by the interacting elements in the system. An evolutionary perspective is useful in suggesting the initial decision rules that affect the emergence of important social norms—the social norms that surround mating, sharing with friends versus family members, gaining status, negotiating with ingroup versus outgroup members, and so on (Kenrick et al., 2003). For example, inclusive fitness considerations make the standard assumptions of market economics largely irrelevant within families and very different for men and women seeking mates than for friends sharing food or information (Kenrick & Sundie, in press). Evolved decision-rules are important not only in affecting social norms but also in shaping social structures: Different natural geometries emerge from the decision-rules associated with friendship networks, mating arrangements, families, and status hierarchies (Kenrick et al., 2002). For example, intrinsic conflict over genetic interest makes it easier to maintain a stable alliance of six or seven same-sex friends than six or seven men married to the same woman. In terms of our earlier metaphor, the mind is a coloring book with multiple pages: Different patterns of lines and different color palettes influence the picture that emerges within each different domain.

Qualitatively different dynamic principles likely apply to coevolutionary processes at several different levels of analysis (Kenrick et al., 2002). Over phylogenetic time spans, for example, the physical traits and psychological preferences within a species will influence one another (internal gestation and nursing young correlates with high selectiveness in choosing mates, for example) and can influence the evolution of traits of conspecifics (selectivity in one sex selects for intrasexual competitiveness in the other, for example). Over the individual lifespan, the existence of particular traits within one person will constrain the development of other traits in that individual (e.g., high physical attractiveness and symmetry in a man facilitate a relatively more unrestricted mating strategy, Gangestad & Simpson, 2000). Over relatively shorter time spans, random variations in decision-biases within the local population will influence the formation of local norms (a relatively high number of local women willing to compromise male commitment for good genes will affect the mating choices of local men and other

women who might have otherwise favored more restrictive local norms).

Why Do Some Continue to Resist Assimilation to the Integrationist Program?

If an evolutionary perspective is flexible enough to incorporate all the different research topics of social and personality psychology, dynamic enough to incorporate the broadest questions about the emergence of human cultural diversity, and powerful enough to keep generating new and interesting empirical hypotheses, why do some psychologists still fight tooth and nail to resist assimilation? The answer to this question is probably fairly complex, but I believe a good part of the answer is this: Resisters still regard the Blank Slate position as somehow morally superior. Many resisters will no doubt insist that they are not Blank Slate theorists. Yet even when they acknowledge the research evidence demonstrating that the slate is not blank, resisters often give away a strong preference for a slate that is as blank as possible, particularly when it comes to their own research neighborhoods.

Consider Eagly and Wood's position on sex differences in mating preferences (Eagly & Wood, 1999; Eagly et al., 2004). Their general position is roughly this: Cross-cultural variations in the size of sex differences in mate preferences cast doubt on the necessity of evolutionary models and instead support an alternative account in which differences in male and female role assignments account for women's preferences for older, high-status men and men's preferences for younger, attractive women. They acknowledge that certain features of these role assignments stem from biological differences—women carry and nurse the offspring; men are physically larger and stronger (Eagly, Wood, & Johannesen-Schmidt, 2004). This is itself one form of an evolutionary model, but it sticks as close to a Blank Slate as possible, yielding only on a few obvious facts about morphology whose denial would strain credibility. Eagly and Wood resist considering how animals' brains and bodies tend to coevolve, so that where there is a structure, there is usually some programming to run it. They also resist considering the many parallel sex differences found in other species (such as intramale competitiveness). And they resist a full consideration of how those sex differences in other species are accompanied by hormonal differences between the sexes and why those hormones are coincidentally also found in humans. If Eagly and Wood merely made the coevolutionary argument that sex role assignments exacerbate initial biological differences between men and women, evolutionarily oriented psychologists would have few problems with their model. But it is clear in reading Eagly and Wood that they find

it somehow preferable to yield as little ground as possible to a brain that does not operate like a Blank Slate (indeed, it is only the bodily structures outside the brain that are sex differentiated; male and female nervous systems are presumed to operate in virtually identical ways as people absorb the culturally assigned roles their particular societies create around the external morphological differences).

Eagly and Wood are surely among the more enlightened of evolutionary psychology's critics; they do their best to argue from data and to keep their political and moral sentiments out of sight (Eagly & Wood, 1999; Eagly et al., 2004). In a recent *American Psychologist* article, Hyde (2005) was more explicit about the moral and political preferences that make resisters long for a slate that is as blank as possible. Hyde advocated that the default position for psychologists ought to be a "sex similarities hypothesis." She acknowledged, with what appears to be some reluctance, that there are a few sex differences that cannot be denied, such as those involving aggression and sexuality, but preferred to focus on a number of forms of affect and cognition for which the sexes do not appear to differ much, if at all. It is noteworthy that the article does not even consider the massive evolutionary literature on why there are sex differences in some areas and similarities in others. Is Hyde unfamiliar with this literature? It is hard to keep up with every research literature tangential to one's own interests, but Hyde is a prominent sex differences researcher who has published chapters in several books right alongside evolutionary accounts of sex differences. Did the *American Psychologist* editor choose reviewers unfamiliar with the pertinent evolutionary literature or biased in ways that led them to ignore it all? In the closing sections of Hyde's article, she argued that even talking about sex differences may be harmful, presumably because it might provide justification for conservative forces who would block women's career progress.

Resistance Is Self-Righteous But May Be Self-Defeating

It seems as if resisters to an evolutionary perspective like to view themselves as freedom riders, valiantly crusading against the massive civil rights setbacks that would ensue if the Darwinian adaptationists got out of hand. But they may be unintentionally a bit more like folks with Confederate flags on their pickups, or like fundamentalist Christians who oppose sex education because they think kids won't do it if they are not made to think of it.

Let's consider a recurrent and rather insulting claim made by opponents of evolutionary psychology, as recently stated by Rose and Rose (2000): "the

political agenda of EP [evolutionary psychology] is transparently part of a right-wing libertarian attack on collectivity, above all the welfare state" (p. 8). Is there any truth to this claim? Having attended the annual meetings of the *Human Behavior and Evolution Society* and the *Society for Experimental Social Psychology*, it seems to me that the only political difference is that the evolutionary group includes more Sierra Club types. My informal observations are consistent with a systematic study comparing political values of graduate students in evolutionary psychology and other areas (Tybur, Miller, & Gangestad, in press). Although a tiny minority of the nonevolutionary students (8.6%) favored George W. Bush before the 2004 election, not a single evolutionist did. Considering a range of other political attitudes, the general picture was the same for both groups: overwhelmingly liberal.

So evolutionary theorists are not themselves political right-wingers, transparently or otherwise. But could it nevertheless be true that their research on sex differences produces results that should be suppressed, or at least deemphasized, because they may be ultimately harmful to egalitarian goals? There are several logical flaws in this argument. It presumes for one thing that right-wing political ideologues really care a lot about scientific facts. A more important problem is that the argument contains a dangerous premise: that equitable treatment of men and women should be based on the lack of psychological differences between the sexes. On that premise, then unless we can suppress all evidence of psychological sex differences, any that gets out to the politicians can be used as a justification for inequity. And is it possible to censor data or theory without losing credibility as scientists? Pinker (2002) eloquently laid out a number of serious problems with the various continuing political misconceptions that have kept the Blank Slate perspective in business long after most psychologists have become convinced that it is factually incorrect. At the very least, there are a lot of reasons to question the default political assumptions that have been used to justify inequitable treatment for research findings that support evolutionary assumptions.

Because evolutionary theorists have been accused for decades of facilitating nefarious political developments (see Segerstrale, 2000, for a review), it seems only fair to consider the other side of this argument. In recent years, the Christian Right has been increasingly championing the position that schoolchildren ought to be required to learn about so-called Scientific Creationism, also known as "intelligent design." Indeed, their president—G.W. Bush—recently came out with public support for this position. Biblical creationists frequently cite the writings of Gould, Rose, and other long-term critics of sociobiology and evolutionary psychology. They use the critiques to ar-

gue that the theory of natural selection is still being debated by scientists. Of course, most antievolutionists probably care little about the logic of the scientific debate; they simply have strong moral convictions that it is good to censor the evidence to which innocent minds are exposed. Sound familiar?

Will All the Resistors Be Assimilated?

The fictional Borg statement that “resistance is futile” is followed by the proclamation that “you will be assimilated.” It is of course doubtful that all the individuals who have resisted evolutionary psychology will themselves be assimilated into the integrationist federation. Indeed, vast social psychological literatures suggest that strongly held opinions to which people are publicly committed are very difficult to change, and evidence against such opinions is likely to fall victim to various forms of schema-biased processing. But if the adaptationist approach continues in the current direction, it will persist in incorporating the good ideas of those who resist it and thereby expand into a more inclusive and integrative perspective. If resistors are open-minded, they will cease persecuting adaptationists as thought criminals and eventually join the federation themselves. If not, the useful aspects of their intellectual culture will eventually be absorbed, and the next generation will learn that we are all in this scientific universe together.

Notes

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Causal Explanations of Human Behavior: From Culture to Psychology or From Psychology to Culture?

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At the beginning of the 21st century, there continues to be much debate regarding the extent to which evolution by natural selection has shaped the diversity of human psychology in the same way it has shaped human physiology and other living systems (e.g., Lewontin, Rose, & Kamin, 1984; Pinker, 2002). There are many sides to this debate, two of which include (a) those who do not employ the principles of evolutionary biology to explain human behavior and, instead, adopt (more or less) the tenets of a standard social science model (SSSM) of psychology (Tooby & Cosmides, 1992) and (b) those who use the logic of natural selection to guide investigations of the human cognitive architecture and the diverse array of behavior it generates. Whereas the former position privileges culture and social structure as causal forces shaping human psychology, the lat-

ter position allows for investigations of how evolved psychological adaptations pattern individual behavior and cultural phenomena. What follows is a brief overview of these two perspectives leading into a discussion of another active front in the behavioral sciences in which causality is being debated: inbreeding avoidance in humans. In the same way cultural patterns of mate preferences reflect the operation of evolved psychological programs that calibrate according to specific environmental contingencies (see target article), culturally expressed sentiments relating to incest, the other side of mating, are also products of our evolved psychological architecture (Lieberman, Tooby, & Cosmides, 2003). Data discussed in the target article by Gangestad, Haselton, and Buss (this issue) as well as those discussed in this article suggest that, at least

for some aspects of human behavior, the arrow of causality points from evolved psychological adaptations to culturally manifest behaviors.

The SSSM of Human Psychology

According to Tooby and Cosmides (1992), the SSSM is a set of assumptions that has shaped (and isolated) the social sciences throughout the last century. Briefly, proponents of the SSSM view social and cultural factors as primary, if not sole, causal forces shaping human behavior (e.g., Frazer, 1908/1910; Geertz, 1973; White, 1948). That is, the diversity of human behavior is a product of few domain-general psychological processes such as “learning,” “imitation,” and “socialization” that guide the absorption and transmission of local rules and norms (i.e., culture; see Tooby & Cosmides [1992] and Pinker [2002] for a thorough discussion of this perspective and its assumptions about human nature). Though many researchers within psychology would not readily categorize themselves as proponents of the SSSM as defined (e.g., stating in objection that they believe the mind does contain specialized “hard-wired” systems for perception and language), many still assume that the arrow of causation regarding human social behavior—including any sex differences that may exist—points from the outer world (e.g., culture, social structure, norms, and so on) to individual behavior and preferences.

One modern instantiation of the SSSM is the biosocial perspective (also known as the social structural theory, social role theory, or social learning theory) discussed by Halpern (2000) and Eagly and Wood (1999). For example, according to Wood and Eagly (2002), “the origins of sex differences are best understood from a biosocial perspective that gives priority to the interaction between the bodily specialization of each sex and the attributes of societies’ economy, social structure, and ecology” (p. 718). The bodily specializations discussed include physiological processes such as placentation and lactation (e.g., Eagly & Wood, 1999) and neuronal pathways and associated neurochemical processes (e.g., Halpern, 2000).

