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Culture and Developmental Plasticity

Evolution of the Social Brain

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he relation between culture and biology emerged as one of anthropology's ▲ first intellectual responsibilities. It remains one of our most frustrating enigmas. The dichotomy of "nature and nurture" has been a persistent obstacle to consilience between the biological and social sciences. Anthropology has traditionally recognized that culture is inextricably linked to the evolution of mind and that the converse is equally important. In this chapter, I review a scenario in which the mind evolved as a "social tool" in an increasingly cultural environment. I posit that the human psyche was designed primarily to contend with social relationships, whereas the physical environment was relatively less important. Most natural selection in regard to brain evolution was a consequence of interactions with conspecifics, not with food and climate. The primary mental chess game was with other intelligent hominid competitors and cooperators, not with fruits, tools, prey, or snow. An extended juvenile period was favored by natural selection because of the need for more time to develop mental competencies used in forming coalitions and other aspects of social competition. "Culture," shorthand for the information acquired and used by minds in social ways, was a

key component of the emerging hominid social environment. Humans are unique in the extraordinary levels of novelty that are generated by the cognitive processing of abstract mental representations. 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. This perspective may reconcile important aspects of the current biology-culture gap because it suggests an evolved human psychology that is creative, dynamic, and responsive to cultural context, rather than being rigidly constrained by domain-specific modules.

Social Sensitivity, Hormones, and Health: Why Can Words Make Us Sick?

Wayonne's dirt bomb struck the bright yellow dress hanging on the clothesline, making an impressive star-shaped smudge. His older cousin Jenny turned angrily from sweeping the house yard to chase him with her broom. Granny Deedee's yell halted their squabble. Jenny's face morphed from stifled argument to guilt, head bowed. She later told me she felt upset because granny did not understand; her frustration was compounded by the rule that she must accept granny's authority without disagreement. Jenny's cortisol (a stress hormone) level, measured from her saliva that I collected several times a day, rose from 1.4 to 4.2 µg/dl. The next day, her secretory immunoglobulin-A levels dropped from 6.04 to 3.6 mg/dl. Four days later, she had common cold symptoms: runny nose, headache, and low-grade fever (see Figure 3.1).

This anecdote contributes to a common pattern. Children in this rural Dominican community are more than twice as likely to become ill during the week following a stressful event (Flinn & England, 2003). People everywhere appear sensitive to their social environments, often with negative consequences for their health (Cohen, Doyle, Turner, Alper, & Skoner, 2003; Maier, Watkins, & Fleschner, 1994; Marmot & Wilkinson, 1999). Mortality rates were appalling during the early 20th century for children in orphanages and hospitals lacking the evolutionarily normal intimacy of the family: "In the last report of the State Board of Charities of New York, it is stated that 57.2 per cent of infants died in infant asylums through the state" (Chapin, 1928, p. 214). It is not just the occurrence of traumatic events that affect health, but the lack of social support, including parental warmth and other factors that influence emotional states. Why should this be so? Why do social interactions, and a child's perceptions of them, affect physiology and

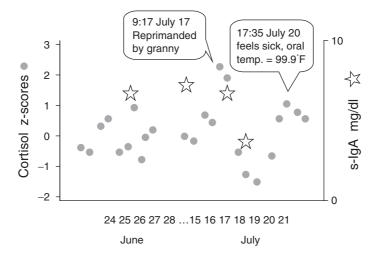


Figure 3.1 Cortisol and s-IgA Levels of a 12-Year-Old Girl Living in Bwa Mawego

morbidity? And, more generally, why is the social environment of such paramount importance in a child's world (e.g., Hirschfeld, 2002)?

In this rural Dominican village that I have lived in and studied over the past 16 years, most of a child's mental efforts seem focused on negotiating social relationships