Perhaps most scientists, evolutionary and social learning included, would agree that the production of any phenotype is an interaction between many components, including one’s ecology, social structure, hormonal condition, and sex. However, for bodily specializations (e.g., female specializations for childbearing and men’s greater size and strength) to impact behavior in specific ways as Wood and Eagly (2002) suggested, there have to be information-processing procedures that use this information (e.g., time and energy costs associated with childbearing), integrate it with specific information from the environment (e.g., pathogen load or indexes of effort and skill required for obtaining a

particular resource), and motivate certain behaviors over others (e.g., motivations for seeking a mate with resources). What is needed is a rigorous description of the kinds of cognitive programs and information-processing procedures involved in the production of behavior. This level of analysis (i.e., an algorithmic level of analysis [Marr, 1982]) is absent from biosocial accounts. Rather, proponents of this view rely on domain-general learning programs to describe how a function is achieved. And although it may be acknowledged that humans and other animals are equipped to learn certain contingencies faster than others, social learning theorists suggest that the

predisposition to learn some behaviors or concepts more easily than others is determined by *prior learning experiences* and the *neurochemical processes* that allow learning to occur (release of neurotransmitters) and change in response to learning. ... Thus, learning depends on what is already known and on the neural structures and processes that undergird the learning and remembering processes. (Halpern, 2000, p. 16, italics added)

That is, explanations are deferred to prior learning experiences, whatever they may be, and are framed in terms of the physical arrangement of our neural system—an important level of analysis, but by no means the only one necessary. Throwing together a bunch of neurons and neurotransmitters within a particular ecology does not a social creature create; social behavior is produced by virtue of the information-processing procedures that, for our species and many others, are instantiated in neuronal pathways and that allow for the interaction with specific components of the ecology, social structure, and so on.

Neural structures in the brain process information, and a complete explanation of a particular behavior requires a description of the kinds of information represented and processed. This can be done independent of any knowledge of the physical instantiation of such processes. It seems theorists who privilege the physical organization of neural structures (e.g., the kinds of hormones and neurotransmitters) and physiology to explain human social behavior jump right over an analysis of the information-processing programs required and in its stead insert placeholders such as “learning” or “socialization.” Any attempt to rigorously specify the kinds of information-processing structures required to perform a particular function (e.g., choosing a mate based on certain environmental and physiological contingencies) would quickly reveal that the processes of learning and socialization are severely underspecified and that specialized systems are required to reliably tailor behavioral responses to local conditions. Specialized systems, however, are highly improbable orderings of matter (e.g., see Tooby,

Cosmides, & Barrett, 2003) and require an explanation for their existence. Evolution by natural selection is the only known causal force that can build complex functional designs—the kind that would be required to “learn” complex behaviors or modify behavior based on environmental contingencies. And so this requires knowledge of how and why complex functional mechanisms come into existence.

An Adaptationist Perspective of Human Psychology

In contrast to the SSSM and more recent social structural models of human psychology, an evolutionary framework suggests the human mind consists of information processing neural circuitry that was selected due to the effects such neural circuitry had on the probability of reproduction and survival over our species' evolutionary history (Tooby & Cosmides, 1990). Recurring selection pressures (e.g., pathogens, individuals of the opposite sex, deleterious recessive mutations, patterns of parental investment, predators, and close genetic relatives) led to the evolution of specialized psychological as well as physiological structures and processes that conferred a selective advantage with respect to each pressure. For example, the presence of pathogens over our species' evolutionary history not only led to physiological processes (e.g., elements of the immune system) for rapid detection and elimination but also psychological processes for avoiding contact with substances that were reliably associated with disease causing organisms such as feces, rotten meat, and spoiled milk (e.g., the cognitive program of disgust).

Pathogens are also hypothesized to have exerted a selection pressure on our mating psychology in at least two ways. First, as discussed in the target article, pathogens are capable of perturbing evolutionary developmental programs, one visible result being a body plan that more greatly deviates from perfect bilateral symmetry (see Gangestad & Thornhill, 1997). Consequently, circuitry guiding mate selection is hypothesized to take this information into account and motivate matings with individuals displaying fewer cues signaling the presence of pathogens (Gangestad & Buss, 1993). Second, pathogens are hypothesized to have been a selective force in shaping inbreeding avoidance mechanisms (i.e., negative mate preferences; Tooby, 1982). Individuals of close common descent are more likely to share similar internal biochemistries. That is, by virtue of having an increased probability of sharing underlying genes, the internal biochemistry of, say, a brother and sister are more similar than the biochemistry of the sister and an unrelated man. Because pathogens are better able to adapt to environments that remain constant from generation to generation (i.e., they become better able to

sequester resources, replicate, and evade components of the immune system), mating with a close genetic relative would have produced offspring that were more susceptible to the harmful effects of pathogens. This is one reason why inbreeding avoidance mechanisms are thought to have evolved (Tooby, 1982).

The purpose of this discussion is to demonstrate how an adaptationist perspective generates hypotheses regarding the kinds of phenotypes (physiological and psychological) that are likely to exist given recurring features of our ancestral past. Furthermore, it allows for the development of potential models of our cognitive architecture. For example, given that pathogens posed the adaptive problem of avoiding contact with and ingestion of substances associated with disease-causing organisms, how did our ancestors know which substances to avoid? What cues correlated with the presence of pathogens? What motivation systems used this information to direct food choice? In general, fleshing out the kinds of information-processing systems required to direct behavior away from random can fortify investigations of human behavior and any variation (e.g., individual or cultural variation) that may arise.

Explaining Individual and Cultural Variation From an Adaptationist Perspective

An understanding of our evolved cognitive architecture provides a legend for interpreting the kinds of variation found within and between groups. For example, many of our psychological adaptations are hypothesized to be sensitive to context and generate behavioral and physiological responses contingent on contextual information. One consequence is that different environments may produce different phenotypes. This has been termed *evoked culture* (Tooby & Cosmides, 1992), and two examples are discussed in the target article (see also Tooby & Cosmides [1992] on patterns of social exchange based on resource variance). As mentioned in the target article, another way groups can become different from one another is through cultural transmission, that is, the passing of information between individuals. But not all information is transmitted—only a subset of all possible beliefs, skills, practices and so forth are transmitted and retained. This narrow state space has led some researchers to suggest that the study of cultural transmission is akin to the study of the epidemiology of representations (Sperber, 1994). If cultural transmission relies on the kinds of representations humans generate and communicate, then an understanding of culture entails the investigation of our cognitive architecture, including the nature of the representations used to process information and guide behavior, a level of analysis not utilized by social learning theorists.

The debate over whether evolutionary principles can be applied to understanding patterns of human behavior seems to become more charged the closer one comes to social behavior (e.g., mating behavior and moral sentiments). For instance, few scientists would likely object to recent findings showing that cultural variation in food preparation is intimately tied to the pathogen load of the environment. Billing and Sherman (1998) sought to understand “why some like it hot” and investigated the use of 43 spices in the meat-based cuisines of 36 cultures. They reasoned that because spices vary in their antimicrobial effects, cultures exposed to greater pathogen loads would utilize a greater number of more potent spices and, specifically, those spices best able to combat the local pathogen composition. They found that as mean annual temperature increased (an index of environmental pathogen load), so too did the percentage of recipes including spices, the number of spices used in total and per recipe, as well as the use of the most potent antimicrobial spices. They tested many alternate hypotheses and concluded that spices help protect foods from pathogens, rendering them safer to eat, and that this is reflected in cross-cultural patterns of food preferences. This example demonstrates how evolutionary hypotheses regarding the kinds of selection pressure that affected human survival and reproduction can help generate hypotheses regarding behavioral variation at the cultural level. If it is possible to explain food choice using these principles, then surely it is possible to apply the same principles to understand other domains of human behavior such as mate choice and moral sentiments.

Summary

Social learning theorists and adaptationist-minded researchers approach the study of human behavior from radically different perspectives. Whereas social learning theorists privilege culture and social structure as the prime causal forces shaping human behavior, adaptationist-minded researchers start with the same biological principles used to study nonhuman behavior to investigate human psychology, including cultural patterns and individual differences. The target article by Gangestad et al. (this issue) discusses how cultural patterns of mate preferences can be explained by considering the kinds of selection pressures that shaped male and female mating psychology (e.g., patterns of parental investment and environmental pathogen load). Oddly, social learning theorists that have voiced strong opposition to this perspective (e.g., Wood & Eagly, 2002) privilege differences in bodily specializations as direct causal forces in shaping mating behavior yet deny the causal role of parental investment theory. But where do they think different bodily specializations came from? Parental investment patterns played a heavy hand in shaping physiological structures (e.g.,

see Trivers, 1972), and if natural selection can differentially shape physical structures in men and women, surely it can also differentially shape psychological processes. In any event, social learning theorists maintain that the culturally derived social roles of men and women shape mating preferences; where roles are more disparate, mating preferences should differ, and where roles are more equal, mating preferences should be more similar. However, Gangestad et al. found little support for this perspective in explaining patterns of cross-cultural mating preferences.

The remainder of this commentary looks at another aspect of mating that can open a window onto the causal factors that play a role in the generation of culturally expressed variation: inbreeding avoidance and the incest taboo. Where do our sentiments relating to incest come from? Does culture or social structure fashion our attitudes relating to incest in the same way proposed for mating preferences (e.g., see Eagly & Wood 1999), or does our evolved psychological architecture pattern moral sentiments and attitudes relating to incest?

Causal Explanations of Human Incest Avoidance: Social Learning or Evolved Psychology?

A Short History of Explanations of Inbreeding Avoidance and the Incest Taboo

At the end of the 19th century, Edward Westermarck (1891/1922), a Finnish social scientist, proposed an explanation for the commonplace observation that family members rarely find one another sexually appealing. Having noted the injurious effects of inbreeding in many species, Westermarck hypothesized that early childhood association, which typically occurs among genetic relatives, serves as an inbreeding avoidance mechanism by triggering the development of a sexual aversion that becomes manifest later during adulthood (Westermarck 1891/1922). This has come to be known as the Westermarck Hypothesis (WH).

In addition to proposing a specialized mechanism that functions to reduce the probability of choosing a close genetic relative as a sexual partner, Westermarck (1891/1922) also proposed an explanation for the origin of the culturally manifest incest taboo. He claimed that the biological systems responsible for the development of sexual aversions between close kin were also responsible for the culturally expressed incest taboo. That is, the explicit cultural prohibitions regarding incest were hypothesized to be a by-product of the natural sexual disinclination that develops between near relatives.

Westermarck's (1891/1922) explanation of the incest taboo differed drastically from the reigning social learning theories of his day, which privileged the cultural incest taboo as the origin, not the consequence, of sexual avoidance behaviors (e.g., Frazer, 1908/1910). In what has become a well-known quote, Westermarck addressed the shortcomings of this alternate explanation:

Moreover, the [social learning] theories in question imply that the home is kept free from incestuous intercourse by law, custom, or education. But even if social prohibitions might prevent unions between the nearest relatives, they could not prevent the desire for such unions. The sexual instinct can hardly be changed by prescriptions; I doubt whether all laws against homosexual intercourse, even the most draconic, have ever been able to extinguish the peculiar desire of anyone born with homosexual tendencies. Nevertheless, our laws against incest are scarcely felt as a restraint on individual feelings. And the simple reason for this is that in normal cases there is no desire for the acts that they forbid. Generally speaking, there is a remarkable absence of erotic feelings between persons living very closely together from childhood. Nay more, in this, as in many other cases, sexual indifference is combined with the positive feeling of aversion when the act is thought of. *This I take to be the fundamental cause of the exogamous prohibitions. Persons who have been living closely together from childhood are as a rule near relatives. Hence their aversion to sexual relations with one another displays itself in custom and law as a prohibition of intercourse between near kin.* (pp. 192–193; italics added)

Though initially well received, the WH and Westermarck's (1891/1922) explanation of the incest taboo gradually fell into disfavor. There were, perhaps, many reasons for this. One main reason was the widespread adoption of the SSSM of human psychology (see Tooby & Cosmides, 1992; Pinker 2002). Whereas the WH implies the existence of content-rich psychological mechanisms designed by natural selection to regulate behavior in adaptive ways, according to the SSSM, the mind is akin to a content-free blank tape that, through processes such as enculturation and socialization, records "relevant" ambient signals from the surrounding social environment, which, in turn, shape an individual's behaviors and attitudes. Applied to the domain of incest, the SSSM (which captures the social learning theories discussed by Westermarck and more recent authors [e.g., Eagly & Wood, 1999]) claims that mere exposure to norms relating to incest automatically generates feelings of sexual disinterest toward family members. The function of this taboo-generated sexual disinterest was thought to have less to do with the dangers of sexual relations within the family (as Westermarck proposed) than the establishment of cooperative relationships between families

via cultural practices such as exogamy (e.g., see Frazer, 1908/1910; Levi-Strauss, 1960; White, 1948).

An Adaptationist Perspective of the WH

From an adaptationist perspective, the WH makes good sense. Due to the selection pressures posed by deleterious recessive mutations and short generation pathogens (Bittles & Neel, 1994; Tooby, 1982), individuals who avoided mating with a close genetic relative and instead chose as a sexual partner someone who did not share a recent common ancestor would have produced healthier, more viable offspring. For this reason, inbreeding avoidance mechanisms are hypothesized to exist in species, including humans, in which close genetic relatives frequently interacted over the lifespan. Indeed, such mechanisms have been found in a number of nonhuman species (Fletcher & Michener, 1987; Hepper, 1991).

What might a human inbreeding avoidance system look like? At least two systems would be required: one that computed genetic relatedness (i.e., a kin detection system) and one that regulated sexual avoidance based on the computed estimates of relatedness. Because it is not possible to directly compare DNA (at least it was not ancestrally), evolution is hypothesized to have shaped kin-detection mechanisms that took as input cues that correlated with relatedness under ancestral conditions. One ancestrally reliable cue to relatedness would have been patterns of childhood coresidence, as the WH suggests. Another cue that would have signaled genetic relatedness is seeing one's biological mother pregnant and caring for (e.g., breastfeeding) a newborn. Indeed, recent investigations have found support for the WH showing that childhood coresidence duration predicts the development of sexual aversions as well as the incidence of sexual behaviors between siblings (e.g., Bevc & Silverman, 2000; Fessler & Navarrete, 2004; Lieberman et al., 2003; Walter & Buyske, 2003; Wolf, 2005). Furthermore, recent evidence suggests that exposure to one's mother caring for a newborn also serves as a cue to siblingship (Lieberman, Tooby, & Cosmides, 2006). Certainly, other cues to siblingship may exist (e.g., facial similarity [e.g., DeBruine, 2002], and olfactory cues based on major histocompatibility complex (MHC) composition [e.g., Wedekind & Furi, 1997]) and it is possible different cues may be used to detect different categories of kin.

The Incest Taboo: Cause or Consequence?

Was Westermarck (1891/1922) correct? Are culturally manifest attitudes (e.g., moral sentiments) relating to incest a by-product of systems guiding the develop-

ment of sexual aversions toward one's own family members? Or, as suggested by traditional SSSM accounts of incest prohibitions, are our moral sentiments a result of the unbiased adoption of ambient cultural norms? These are empirical questions, capable of being explored using the tools of modern behavioral science. If Westermarck was indeed correct and culturally expressed moral sentiments relating to incest are a reflection of underlying biological systems for inbreeding avoidance, then the cues the human mind uses to detect kin and to regulate sexual avoidance should explain the patterns of moral sentiments relating to incest. If, on the other hand, social learning theorists (e.g., Wood & Eagly, 2002) are correct and individuals "learn" preferences based on their social role, then these cues should not necessarily explain patterns of moral sentiments. Rather, culturally transmitted values, either from one's peers or from one's family members, should predict an individual's moral sentiments.

In recent studies, coresidence duration with an opposite-sex sibling has been found to predict the level of moral opposition to third-party sibling incest (Fessler & Navarrete, 2004; Lieberman et al., 2003). These findings support Westermarck's (1891/1922) original notion that the culturally manifest incest taboo and related sentiments are a product of the same mechanisms guiding the development of a sexual aversion toward one's own family members. However, this finding could be marshalled as support for social learning theories: Coresidence duration may predict moral sentiments not because it regulates the development of sexual aversions based on estimates of kinship, but rather because coresidence duration tracks opportunities for the cultural transmission of norms. An alternate hypothesis, then, is that the cultural transmission of sexual attitudes from parents and peers should predict moral sentiments relating to incest. However, as Lieberman et al. (2003) have shown, they do not: Parental attitudes regarding sexuality and an individual's own attitudes regarding sexuality, attitudes that may have been shaped by peers or family members, do not predict moral sentiments relating to incest. In contrast, coresidence duration does predict moral sentiments relating to incest, even after the effects of parental and personal attitudes are statistically removed.

Social learning theorists could suggest, however, that family social structure is the important dimension, not coresidence duration per se. Families with more traditional values and structures may be less likely to divorce, leading to greater coresidence periods for the children. If this is the case, then the sex of the children should not matter; traditional family structure or not, sex is determined by a genetic coin flip. Consequently, coresidence with same- and opposite-sex siblings should generate similar patterns of moral sentiments. They do not. Whereas coresidence duration with an opposite-sex sibling

predicts moral sentiments, coresidence duration with a same-sex sibling does not (see Lieberman et al., 2003). Although difficult to explain from a social learning perspective, this makes sense based on evolutionary hypotheses: Systems regulating sexual behavior should target members of the opposite sex (assuming heterosexuality).

One last possibility is that social learning theorists might suggest family composition matters such that, in families in which both sons and daughters exist, parents are communicating different rules about sexual behavior compared to families in which only sons or only daughters exist. If this is the case, then to the extent that coresidence tracks a separate variable having to do with the communication of norms, it should do so regardless of birth order. That is, coresidence, if truly a proxy for a "norm transmission" variable, should predict moral sentiments regardless of whether an individual in an opposite-sex sibling pair is older or younger. However, adaptationist hypotheses suggest that coresidence duration may be a cue used to detect older siblings and not, necessarily, younger ones. This is because other, more reliable cues may have been available for detecting younger siblings, namely, seeing one's mother pregnant and breastfeeding a newborn. Because the arrow of time forbids younger siblings from seeing their older siblings being born or breastfed, coresidence may be the best cue available for assessing the relatedness of older siblings. Therefore, coresidence duration with an older sibling should predict moral sentiments relating to incest whereas coresidence duration with a younger sibling should not. And this is exactly the pattern found. Moreover, it holds after controlling for sibling age to ensure that opposition is not a result of the presence of prepubescent siblings (see Lieberman et al., 2006). Taken together, these findings militate against social learning hypotheses and suggest that evolved psychological adaptations for guiding mating behavior pattern culturally expressed sentiments relating to incest and not the other way around.

Conclusion

From a social learning perspective (e.g., Eagly & Wood, 1999), mating preferences, including any sex differences that might arise, are due to interactions between physiological specializations and particular attributes of the environment. To the extent there is any scientific merit to this approach, this interaction should specify the entire scope of mate preferences, from those traits preferred in a mate (see target article) to those avoided. That is, the interaction between physiology and the environment (e.g., culture and local resources) should explain the patterns of sexual avoidance and related attitudes in the same way it explains

the patterns of sexual preferences and related attitudes. But, as the target article and this discussion suggest, social learning theories do not explain the patterns of variation found in mate preferences or moral sentiments relating to incest.

The structure of mate choice in humans as well as other social behaviors in humans will, of course, rely on a multitude of factors. However, specific hypotheses are required to rigorously investigate why and how various factors influence behavior and related attitudes. The principles outlined by an adaptationist framework provide a robust set of guidelines for the generation of specific hypothesis regarding ultimate causation as well as the generation of cognitive models specifying proximate procedures that give rise to the array of individual behaviors and, consequently, patterns of cultural variation.

Note

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Cultural Influences on Human Mating Strategies: Evolutionary Theories, Mechanisms, and Explanations of Change

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Gangestad, Haselton, and Buss (this issue) offer a compelling case for viewing much of human culture as reflecting, amplifying, and ultimately resulting from our evolved psychological architecture—our human nature. At times, this human nature produces cultural universals (e.g., language acquisition, emotional expressions, incest avoidance; see Brown, 1991). Domain-general learning mechanisms and the standard social science model simply cannot account for the breadth of observed cultural universals, especially when these universals are compared to the “ethnographic hyperspace” of human cultural possibilities (Cronk, 1999). Other times, our universal human nature interacts with environmental contingencies and personal circumstance and results in cultural variation. For example, preferences, norms, and values in the realm of mating culture can vary as a result of human nature responding in specially designed ways to local ecological information (Gangestad & Simpson, 2000; Schmitt, 2005). Gangestad et al. show that the cultural emphasis on physical attractiveness and intelligence in mate preferences intensifies (i.e., is evoked) when local ecologies are high in pathogens, precisely when both physical attractiveness and intelligence would provide critical adaptive insights into a potential mate’s genetic quality.

Unfortunately, most psychologists seem unable or unwilling to acknowledge evolutionary or natural explanations of cultural variation. Any confirmation of a trait’s cultural variability is, instead, taken as *de facto* evidence that nature is largely irrelevant and the trait’s origins reside solely within the realm of nurture. It is only when features of humanity demonstrably transcend 100% of all cultures (an exceedingly stringent requirement given the limitations of the ethnographic method, the conditional nature of many psychological adaptations, as well as basic measurement error; see Schmitt & Pilcher, 2004) that the potential influence of nature is recognized. The calls of Gangestad et al. (this issue) for finally dispensing with this false “nature versus nurture” dichotomy that plagues academic psychological thought are welcome, and one hopes they will be heeded.

There are additional problems with the way psychologists have thought about culture and cultural variation. Historically, social scientists have conceived of culture as the transmission and sharing of patterns of human cognition, emotion, and behavior. For most cross-cultural psychologists, culture is also viewed as a prospective explanatory force, a first cause. Culture ex-

ists, and then human psychology results. Several serious problems exist with this standard view of culture. First, there are definitional and circularity issues. Cultures cause the sharing of human psychology, but cultures *are* the sharing of human psychology. Second, not all people within a culture share the same features of human psychology. Variations within cultures along the dimensions of sex, age, and status lead to skepticism about the legitimacy of culture as a causal force. Third, all cultures change over time. Without a mechanism for explaining why cultures change, any theory of culture and its influence on human psychology is necessarily incomplete (Cavalli-Sforza & Feldman, 1981; Ross, 2004).

Because of these and other serious limitations, many social scientists during the middle of the last century became disenchanted with culture as an explanatory tool. Culture became an “essentializing” concept that failed to acknowledge multicultures, cocultures, and cultural change. Fortunately, evolutionary approaches to culture offer a legitimizing reason to revive the study of culture, both as a cause and as a consequence of human nature. This is because evolutionary perspectives on culture provide three important improvements from classic cross-cultural psychology and cultural anthropology. First, evolutionary psychology offers theories for why cultures vary in the ways that they do. Gangestad et al. (this issue) theorize that cultural variations in the desire for physically attractive mates result from ecological differences in pathogen prevalence. Second, evolutionary psychology perspectives offer mechanisms for why cultural variations exist. Gangestad et al. explain the mechanism of cultural variation in mate preferences is a conditional if-then adaptation within our universal psychological repertoire. If environments have high pathogen prevalence, then our mating desires adaptively emphasize physical attractiveness. If the local environment has low pathogen prevalence, then our adaptive desires de-emphasize physical attractiveness in potential mates. Third, evolutionary psychology perspectives offer explanations of cultural change. When levels of pathogen prevalence shift, the corresponding emphasis on physical attractiveness should shift as well.

In my own research on psychological adaptations toward short-term mating (Schmitt, 2005), evolutionary perspectives offer explanations for within-cultural variability (e.g., sex and individual differences in seeking multiple short-term mates; Buss & Schmitt, 1993), between-cultural variability (e.g., female-biased sex

ratios lead relatively rare men to have more relational power, and they are able to successfully insist on short-term mating; Pedersen, 1991), and cultural change over time (shifts in sex ratios as well as the need for paternal investment can lead to shifts in short-term mating; Gangestad & Simpson, 2000). All of these evolutionary perspectives possess the ability to explain cultural universals and variations, something very much missing from standard psychological accounts of short-term mating (Schmitt, 2005).

If psychologists continue to treat culture as simply an independent variable that is a first cause of human cognition, emotion, and behavior, the psychological science of culture will linger. Neither should social or cultural causes be treated as independent of biological or evolved causes. Instead, we need to fully explore and ultimately acknowledge the evolved psychological architecture that constitutes human nature and recognize that the conditional nature of human psychological adaptation gives rise to predictable forms of cultural variability. It is not the case that every evolutionary theory of cultural variation will turn out to be correct, as Gangestad et al. (this issue) demonstrate with the disconfirmation of Wood and Eagly's (2002) biosocial theory of human sexuality and culture. Neither will all aspects of culture (e.g., unique historical events) be subject to evolutionary explanation, at least in terms of genetic evolution. However, at this point in time all psychologists should dispense with dichotomous nature–nurture explanatory thinking and fully recognize that evolutionary psychology has the potential to transcend the tired old paradigms of the standard social science model and its view of learning culture as a first and only cause. Only by combining genetic and cultural levels of evolution in sophisticated ways will a more complete explanation of human psychology be possible (Boyd & Richerson, 1985; Lumsden & Wilson, 1981).

Finally, in addition to evoked and transmitted aspects of culture mentioned by Gangestad et al. (this issue), further thought within evolutionary psychology needs to be given to anticipated culture. That is, many psychological adaptations were designed to function in foraging cultures, and the development of fully functioning adaptations may require contact with certain environmental inputs particular to those cultures. Many aspects of modern culture are certainly similar to foraging cultures, but the differences need to be more fully incorporated into evolutionary theories of culture

and psychology. Moreover, our human nature likely anticipates being exposed to reliable nurturing from human culture (e.g., language acquisition adaptations anticipate exposure to language). In this way, important aspects of human culture may be considered extensions of our evolved phenotype. Just as webs are an extension of the phenotype of spiders, just as nests are to birds and dams are to beavers, cultures (both universal and variable) are extensions of the evolved phenotype of humans (Dawkins, 1982).

Note

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Cross-Cultural Universals and Variations: The Evolutionary Paradox of Informational Novelty

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Psychological Universals and Adaptive Variation

The identification of universals in a species is an important method for inferring adaptive design (Mayr, 1982). Among humans, large (~1300cc) brains and habitual upright bipedal locomotion are ubiquitous traits that distinguish us from our primate relatives, providing important clues about hominin evolutionary history. The identification of psychological universals is similarly useful (Brown, 1991; Ekman, 1993; Norenzayan & Heine, 2005) and has been emphasized by the evolutionary psychology paradigm (e.g., Buss, 1995; Tooby & Cosmides, 1990).

The identification of variation can also be a powerful scientific tool. For example, different color morphs of *Heliconius* butterflies suggest advantages for distinctive aposematic color patterns (Langham, 2004), maintaining allelic diversity at relevant loci. In addition to genetic differences, phenotypic variation usually involves ontogenetic responses to the environment (West-Eberhard, 2003). Gangestad, Haselton, and Buss (this issue) note the flexible production of melanin in melanocytes in response to solar radiation. Other classic examples include seasonal changes in cryptic fur coloration in the arctic hare, production of a protective shield in *Daphnia* in response to predation risk (Agrawal, Laforsch, & Tollrian, 1999), and the canalization of migratory locusts into short-winged nondispersing or long-winged dispersing adult morphs contingent on exposure to crowded conditions as juveniles (for a general discussion, see Schlichting & Pigliucci, 1998). Learning constraints follow similar “reaction norms” (e.g., Garcia, 1974). The phenotypic variations associated with human culture, however, present some added complexities for inferring evolutionary design.

The Problem of Culture

Vygotsky (1978) observed that children are especially tuned to their social worlds and the information that it provides. More recent evolutionary theorists of the mind suggest a complementary adaptive logic: The social world is a rich source of useful information for cognitive development. The human brain has been designed by natural selection to take advantage of this bonanza of data (e.g., Alexander, 1987; Belsky, 2005; Bjorklund & Pellegrini, 2002; Flinn, 2006; Tooby &

Cosmides, 1992). Some, perhaps in a gesture of appeasement to the cultural *tabula rasa* old guard, would have culture running off in its own evolutionary system with its own separate (but linked!) inheritance mechanisms (for reviews, see Dawkins, 1982; Durham, 1991; Henrich & McElreath, 2003; Richerson & Boyd, 2005). Others advocate a more restrictive grounding in the biology of learning (e.g., Galef, 2004; Gottlieb, 2002; Shettleworth, 1998; Tomasello, 1999), viewing culture as a rather special type of phenotypic plasticity (Alcock, 2005; Coe, 2003; Flinn, 1997; Flinn & Alexander, 1982). Gangestad et al (this issue) exemplify this latter paradigm, modeling culture—with mate choice as a specific component—as a compilation of flexible responses by individuals to specific environmental contingencies, analogous to the biological concept of reaction norms and consistent with the basic premises of evolutionary psychology (e.g., Daly & Wilson, 1983).

Here I aim to push this evolutionary perspective beyond the concept of “evoked culture” as constrained response to variable environments guided by specialized psychological modules. Startling advances in the understanding of the evolutionary basis of the phenotype, captured in part by the emergent field of “evo-devo” (evolutionary developmental biology) and its re-emphasis of the complexity of ontogeny (West-Eberhard, 2003), have apparent relevance to this question of culture and its variants (e.g., Heyes, 2003).

Culture may be viewed as a highly dynamic information pool that coevolved with the extensive information-processing abilities associated with our flexible communicative and sociocognitive competencies (Alexander, 1979). With the increasing importance and power of information in hominin social interaction, culture and tradition may have become an arena of social cooperation and competition (Coe, 2003; Flinn, 2004; see also Baumeister, 2005; Sternberg & Grigorenko, 2004).

The key issue is novelty. One of the most difficult challenges to understanding human cognitive evolution, and its handmaiden culture, is the unique informational arms race that underlies human behavior. The reaction norms posited by evolutionary psychology to guide evoked culture within specific domains may be necessary but insufficient (Chiappe & MacDonald, 2005). The mind does not appear limited to a predetermined Pleistocene set of options—such as choosing mate A if in environment X but choosing mate B if in environment Y—analogous to examples of simple phenotypic plasticity (MacDonald & Hershberger,

2005). The human jukebox does not just keep the same old selection of tunes; the Beatles displaced Elvis, and so forth.

Keeping up in the hominin social chess game required imitation. Getting ahead favored creativity to produce new solutions to beat the current winning strategies. Random changes, however, are risky and ineffective. Hence the importance of cognitive abilities to hone choices among imagined innovations in ever more complex social scenarios. The theater of the mind that allows humans to “understand other persons as intentional agents” (Tomasello, 1999, p. 526) provides the basis for the evaluation and refinement of creative solutions to the never-ending novelty of the social arms race. This process of filtering the riot of novel information generated by the creative mind favored the cognitive mechanisms for recursive pattern recognition in the open domains of both language (Deacon, 1997; Nowak, Komarova, & Niyogi, 2001; Pinker, 1994) and social dynamics (Flinn & Ward, 2005; Geary, 2005). The evolutionary basis for these psychological mechanisms underlying culture appears rooted in a process of “runaway social selection” (Alexander, 2005; Flinn, Alexander, & Coe, 2006).

Runaway Social Selection

Darwin (1871) recognized that there could be important differences between (a) selection occurring as a consequence of interaction with ecological factors such as predators, climate, and food, and (b) selection occurring as a consequence of interactions among conspecifics (i.e., members of the same species competing with each other over resources such as nest sites, food, and mates). The former is termed *natural selection* and the latter *social selection*, of which sexual selection may be considered a special subtype (West-Eberhard, 1983). The pace and directions of evolutionary changes in behavior and morphology produced by these two types of selection—natural and social—can be significantly different (Alexander, 1974, 2005; R. A. Fisher, 1930; West-Eberhard, 2003).

Selection that occurs as a consequence of interactions between species can be intense and unending, for example with parasite–host red queen evolution (Hamilton, Axelrod, & Tanese, 1990). Intraspecific social competition may generate selective pressures that cause even more rapid and dramatic evolutionary changes. Decreasing constraints from natural selection, combined with increasing social competition, can generate a potent runaway process. Human evolution appears characterized by such circumstances (Alexander, 2005; Flinn, Geary, & Ward, 2005). Humans, more so than any other species, appear to have become their own most potent selective pressure via social competition involving coalitions (Alexander, 1989; Geary & Flinn, 2002; Wrangham, 1999; e.g., Chagnon, 1988) and dominance

of their ecologies involving niche construction (Deacon, 1997; Laland, Odling-Smee, & Feldman, 2000). The primary functions of the most extraordinary human mental abilities—language, imagination, self-awareness, Theory of Mind (ToM), foresight, and consciousness—involve the negotiation of social relationships (Adolphs, 2003; Geary, 2005; Siegal & Varley, 2003; Tulving, 2002). The multiple-party reciprocity and shifting nested subcoalitions characteristic of human sociality generate especially difficult information-processing demands for these cognitive facilities that underlie social competency. Hominin social competition involved increasing amounts of novel information and creative strategies. Culture emerged as a new selective pressure on the evolving brain.

Evolution of the Cultural Brain

The human brain is a big evolutionary paradox. It has high metabolic costs, it takes a long time to develop, it evolved rapidly, it enables behavior to change quickly, and it generates unusual levels of informational novelty. As noted earlier, its primary functions include dealing with other human brains (Adolphs, 2003; Gallagher & Frith, 2003; Siegal & Varley, 2002; Tulving, 2002). The currency is not foot-speed or antibody production but the generation and processing of data in the social worlds of the human brains’ own collective and historical information pools. Some of the standout features of the human brain that distinguish us from our primate relatives are asymmetrically localized in the prefrontal cortex, including especially the dorsolateral prefrontal cortex and frontal pole (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001; Nimchinsky, 1999; Semendeferi et al., 2001; Zilles et al., 1996; for a review, see Geary, 2005). These areas appear to be involved with “social scenario building” or the ability to “see ourselves as others see us so that we may cause competitive others to see us as we wish them to” (Alexander, 1990, p. 7; cf. Bekoff & Sherman, 2004) and are linked to specific social abilities such as understanding sarcasm (Shamay-Tsoory, Tomer, & Aharon-Peretz, 2005) and morality (Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005). An extended childhood seems to enable the development of these necessary social skills (Flinn, Ward, & Noone, 2005; Joffe, 1997). Learning, practice, and experience are imperative for social success. The information-processing capacity used in human social competition is considerable and perhaps significantly greater than that involved with foraging skills (Roth & Dicke, 2005).

Evolution of the Cultural Child

The altricial (helpless) infant is indicative of a protective environment provided by intense parental and

alloparental care in the context of kin groups (Chisholm, 1999; Flinn & Leone, in press; Hrdy, 2005). The human baby does not need to be physically precocious. Rather than investing in the development of locomotion, defense, and food acquisition systems that function early in ontogeny, the infant can work instead toward building a more effective adult phenotype. The brain continues rapid growth, and the corresponding cognitive competencies largely direct attention toward the social environment. Plastic neural systems adapt to the nuances of the local community, such as its language (Alexander, 1990; Bjorklund & Pellegrini, 2002; Bloom, 2000; Geary & Bjorklund, 2000; Geary & Huffman, 2002; Small, 1998, 2001). In contrast to the slow development of ecological skills of movement, fighting, and feeding, the human child rapidly acquires skill with the complex communication system of human language (Pinker, 1999). The extraordinary information-transfer abilities enabled by linguistic competency provide a conduit to the knowledge available in other human minds. This emergent capability for intensive and extensive communication potentiates the social dynamics characteristic of human groups (Deacon, 1997; Dunbar, 1997) and provides a new mechanism for social learning and culture. The recursive pattern recognition and abstract symbolic representation central to linguistic competencies enable the open-ended, creative, and flexible information-processing characteristic of humans, especially of children.

Reconciling Domain-Specific Modularity With Informational Novelty

Humans are unique in the extraordinary levels of novelty that are generated by the cognitive processing of abstract mental representations. Human culture is cumulative; human cognition produces new ideas built on the old. To a degree that far surpasses that of any other species, human mental processes must contend with a constantly changing information environment of their own creation.

Cultural information may be especially dynamic because it is a fundamental aspect of human social coalitions. Apparently arbitrary changes in cultural traits, such as clothing styles, music, art, perceptions of beauty, food, dialects, and mate choice decisions, may reflect information “arms races” among and within coalitions. The remarkable developmental plasticity and cross-domain integration of some cognitive mechanisms may be products of selection for special sensitivity to variable social context (e.g., Boyer, 1998; Carruthers, 2002; Sperber & Hirschfeld, 2004). Human culture is not just a pool or source of information; it is an arena and theater of social manipulation and

competition via cooperation. Culture is contested because it is a contest.

The effects of coalition conformity and imitation of success may drive culture in directions difficult to predict solely on the basis of simple functional concerns or evolved psychological mechanisms. This social dynamic would explain the apparent lack of a simple biological utilitarianism of so much of culture and the great importance of historical context and social power (e.g., Wolf, 2001). Deconstruction is a complicated but necessary enterprise, for we are all players in the social arena. The twist is that we are evolved participants.

This perspective may reconcile important gaps between the evolutionary psychological paradigm and the more history-oriented anthropological approaches (e.g., Richerson & Boyd, 2005) because it suggests an evolved human psychology that is creative, dynamic, and responsive to cultural context (e.g., Kenrick, Li, & Butner, 2003), rather than being more rigidly constrained by domain-specific modules.

Culture and Mate Choice: Context-Specific and Context-General Conditional Responses

Beauty appears to have some cross-culturally universal components (Jones, 1996; Kenrick & Keefe, 1992). Health, youth, fertility, and status have near-ubiquitous appeal. Romantic attachment involves the same hormones and neurotransmitters and the same locations in the brain (Bartels & Zeki, 2004; H. Fisher et al., 2002). The devil is in the details. Evolutionary psychology has tended to focus on a limited set of mate choice criteria, largely based on research among industrialized global cultures. Analyses of variation in mating systems from human behavioral ecology have tended to focus on associations between subsistence practices, control of material resources, and male–female reproductive strategies (e.g., Borgerhoff Mulder, 1991; Geary & Flinn, 2001; Hill & Hurtado, 1996; Smith, Borgerhoff Mulder, & Hill, 2001). For example, mating relationships tend to be less stable and less exclusive in societies with subsistence ecologies that lack important resources individual men can monopolize (Flinn, 1981). Moreover, individual variability of mating relationships within a society also tracks resource control (e.g., Flinn, 1986, 1988, 1992). Gangestad et al (this issue) reiterate the importance of this type of flexible evoked culture response to the material world.

The importance of kin-based coalitions for the control of social and material resources, and the resultant nuances of human mating systems in traditional societies (Chagnon, 1997; Flinn & Low 1986; Irons, 1983), however, have not yet been incorporated into a comprehensive theoretical framework in evolutionary psy-

chology. The awareness of these shortcomings, and the interest in a broader cross-cultural database advocated by Gangestad et al. (this issue), are potential great strengths that will go far to advance our understanding of the nature of human psychology and its adaptive variations. This synthesis also portends renewed interdisciplinary efforts among anthropology, biology, and psychology across a broad range of research questions that may help resolve concerns that “many psychologists have not been studying human nature—they have been studying the nature of educated, middle-class, young adult Westerners (or the children of such people)” (Norenzayan & Heine, 2005, p. 765).

Note

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Evolution and Transmitted Culture

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It is a truism that cultures, or widely distributed ideas, practices, and their material effects, exist in all human populations, vary markedly from one group to another, and shape human lives in profound ways. Linguistic dialects, cooking methods, technology, calendars, time-keeping devices, writing, formal schooling, folktales, religious beliefs, agricultural practices, and, as recent evidence indicates, even basic psychological processes such as selfways and cognitive tendencies vary across groups and form the bulk of human activity in all societies in the world.

Culture is an evolutionary puzzle for two reasons: (a) No other unitary species in the world shows the extent of intergroup variation in behavior that is seen in humans, and (b) this intergroup variation is largely independent of reproductive events. What accounts for this variation? It cannot be genetic differences. Although there is considerable evidence from behavioral genetics that individual differences in behavior within any given group are partly genetic (e.g., Plomin, Owen, & McGuffin, 1994), genetic differences between human groups are too small and behavioral variation between groups too large for genetic evolution to explain most human intergroup variation. Moreover, two groups of genetically similar individuals who live in different or even similar environments end up with radically different beliefs and behaviors. Nongenetic explanations are needed. Gangestad, Haselton, and Buss (this issue), are right that evolutionary processes that do not invoke genetic differences can shed light on why and how cultural variation emerges.

Cultural Variation in Psychology

In most of psychology as well as anthropology, culture is treated as a given. Psychologists interested in culture have tended to focus on the extent to which cultures vary and how this variation affects not just the superficial content of beliefs and behaviors but the very nature of basic domain general psychological processes, including the self (Markus & Kitayama, 1991; Triandis, 1989), cognition (Medin & Atran, 2004; Nisbett, Peng, Choi, & Norenzayan, 2001), attention and perception (Nisbett & Miyamoto, 2005), motivation (Heine, Lehman, Kitayama, & Markus, 1999), and emotion (Mesquita, 2001; Nisbett & Cohen, 1996).

This is understandable. For most of its modern history, psychology has faced a daunting cultural challenge. The vast bulk of empirical research in psychology, with some notable exceptions, many originating from evolutionary psychology (e.g., Buss, 1989; Daly & Wilson, 1988), has been conducted with an astonishingly narrow subset of the world's population: Western, middle-class, industrialized, secular people (and their children). Needless to say, this subgroup is a culturally unrepresentative sample of the world and comprises a small percentage of the world's population. As a result, until recently the invariance of psychological processes was assumed as a given, and little was known about the extent to which psychological theories and findings would generalize to the rest of the world's population, and in fact many of the central theories and findings of psychology do not travel well (see Norenzayan & Heine, 2005, for a discussion of universals and cultural differences). This picture has been

changing slowly. Growing cross-cultural research promises to expand the psychological database to encompass the world's cultural diversity, and, as a result, theories about human behavior can gain greater accuracy and generality, placing psychological science on firmer empirical foundations.

But culture is not just the *explanans* but also the *explanandum* of social science. It is a thing that must be explained. Why does culture exist at all? Are there phylogenetic homologies of culture in other species? How does culture emerge, and what are the psychological mechanisms by which beliefs and behaviors achieve cultural stability in a population of minds? Why are some distributions of beliefs and behaviors more culturally prevalent than others? How do culturally acquired beliefs interact with innate tendencies? These are important questions about culture that invite psychologists to treat culture as an emerging process as well as a causal force in human psychology (Kameda, Takezawa, & Hastie, 2003; Lehman, Chiu, & Schaller, 2004; Norenzayan, Schaller, & Heine, 2006; Schaller & Crandall, 2004).

Evoked and Transmitted Cultural Variation

As Tooby and Cosmides (1992) have proposed, from an evolutionary perspective, there are two known processes that offer a naturalistic account of how culture emerges: (a) Culture can be evoked by local environmental triggers acting on the same underlying psychology (evoked culture); (b) culture can travel from mind to mind by processes of transmission, analogous, but not identical, to Darwinian genetic evolution (transmitted or epidemiological culture, e.g., Sperber, 1996). To illustrate how evoked culture operates, Tooby and Cosmides discussed how the same food-sharing mechanism can lead to different cultural norms depending on the degree of variability in foraging success. Egalitarian norms for food sharing and sanctions against hoarding are strong where foraging or hunting success is highly variable across time, but not when the supply of food is relatively stable. In their article, Gangestad et al. (this issue) admirably elaborate on the notion of evoked culture to explain cultural variation in mate preferences. In this case, the authors argue that the same underlying mate preference for indicators of health interacts with an ecological cue to produce cultural variation—where parasite prevalence is high, features signaling health are more important and diagnostic of underlying health, and as a result attractive mates are preferred more strongly than in regions with low parasite prevalence.

Transmitted or epidemiological culture, in contrast, is prototypically what most social scientists consider culture (Nisbett, 2003; Richerson & Boyd, 2005;

Sperber 1996). This refers to the fact that genetically similar people living in similar environments may possess strikingly different beliefs and practices that they acquire from others in their group. Culture emerges when information is transmitted not genetically but socially through social learning mechanisms such as mimicry, imitation, and instruction (Tomasello, Kruger, & Ratner, 1993), as well as a byproduct of communicative processes such as gossip, conversations, and telling of stories (Schaller, 2001). With significant assistance from other human beings, people acquire and transmit substantial amounts of information that subsequently alters their behavior in profound ways. Growing research points to some rudimentary forms of cultural transmission in other species, particularly chimpanzees, who exhibit culturally variable traditions in some 39 behaviors (Whiten, 2005). However, cultural transmission in humans is so massive and rapidly cumulative that many evolutionary scientists consider it a species-specific second system of inheritance in humans, distinct from, but interacting with, genetic inheritance (Richerson & Boyd, 2005; Tomasello, 1999). Richerson and Boyd went so far as to argue that transmitted culture is an adaptation and that babies are born biologically prepared to rapidly learn the beliefs and practices of their social group. A learning bias that adopts the most common behaviors of the ingroup may have been selected in the ecologically fluctuating ancestral environment in which human psychology evolved. Whether or not transmitted culture can best be considered a naturally selected adaptation, psychological research grounded in evolutionary science can shed light on this powerful but poorly understood engine that drives culture.

Although Gangestad et al. (this issue) are careful to note that cultural variation is likely to be the result of both evocation and transmission, like Tooby and Cosmides (1992) and many evolutionary psychologists, they privilege the notion of evoked culture as the central evolutionary framework to explain cultural variation. Of course, evoked culture is a welcome development that promises to engage evolutionary psychology with cultural psychology and may encourage fruitful new avenues to explain not just psychological universals but cultural variation as well. But why have evolutionary psychologists been wary of the concept of transmitted culture? Is transmitted culture a Trojan horse that, once invited in, would unleash conceptual anarchy and unravel the project of anchoring psychology in an evolutionary framework? On first thought, it might seem so. Many of the cultural elements that spread in a population are, at best, arbitrary conventions such as dress code, whether to eat horse meat or dog meat, or whether to serve the said meat as a sizzling steak or boil it into a goopy goulash. At worst, they are Darwinian nightmares, competing with genetic interests and even undermining them, such as

when the idea of celibacy, suicide, the practice of using contraceptives, eating rotten foods, or writing scientific articles instead of having children succeed in colonizing a large number of minds.

But no need to worry about transmitted culture! Even if a significant part of the content of culture may be fitness-neutral or in some cases may even compete with genetic fitness, evolutionary thinking is essential for our understanding of (a) the evolved psychological capacities that power cultural transmission and (b) whether cultural elements themselves are subject to a secondary evolutionary process—variation, selection, and retention analogous to natural selection. Evolutionary thinking is also essential to understand how genetic and cultural evolution influence each other. In the rest of this article, then, I aim to give transmitted culture its due, with two goals in mind. With evolutionary psychologists in mind, I argue for the centrality of transmitted culture in accounting for a significant, perhaps overwhelming, bulk of human variation on the planet. With cultural psychologists in mind, I argue for the importance of evolutionary science in explaining cultural transmission as one of the central mechanisms of human cultural variation.

Evolved Capacities for Transmitted Culture

The set of psychological capacities that allowed humans to learn from others and calibrate their behavior to the cultural group in which they live are rooted in evolutionary processes. There is already a great deal of good theoretical work, mostly from anthropology, about such capacities (Boyd & Richerson, 1985; Richerson & Boyd, 2005; in psychology, see Tomasello et al., 1993). Several independent mechanisms that may contribute to transmitted cultural differences have been proposed and examined. The simplest of those is social learning, which allows humans to imitate other humans without any particular bias as to who gets to be the model of imitation. This mechanism could have been selected for, because individuals in a group live in more or less the same environment and are likely to face similar survival challenges. By allowing individuals to imitate the behavior of others, social learning can evolve by freeing individuals from the costs of trial and error learning, as long as the alternative cost of imitating maladaptive behaviors are not too high.

Another mechanism identified by Henrich and Boyd (1998) is “conformist transmission,” which, unlike simple social learning, is biased toward adopting the most common behaviors in a group. Such conformist transmission is robust in environments that fluctuate within space and over time and may have been selected for in the human ancestral environment that seems to

have been quite unstable, for example in weather and in availability of food supply (see Richerson & Boyd, 2005). Finally, a form of biased transmission may have evolved that is sensitive to the success or prestige markers of individuals, such that successful individuals in a group are more likely to be imitated (Henrich & Gil-White, 2001). Although social psychologists have examined similar social influence processes, there has been insufficient effort to ground this research in an evolutionary framework. Most likely, there are several, psychologically distinct, flexible transmission mechanisms that optimally operate in different social contexts. It is up to evolutionary social psychology to generate hypotheses regarding the behavior of these mechanisms, examine their boundary conditions, and link them to known culturally acquired beliefs and behaviors. Such work is mutually relevant to both evolutionary psychology and cultural psychology and promises to enrich both fields as well as psychology more broadly.

Cultural Evolution

Clarifying the psychological mechanisms of transmitted culture is only part of the evolutionary story of culture. Once transmission mechanisms give rise to cultural forms of learning, they open the floodgates to cultural evolution. Cultural elements then enter into what is probably a secondary evolutionary process in humans that is distinct from genetic evolution but interacts with it in complex ways. This is because evolution is substrate-neutral (Dennett, 1995). Any entity—be it DNA, computer viruses, or mental representations—capable of replication, selection, and retention is likely to undergo Darwinian processes. Cultural evolution is a hotly debated topic, and several theoretical issues still remain open. One issue that has received attention is the accuracy of cultural transmission. Unlike genetic transmission, cultural transmission has low fidelity (Atran, 2001). Whereas genetic transmission is largely a process of faithful replication, cultural transmission is more akin to transformation or inference (Sperber, 1996; see also Boyer, 1994). At every instance of cultural transmission from one individual to another, cognitive and emotional biases transform the mental representations. For example, a folktale or an urban legend that is told and retold is not preserved in identical form across minds the same way DNA replicates from parent to offspring. Rather, each act of transmission is a systematic reconstruction, and several versions of the same folktale or urban legend emerge in oral traditions. Nevertheless, quasi-stable cultural traditions do emerge over time, either because these psychological biases systematically push beliefs into certain regions or what Sperber called “attractors,” or because, as Henrich and Boyd (2002) argued, stable

cultural beliefs at the population level can plausibly emerge even if transmission is low-fidelity at the individual level.

Either way, these cognitive and emotional biases render psychology central to the study of cultural evolution (see, e.g., Boyer & Ramble, 2001; Heath, Bell, & Sternberg, 2001; Norenzayan, Atran, Faulkner, & Schaller, 2006). Here again, psychology informed by evolutionary thinking can contribute to our understanding of how ideas achieve cultural success. The cultural prevalence of supernatural beliefs such as ghosts and Gods, for instance, can be understood as by-products of cognitive and emotional programs that were designed for other purposes, such as agency detection, memory, and existential fears (e.g., Atran & Norenzayan, 2004; Boyer, 1994; Guthrie, 1993).

Furthermore, cultural evolution is essential for our understanding of human nature because it sheds light on many (culturally altered) behaviors that are otherwise quite puzzling from the standpoint of genetic evolution or evoked culture. Evolutionary psychologists correctly point out that human mental adaptations were selected for in the ancestral environment, not in the modern cultural environment, and therefore they could be maladaptive today. But why did the modern cultural environment become so astonishingly different from the ancestral environment in less than 10,000 years? The answer is cultural evolution. For example, populations exposed to higher education are less likely to have offspring, which means that the practice of higher education can spread in populations even though it has the net effect of reducing genetic fitness (Richerson & Boyd, 2005). The most compelling naturalistic explanation for such effects is cultural evolution.

Back to Evoked Culture

Although evoked and transmitted culture are theoretically distinct processes, it is notoriously difficult to disentangle the two. In their framework, Gangestad et al. (this issue) tested variation in parasite prevalence against variation in gender inequality to explain mate preferences. Although parasite prevalence clearly is an evoked variable (characteristic of the environment), it is unclear whether gender inequality is best construed as the product of evocation or transmission. As Gangestad et al. discuss in some detail, there are various competing explanations for gender inequality across cultures in the first place. When men produce more surplus calories (usually by hunting) than women, gender roles diverge. Men and women may engage in different activities because of evocation (ecological factors) or transmission (how boys and girls are socialized and trained in the society). Most likely it is both. Therefore, Gangestad et al. provide evidence that evocation does account for cultural varia-

tion in mate preferences, but their design does not allow for a clear test of whether transmission contributes to this variation.

Indeed, Gangestad et al. (this issue) point to the issue of the inseparability of evoked and transmitted culture when they discuss Nisbett and Cohen's (1996) work on the culture of honor. The southern United States, as well as the Mediterranean region, has a tradition of honor, in which toughness and aggressive response to insults is prized in a way that it is not in the northern United States or in most of northern Europe. The origin story of this difference is in fact evoked culture: Where wealth is easily stolen, as in ecologies supporting herding economies, men are more deeply preoccupied with maintaining their honor or reputation for toughness. The U.S. South was settled by Scotch Irish herders, whereas the U.S. North was settled mostly by European farmers, and as a result a tradition of honor is prevalent in the South but not in the North. But cultural differences persist even when the original economic conditions disappear. Culture of honor continues to flourish in industrialized Houston, even though herding is a thing of the past. The best explanation for the persistence of honor cultures is social transmission, and indeed a variety of evidence supports this view (Nisbett & Cohen, 1996; see also Cohen, Vandello, Puente, & Rantilla, 1999). Perhaps a common scenario across cultures is that ecological differences evoke an initial response that adaptively varies but then is picked up by processes of transmitted culture, amplified, and perpetuated even when the initial conditions are no longer present.

How, then, can we disentangle the relative contributions of evoked and transmitted culture? Richerson and Boyd (2005) proposed the ideal "common garden experiment": Take two groups of individuals with very different cultures, say, Inuit fishermen and Ache foragers, and switch them around—some Inuit move into the rainforests of Paraguay and some Ache move into the icy fringes of Greenland. Would the Ache foragers in Greenland begin to resemble the Inuit more than they would resemble their Ache compatriots in Paraguay, as the evoked culture explanation would predict? Or would they remain more like their Ache compatriots and, without the cultural repertoire of arctic survival, quickly perish in the harsh climate, as the transmitted culture explanation would maintain?

In the absence of such a naturalistic experiment, what can researchers do? One approach is to hold one variable constant while examining the effect of the other variable. Comparing groups living in similar environments but with different beliefs and practices allows researchers to isolate the effects of transmitted culture. The Amish of the U.S. Midwest, for example, live in the same ecological environment as neighboring German-ancestry farmers but to this day have maintained beliefs and practices that are markedly different.

The complementary strategy would be to measure the effects of a novel ecological variable on a group that shares the same culture (e.g., by examining how farmers in the U.S. North living in a farming community differ from farmers who have migrated to a new environment in which they adopt herding). Psychologists interested in cultural variation have been slow in adopting such research questions that are ultimately important in isolating the mechanisms of cultural variation. These questions can be fruitfully examined by studying immigrant populations who move to an ecologically different setting and conversely by tracking cultural evolution in several groups who live in similar ecological circumstances.

For example, one interesting study (Rice & Steele, 2004) compared the average subjective well being (SWB) of European countries with various European ethnic groups in the United States whose ancestry is derived from these countries. Cultures across countries differ markedly in their average SWB, and it was found that the relative differences in SWB among these American ethnic groups, although smaller, were nevertheless preserved even after generations of living in the same country, under similar ecological conditions of American middle-class life. Because group differences in SWB in these samples are likely not genetic, such a finding supports the idea that an important psychological variable such as SWB is transmitted socially across generations and can persist for a long time even in a different environment.

Conclusion

In the past two decades, both cultural psychology and evolutionary psychology have enjoyed marked growth. Cultural psychologists have been documenting the extent of cultural variation in psychological functioning. Evolutionary psychologists have been documenting the species-specific mental architecture that evolved to solve adaptive problems in the ancestral environment. Yet evolutionary explanations for how culture emerges in the first place, as well as for cultural differences, have been relatively neglected in cultural psychology and are beginning to be addressed only recently. Conversely, empirical work on cultural variation has been relatively neglected in evolutionary psychology. Greater interest in the scope and nature of cultural variation among evolutionary psychologists, and greater interest in evolutionary explanations in cultural psychology, are a welcome development that stands to strengthen psychology as a science. Evolutionary considerations that underlie processes of both evoked and transmitted cultural variation are an exciting point of convergence between these two fields and are an important scientific

advance for a psychology that encompasses the world's cultural diversity.

Notes

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Evoked Culture and Evoked Nature: Coevolution and the Emergence of Cultural Animals

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Arguments about whether behavior is best explained by invoking nature or culture have been a staple of social sciences for decades. Declaring them over and resolved, especially in the form of both sides' repeated claims to have won, has not brought them to an end. In work such as the target article by Gangestad, Haselton, and Buss (this issue), however, one can begin to get a glimpse of how a conceptual integration might occur. As they suggest, cultural variation is not a prime-mover sort of autonomous explanation for behavior but rather a well-documented phenomenon that itself calls for explanation. The authors propose that evolutionary theories can potentially offer a powerful basis for explaining cultural variation.

Our enthusiastic support for the target article's line of argument is accompanied by a sense that the nature–nurture debates are not likely to be ended even if conceptual integration continues apace. The practical issues concerning proximal causation, for example, likely will continue to revive debates as to how much a

change in cultural conditions or socialization practices can alter problem behaviors. Can murderers and sex offenders be rehabilitated to become model citizens? Can race differences in intellectual performance be eliminated? Do women inevitably make better parents, lovers, and leaders than men?

Our purpose in this brief comment is not to dispute or criticize the thoughtful arguments made by Gangestad et al. (this issue) so much as to offer complementary ideas that can possibly advance the project of integrating nature and culture within the same theory. We suspect that researchers sympathetic to culture will regard the target article—and similar efforts to explain culture by invoking nature—as a sort of hostile takeover. It might be easy for cultural sympathizers to read this work as saying that evolution can explain everything, including culture. Perceptions of hostile takeover can perhaps be softened, however, by suggesting that culture has also influenced nature, thus augmenting “evoked culture” with “evoked nature.”

In a model of human nature based on a survey of psychological research findings, Baumeister (2005) concluded that the most apt integrative formula would treat the human psyche as exceptionally well designed for culture. Humans have the same basic wants and needs as most other animals, but the ability for humans to live in culture changes the strategies by which they set out to satisfy these basic goals. That is, moving beyond the long-standing notion that humans are simply social animals, the most all-encompassing explanation of what is distinctive about humans would depict them as cultural animals.

To argue that culture influenced (evoked) nature, several conceptual refinements are necessary. First, the importance of culture is not limited to cultural differences. In practice, the vast majority of theorizing about culture emphasizes differences, and whenever one sees the word *culture* in the title of a psychology talk or article, one can bet with confidence that cultural differences will be the theme. But, of course, cultural differences come and go too rapidly to become encoded in genes—hence the conventional wisdom that culture could not have influenced nature. If we look at culture per se instead of cultural differences, however, then it does become plausible that culture may have influenced human nature. The fact of living in culture has been part of human life all over the world and throughout its history (and prehistory).

Is it possible that culture evoked nature in some aspects of human psychology? That question brings up the second conceptual refinement. Baumeister (2005) speculated that culture may have been a selection factor in human evolution. There are several indications that culture has played a crucial role in shaping human evolutionary processes. One indication is the accumulating evidence that the beginnings of culture can be found in nonhuman species (e.g., De Waal, 2001). To be sure, these fall far short of the sophistication of human culture. Nevertheless, if nonhuman primates have rudimentary culture, then culture may have provided some of selection factors in the development of *Homo sapiens*. Another indication is that, although cultural differences often take scientific center-stage over cultural similarities, there are also a great many important similarities across cultures. At least some of these similarities may reflect important universals in human group psychology, universals that have played a role in shaping the evolution of individual human minds.

Culture would have changed the selection pressures on human evolution—that is, culture changed what traits were important for reproductive success among humans. Humans who were best able to navigate the challenges and opportunities of culture would have been most successful at passing on their genes. For example, once hominid groups engaged in social exchange, then individuals who were more capable at social exchange

may have reproduced more effectively. By fundamentally changing the nature of group-level interpersonal dynamics, the advent of culture modified the rules of the natural selection game. What emerges, then, is a picture of gene-culture coevolution, in which biological evolution selects for cultural beings whereas culture shapes the fitness landscape on which evolution operates (cf. Lumsden & Wilson, 1982). Put another way, once culture began to emerge, evolution likely selected for traits that helped individuals reap the novel benefits and avoid the novel dangers of cultural life. Individual humans, in turn, would have possessed stronger and stronger cultural capacities over time, which would have reinforced the further development of culture. Thus, the biological evolution of the human mind and the evolution of human culture are very likely to have reinforced one another throughout history.

Several universal aspects of culture may have changed the fitness landscape in which humans evolved. Language and symbolic thought, for example, are apparently universal features of human culture, and moreover they are rather distinctively human (Pinker, 1994). Some nonhuman animals do communicate with each other, typically with simple grunts or barks, but most linguists balk at stretching the term *language* to cover such communication. The cultural animal style of argument is that small, incipient patterns found in prehuman creatures opened up styles of interactive behavior that proved so adaptive that natural selection cultivated them into major, central, distinctively human traits. Applied to language, the argument would be that the beginnings of oral and auditory communication in other animals opened up the possibility for richer and more effective social life, and so improvements in the ability to communicate in that way conferred important adaptive benefits.

Hence it is likely that language shaped the manner in which human biological evolution occurred. We doubt that the adaptations for human speech—the vocal apparatus capable of producing thousands of distinct sounds, the ear capable of hearing subtle differences, and the brain capable of grammar and vast vocabulary—occurred all at once. Rather, once hominids began to talk, then individuals who were biologically better suited to language use survived, flourished, and reproduced better than their linguistically inept peers. In this way, what is undeniably a cultural and learned reality—language—could have guided the selection of biological traits.

An alternative view is that biological adaptation fully preceded the development of culture and simply made possible its development. Applied to language, this view entails that humans evolved their marvelous vocal apparatus, fine-resolution hearing, and grammatical brain first, and only after these were fully ready did people invent language. This strikes us as postulating a stroke of luck so extraordinary as to suggest intelligent

design. (One would have hoped, however, that an intelligent designer would have given all humans the same language, thereby sparing us endless misunderstandings, hassles, and translation costs!) But it seems much more plausible that language and its biological underpinnings evolved in concert.

The view of culture as a biological strategy can also be used to explain the eventual success of our own species over its rivals. Human evolution was hardly a straight path, and in fact most evidence now points to various versions of human beings evolving in different parts of the globe. In single hand-to-hand combat, our Cro-Magnon ancestors might have found Neanderthals to be formidable opponents (indeed, the Neanderthals are believed to have had both larger brains and greater physical strength than *Homo sapiens*), but Neanderthal culture was no match for ours. The Neanderthal incapacity for role differentiation and division of labor would have crippled their ability to create an economic culture, and this alone could explain why they went extinct when competing against the economically competent *Homo sapiens* (Horan, Bulte, & Shogren, 2005).

The importance of role differentiation (for economic life in culture) suggests one small refinement of the argument by Gangestad et al. (this issue). They say that what scientists call culture is a matter of “within-group similarity and between-group difference.” Similarity is undoubtedly an important aspect of culture, especially with regard to shared practices, beliefs, values, and the like, but a full understanding of culture most likely has to recognize within-group differences—even to the extent of proposing that culture promotes within-group differentiation. Culture is a system, and a system consisting of identical parts is not going to produce the kinds of system gain that a system of highly specialized, differentiated parts can have. (That’s apparently what doomed the Neanderthals.) As evidence, it is probably sufficient to look at one of the biggest themes of cultural change across the centuries, namely the relentless movement toward ever greater specialization inside of ever larger systems. Culture makes us all increasingly different from each other, at least in terms of our increasingly narrowly specialized roles within the larger community.

A great strength of the Gangestad et al. (this issue) article is in pointing the way to how cultural differences could have emerged in response to local conditions. Baumeister (2005) rather vaguely suggested that cultural differences represented different solutions to the same problems, but without much basis for explaining why one solution might prevail in one place and another elsewhere. As Gangestad et al. (this issue) indicate, differences in food availability, sex ratios, and

other environmental conditions can make different approaches and solutions more effective in some places than others, thereby contributing to the immense variation in human culture.

The view that humans evolved for culture depends on the gradual construction of what Gangestad et al. call “an intricately designed, environmentally sensitive psychological architecture.” That remarkable architecture is what makes humans special. Most plausibly, that architecture came into being under evolutionary selection pressures that included the emergence of a new kind of social system, such that whoever was most capable of taking part in that system and contributing to it was most likely to pass on his or her genes.

Four biological advantages of culture were suggested by Baumeister (2005): language and the resultant improvement in capacity for both communication and thought; intergenerational progress based on the accumulation of knowledge; division of labor and its resultant gains in efficiency; and economic exchange, which increases material wealth and hence well-being. Those are perhaps the universal benefits of culture, which all cultures manage to confer. Local environmental contingencies can then evoke important differences in how cultures provide those benefits and capitalize on those advantages. But also, those benefits of culture may have been decisive in evoking the further development of human nature so as to capitalize on them. In this way, we can follow Gangestad et al. (this issue) toward explanations of both the universal and the culturally relative aspects of the human experience.

Note

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Three Ways That Data Can Misinform: Inappropriate Partialling, Small Samples, and Anyway, They're Not Playing Our Song

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Gangestad, Haselton, and Buss (this issue) have contributed a provocative analysis of cultural variation in mate preferences. We applaud their advocacy of an interactionist perspective on mate selection that takes nature and nurture into account simultaneously. We, like they, reject artificial dichotomies between evolved dispositions and environmental influences. As they acknowledge, our debates with them center on the details of our respective interactionist theories, especially the ways in which evolutionary processes calibrated the human psychological dispositions that are manifest in mate preferences among modern humans. To advance this debate, we begin by briefly reviewing our theory and critiquing Gangestad et al.'s evolutionary psychology theory.

Our comment then addresses three flaws in Gangestad et al.'s (this issue) empirical demonstrations that lead them to conclude support for their own evolutionary psychology theory over a biosocial account (Wood & Eagly, 2002). The first is the partialling fallacy, whereby Gangestad et al. control the status of women for its socioeconomic and ecological determinants in their attempt to show that this variable is not relevant to mate choice. The second is the small sample shortcoming, whereby their analyses are compromised by too many variables given the small number of cases. The third is their use of obsolete predictors, whereby they represent pathogen prevalence with old data in their attempt to show the relevance of this variable to mate choice.

Social Structural Origins of Sex Differences in Mating Preferences

Behavior Patterns as Emergent

The human capacity to benefit from a fairly wide range of mating opportunities optimizes possibilities for reproduction and survival, just as the human capacity to thrive on many different types of foods favors survival in widely differing environments. The study of human food preferences details the way that these preferences emerge from the interaction between biological predispositions and properties of the environment (e.g., Rozin, 2000; Stricker, 1990). Specifically, human food practices appear to depend on the options inherent in local conditions, within the limits set by spe-

cies-wide evolved preferences (e.g., sweet foods) and aversions (e.g., rotting food). Humans thus learn what foods are available and healthful in their environments, and this learning is culturally shared. Food preferences are an emergent product of evolved dispositions and other influences rather than preprogrammed through evolution and merely contingently emitted in response to environmental conditions.

Mating preferences follow a similar logic. They are an emergent product of the evolved characteristics of the human species, individuals' developmental experiences, and their situated activity in society. Beliefs about the costs and benefits of mating are socially transmitted and shared within cultures. Not only humans, but other vertebrate species, including birds and fish, have mating preferences that reflect learning from observing others' sexual behavior and mate choices, along with other forms of social transmission of these preferences to conspecifics and across generations (Freeberg, 2000). For example, female quail apparently acquire a preference for an experimentally altered male wearing a feather headdress after observing another female's apparent choice to mate with such a male (White, 2004). The learning mechanisms that allow for socially transmitted assessments of the costs and benefits of mating not only alter selection pressures and subsequent evolution but themselves represent a kind of evolutionary process (Freeberg, 2000).

Roles as Channeling the Costs and Benefits of Behaviors

Among humans, much of the learning of the costs and benefits of behavior is channeled through men's and women's social roles, which divide labor between the sexes. Roles are especially relevant to understanding sex differences in mating and other behaviors. Differing role obligations and opportunities cause men and women to experience differing costs and benefits of mating choices and consequently to value different types of relationship partners (Eagly & Wood, 1999; Wood & Eagly, 2002).

Several processes mediate between the division of labor and typical male and female behaviors. The differing roles of men and women foster the formation of distinctive gender roles, by which people are expected to have characteristics that equip them for activities

typical of their sex. For example, to facilitate caring for young children, women are expected to be nurturing and kind, and to facilitate participation in warfare, men are expected to be aggressive and brave. Gender roles, along with specific roles (e.g., occupational, family) then guide behaviors, including sexual behavior. The effects of roles on behavior are in turn mediated by developmental and socialization processes as well as by processes involved in social interaction and self-regulation. In addition, biological processes such as hormonal changes orient men and women toward certain roles and facilitate role performance.

The social roles of men and women are themselves powerfully influenced by the evolved physical attributes of the sexes and related behaviors, especially women's childbearing and nursing of infants and men's greater size, speed, and upper-body strength (Wood & Eagly, 2002). These evolved sex differences interact with the prevailing social, economic, technological, and ecological forces to yield a division of labor that reflects the ease and efficiency with which each sex performs life tasks.

To illustrate this theory's power, Wood and Eagly (2002) discussed the tendency across many societies for men and not women to hunt large game. The crux of their argument is that women's gestation, nursing, and care of infants limit their ability to perform tasks such as hunting that require speed, uninterrupted periods of activity, or long-distance travel away from home. This account is compatible with the small percentage of known foraging societies in which women regularly hunted large game. In one of the most extensively investigated examples, women of the Agta in the Philippines, assisted by dogs, hunted wild pigs and deer (Estioko-Griffin & Griffin, 1981). Because the Agta lived in a relatively resource-rich environment with game available in close proximity to home, hunting and child care were not incompatible. Women took infants along with them and left weaned children at home until they were old enough to join the hunt.

Comparison With Gangestad et al.'s Evolutionary Psychology Theory

In Gangestad et al.'s (this issue) theory, evolution has designed the human mind to have domain-specific dispositions that are contingent on environmental input. They offer the analogy of the jukebox based on humans' capacity to deliver a selection of preprogrammed responses, depending on the directions from environmental inputs. In contrast, our evolutionary theory assumes far more flexible emergent responses that reflect learning from environmental input, developmental experiences, and evolved dispositions.

We assume that human psychology has evolved to favor the emergence of new preferences with changing circumstances. As Foley (1995–1996) explained, even

humans' early ancestral environments were characterized by a diversity of habitats and associated challenges of reproduction and survival. If evolution endowed humans with prepackaged contingent preferences that maximized outcomes tailored to past evolutionary pressures, they would be ill-equipped to generate innovative solutions to changing environments. A human mind preprogrammed with many domain-specific adaptations would be too rigid to respond effectively to the novel conditions that humans have encountered as their environment has shifted in response to ecological changes, population growth, and the development of complex economies and technology. Less flexible species than humans are more vulnerable to extinction in novel environments.

Our emphasis on humans' behavioral plasticity and the wide range of environments in which they can thrive does not suggest a blank slate so much as evolved dispositions that depend on social and environmental input for the form in which they are expressed in behavior. A more compelling account of human mating preferences than a mechanistic jukebox model of environmentally evoked dispositions maintains that such responses emerge flexibly from multiple influences, given humans' unique adaptation for culture. This evolutionary reasoning recognizes that human cultural traditions, unlike the cultures of other primates, accumulate contemporaneously and over historical time (i.e., the ratchet effect). As an example of this reasoning, Tomasello (1999) proposed that the distinctly human forms of social learning that yield pooling of cultural knowledge emerged largely from a single evolutionary event, which he described as the evolution of humans' ability to understand others as intentional agents like the self. Given this capacity, humans' genetic heritage does not carry the burden of specifying the detailed outcomes evident in contemporary human behavior. Instead, mating preferences, like many other aspects of human behavior, can be understood as emergent from uniquely human forms of social learning in interaction with evolved dispositions and particular developmental and societal contexts.

Relevance of Cross-Cultural Patterning of Human Mate Preferences

Our dynamic framework draws attention to the division of labor within a society as an influence on mating preferences (Eagly & Wood, 1999). The criteria that women and men use to select mates reflect the divergent responsibilities and obligations inherent in their social roles. In societies with a strong division between male providers and female homemakers, women should seek a mate who is a good provider because they are reliant on men to garner resources for them and their children. Men should seek a mate who is a

skilled homemaker and child caretaker because their children's ability to thrive and to some extent their own ability to do so depend on women's mastery of domestic tasks. The provider-homemaker marital system should also favor sex differences in age preferences. These preferences emerge because older men are likely to have acquired resources, and younger women, are likely to lack resources, and thus to value marriage and older partners with resources. However, all of these sex differences in mate preferences would lessen to the extent that the provider-homemaker division of labor erodes and women and men are similarly placed in the social structure.

In a test of these predictions (Eagly & Wood, 1999), we reanalyzed the same data that have once more been reanalyzed by Gangestad et al. (this issue). The data are from Buss's (1989) study of the mate preferences of young adults from 37 diverse, primarily urbanized, cash-economy cultures, with 54% from Europe and North America. In our reanalysis, we represented the social position of women and men by two nation-level indexes available from the United Nations (United Nations Development Programme, 1995). The more relevant of these two indexes, the Gender Empowerment Measure (GEM), represents the extent to which women participated equally with men in economic, political, and public decision-making roles. The second index, the Gender-Related Developmental Index (GDI), reflects the equality of the sexes in basic access to health care, education and knowledge, and income. Although these indexes are useful, neither is fully adequate to represent the male-female division of labor.¹

Consistent with the prediction that mate preferences reflect each sex's attempts to maximize outcomes within their environments, women's preferences for older mates and mates with resources and men's preferences for younger mates and mates with housekeeping and cooking skills were more pronounced in societies with less gender equality, as represented by the GEM and GDI. Providing additional evidence that the preferences of men and women were a common response to a sex-typed division of labor, the sex differences in mate preferences tended to coexist within societies: In societies in which women expressed especially strong preferences for mates with resources and older mates, men also expressed especially strong preferences for mates with domestic skills and younger mates. Nonetheless, because a gender-equal division of labor had not been attained in any of the societies in

Buss's (1989) data set, the sex differences in mate preferences were present to some degree in all of the sampled societies.

In contrast to our biosocial analysis, Gangestad et al. (this issue) propose that mate preferences are pre-programmed, evolved dispositions that are evoked by attributes of the current environment that were associated with fitness in our ancestral past. Their reanalysis of Buss's (1989) cross-cultural data to address this idea suffers from three serious errors that compromise their conclusions. These involve the misspecification of predictors through inappropriate partialling, the overly small samples given the number of predictors in their models, and the use of obsolete pathogen data.

The Partialling Fallacy

The partialling fallacy is a form of specification error that occurs when predictors in regression are not meaningfully distinct (Gordon, 1968). If regression models include controls that themselves capture the meaning of key predictors, then the equation retains too little of the predictors to allow for interpretation. On a statistical level, such inappropriate partialling inflates the standard errors of the regression coefficients and thereby compromises replicability of the analyses (Gordon, 1968). Gangestad et al. (this issue) fell prey to this error when they imposed statistical controls for income, latitude, and region in their regression analyses, ostensibly to remove confounds and thereby obtain purer measures of Eagly and Wood's (1999) key predictor, the division of labor between the sexes. With these controls, the remaining predictor is uninterpretable and assumes undesirable statistical properties.

Before probing this critique of Gangestad's (this issue) analyses, let us illustrate this point by examining an even more obvious example of the partialling fallacy (Ezekiel & Fox, 1959). A study conducted to determine the size standards for children's clothing predicted these standards from various body measurements as well as age and sex (see data in O'Brien & Girshick, 1939). The key statistical predictors turned out to be height and girth at the hips. Once these variables were controlled, age contributed no net effect. A researcher following Gangestad et al.'s regression logic (see footnote 6) would conclude that age is irrelevant to the sizing of children's clothes. Given that age, height, and girth at the hips are intrinsically and causally linked, even a moment's thought reveals the causal relevance of children's age to their clothing sizes, saving virtually all interpreters of the data from such a conclusion.

Now, concerning status of women, the male-female division of labor and patriarchal social structure are intrinsically tied to economic development in world societies because societal modernization produces system-

¹The GDI, indexing the relative access of women and men to societal resources, provides only an indirect measure of gender equality. Even the GEM measure is inexact because it indexes the extent to which women hold seats in parliaments and have technical and managerial occupations, without taking into account the authority associated with these roles. Women and men are counted if they hold managerial or technical roles, regardless of the placement of these roles in organizational hierarchies.

atic changes in the social position of the sexes. As Inglehart and Norris (2003; see also Inglehart, 1997) explained, modernization has proceeded in two phases as societies have moved from agrarian economies to more modern forms. In the first, or industrialization, phase, women enter the paid workforce, and fertility rates fall dramatically. Although women gain basic political rights such as the vote, their power and status remain relatively low, and most aspects of the division of labor continue unchanged. In the second, or postindustrial, phase of modernization, women gain access to management and the professions and increase in political influence. Equality of the sexes increases with the weakening of the division of labor in the home, family, and workplace and the replacement of the traditional breadwinner–homemaker family by a wide variety of adult living patterns.

This postindustrial stage prevails only in the more advanced industrialized societies, which are characterized by the greatest wealth and the highest levels of human capital. Wealth varies dramatically depending on whether societies are in the postindustrial, industrial, or agrarian phase of development. In 1998 a sample of 191 nations whose modernization was defined by the composite Human Development Index (United Nations Development Programme, 1995), the gross domestic product per capita was \$29,585 in postindustrial nations, \$6,314 in industrial nations, and \$1,098 in agrarian nations (Inglehart & Norris, 2003). The close association that exists between economic development and gender equality is consistent with Inglehart and Norris's prediction of attitudinal support for gender equality across 55 nations assessed between 1995 and 2001 from nations' income. Per capita gross domestic product was correlated .61 with support for gender equality, which was in turn correlated .84 with the GEM. Thus, societal income is closely and meaningfully related to gender equality.

What does geographic location have to do with the division of labor? Region and latitude are correlated with the division of labor because some nations are more favorably situated for modernization due to their geography and ecology. The arguments for the importance of geography and ecology, interacting with technological developments, have been set forth by many scientists, most popularly by Diamond (1997). Certain societies possessed the natural resources that contributed to economic development, along with the geography that facilitated trade and the communication of innovations. As historians and social scientists have extensively documented, such advantages have propelled some societies, especially those of North America and Europe, into the industrial and then the postindustrial stage. It is thus understandable that gender equality is related to region and latitude.

Our reasoning about the intrinsic linkages of gender equality to nations' wealth, region, and latitude is consistent with the correlations of these variables with the GEM and GDI United Nations indexes of equality shown in Appendix A of Gangestad et al. (this issue). Nations' income and latitude are highly correlated with gender equality (r s range from .63 to .75), and the various geographic regions show more modest associations. With this pattern, specification errors occur when the gender equality indexes are partialled for income, latitude, or region in predicting mate preferences. Because Gangestad et al.'s regression models are subject to specification errors that arise from controlling gender equality for its determinants, it is understandable that few significant results remain for the GEM and GDI indexes in Tables 1, 2, and 3, in which the authors report the findings predicting preferences from these indexes.

Additional complexities arise because it is impossible to discern exactly what controls Gangestad et al. (this issue) instituted for each analysis reported in Tables 1, 2, and 3. The authors evidently instituted differing controls across the analyses (see footnote 5), making the various analyses noncomparable. They report that their first-stage analyses were regressions that "examined the contributions of income, geographical region, and distance from the equator. If a variable accounted for significant variation, it was retained for the second stage of analysis." In the second-stage analyses, aspects of which are reported, some regressions might have controlled, for example, for one or more of the dummy-coded region variables and other regressions for latitude or income. Although the details of these analyses remain unreported, Gangestad et al.'s description of their method implies that analyses on each dependent variable included a distinct set of control variables and that these variables changed across the analyses. Because interpretation of the effects of the gender equality and pathogen prevalence predictors depends on the specific controls included, it is unclear how to interpret the effects reported by Gangestad et al.

In their unusual analysis strategy of including multiple and varying controls for national wealth and geographic location, Gangestad et al. (this issue) deviate from earlier research. Low's (1990) analysis linking pathogen stress and the prevalence of polygynous marital systems reported some analyses controlling for geographic region and other analyses controlling for latitude but did not include multiple controls and did not control on national income.

In sum, given that gender equality is but one component of a set of intrinsically linked societal factors, it is inappropriate to partial out the influence of these other factors when interpreting the effects of this variable. Nations' gender equality, as one aspect of social struc-

ture, is embedded in a complex of linked features of the economy, polity, and family.

The Small Sample Shortcoming

The small samples available for Gangestad et al. (this issue) to test their regression models provide additional reason to question the reliability of the findings reported in Tables 1, 2, and 3. Regression analyses are made unstable by inadequate sample size in relation to the number of predictors included in the analysis. Although Gangestad et al.'s report obscures the details of their analyses, the first-stage analyses apparently entered seven predictors (income, latitude, regional contrasts 1 through 5). The second-stage analyses had fewer predictors, evidently just over three on the average (control variable, GEM, and pathogen prevalence), but the range of the number of predictors is unreported.

Although the aggregated data represented in Buss's (1989) 37 cultures study possess particular statistical properties, the models used in Gangestad et al.'s (this issue) analyses are presumably subject to the standard requirements of regression procedures. In a classic analysis of the sample sizes necessary for adequate power in regression models, Green (1991) evaluated numerous rules of thumb that have been used by researchers over the years. He concluded that detection of a medium-sized effect with power equal to .80 in multiple regression requires a sample size greater than $50 + 8p$, where p is the number of predictors. With a sample size of 37, the analyses were inappropriate even in the second stage of the regressions and more so in the first stage. In recognition of the small sample size and relatively low power, the authors report that they used a liberal alpha equal to .10 to determine statistical significance. However, this decision rules is inadequate to address the problem of instability of findings given samples too small for the number of predictors.

Anyway, They're Not Playing Our Song

Gangestad et al. (this issue) based their analysis of parasite prevalence on old parasite data contained in books by Craig and Faust (1943), Rodenwaldt (1952), and Simmons et al. (1944–1954). The jukebox analogy implies that contemporaneous local conditions elicit the preprogrammed preferences that control mating. The data that Gangestad et al. (this issue) used from “the first half of the 20th century” have uncertain relevance to the mate preferences of late 20th century humans. These outdated eliciting conditions can't play the right song.

One reason for using older estimates of parasite prevalence might be that sexual behavior changes only with considerable lag as the environment changes. Therefore, earlier parasite data might be preferable to parasite data more contemporaneous with the 1982–1986 dates when mate preferences were assessed (see Gangestad & Buss, 1993). However, this lag appears to be relatively small. Typical mating practices can change quite rapidly along with other social changes that bring an increase in the status of women. Illustrative of such change in the 20th century in the United States, a meta-analysis of data from 1943 through 1999 showed extremely large shifts toward more sexual activity beginning at earlier ages, especially among girls, and considerably greater approval of premarital intercourse (Wells & Twenge, 2005). By 1999, the once quite different sexual behavior and attitudes of young men and women appeared to have become virtually identical.

If more modern data on parasite prevalence were not available, Gangestad et al. (this issue) might be justified in relying on old data. However, prevalence indicators contemporaneous with the dates of the mate preference assessments are widely available. In fact, Low (1994) included sources from the 1980s (e.g., Markel & Voge, 1981) in her cross-cultural analyses of pathogen prevalence, and she attempted to match the date of each culture's parasite data to the time period of the other data in her analysis.

The importance of coordinating the dates of the parasite estimates and the mate preference assessments is highlighted by evidence of the volatility of parasite distributions across the 20th century. Part of this instability comes from inexact assessments, given that early estimates of the prevalence of parasites often were based on informal assessments rather than on reports from national health agencies and other reliable sources.² More important, the actual prevalence has shifted as the parasites have evolved and as events have transpired to increase or decrease their incidence. In recognition of the speed of adaptation of parasites and hosts, evolutionary theorists have posited the red queen hypothesis, suggesting that, like the red queen in Lewis Carroll's book, *Through the Looking Glass*, interacting species must evolve continuously to keep up, even in a constant physical environment (see Ridley, 1994).

²Several developments have increased the precision of estimates of parasite prevalence across world geographic regions. The accuracy of data has benefited from “sentinel” practices whereby general practitioners in many nations report the diseases that they have diagnosed, international agreements mandate the reporting of some diseases, and the World Health Organization (2004) systematically records the distributions of diseases (Cliff et al., 2004). Taking advantage of these improvements, the Global Infectious Diseases and Epidemiology Network database indexes 337 human parasitic and infectious diseases in 224 nations and updates these estimates weekly based on a range of sources.

Additional impetus for increased or decreased incidence comes from the changes in humans' and parasites' environment during the period from the early to the late 20th century. Reduction of parasites has been achieved during some periods in particular regions due to pesticides, population shifts, environmental manipulations, increased health infrastructure, and accessibility of drug treatments. In other regions at other points in time, parasite incidence has increased due to reduced financial support for eradication, loss of public health infrastructure, overpopulation, climate change, and evolution of parasite resistance to insecticides and drugs. For reviews of the multiple effects of human activity and climatic change on the epidemiology of parasitic zoonoses affecting humans, see Cliff, Hagggett, and Smallman-Raynor (2004), Gramiccia and Gradoni (2005), and Macpherson (2005).

The volatility of parasite data is evident in Cliff et al.'s (2004) comparative mapping of the incidence of malaria at the middle and end of the 20th century, especially in the considerable retreat of malaria from areas such as coastal South America and China. In addition, Gubler (1998) noted that four of the diseases in Gangestad et al.'s (this issue) analysis (i.e., filariasis, trypanosomiasis, leishmaniasis, and malaria) that are transmitted through blood-sucking arthropods such as mosquitoes were effectively controlled outside of Africa by the 1960s, largely due to insecticides. However, he also indicated that for a number of reasons these diseases reemerged in the next 20 years and reached epidemic levels in particular world regions. As another example of change, researchers in the Zhejiang Province of China reported a 72% reduction in the prevalence of 26 species of human parasites between 1987–1989 and 1998–1999 (Tu et al., 2001). This shift consisted of a decrease from an 80% infection rate to 23%, based on biological measurements of multiple samples of individuals. Given this considerable volatility of parasite infections, a valid test of the possibility that mate preferences are contingent on pathogens requires careful documentation of the prevalence in each world region contemporaneous with the timing of the assessment of mate preferences.

It is additionally interesting to note that Gangestad et al.'s (this issue) interpretation of pathogen effects may itself suffer from specification error because pathogen distribution and diversity are moderately strongly associated with latitude (Guernier, Hochberg, & Guégan, 2004). In Gangestad et al.'s data, these relations are represented by the correlations of pathogen prevalence with geographic region and latitude (see Appendix A). In general, parasitic and infectious diseases become more common and diverse at lower latitudes. The power of latitude as a predictor is due to various covarying bioclimatic factors. Investigation of a number of such variables within the database of the Global Infectious Diseases and Epidemiology Network (2005) found that the best predictor of pathogen

species distribution is the annual variation of precipitation around the mean (Guernier et al., 2004). Many pathogens appear to be adapted to climatic patterns of strongly contrasting wet and dry seasons, which are more common nearer to the equator. In addition, mean annual temperature predicted some groupings of pathogens, as did mean annual precipitation.

Given that climate is important to the diversity and occurrence of human pathogens and that the relevant climatic variables are correlated with latitude, we wonder how to interpret pathogen prevalence data controlled for region or latitude—the key proxy variables that represent the bioclimatic factors causally related to pathogens. Adding controls for latitude or region in the analyses in Tables 1, 2, and 3 does not make the pathogen predictor easier to interpret. Instead, the resulting pathogen variable represents the variability in early 20th century pathogen distributions that is not predictable from latitude. This analysis thus provides a classic demonstration of the partialling fallacy, and the results do not yield clear interpretation.

Conclusion

The analyses provided by Gangestad et al. (this issue) do not contribute meaningfully to the debate about the causes of mating preferences. The jukebox theory and ideas about contingently expressed dispositions, although advancing evolutionary psychology toward the recognition of cultural variation, fail to acknowledge the emergent quality of these preferences. These preferences reflect evolved physical attributes and psychological dispositions, including the uniquely human abilities that have fostered behavioral flexibility and enabled complex societies. Humans' evolved characteristics, together with their developmental experiences and situated activity in society, shape their mating preferences, including sex differences in these preferences.

Notes

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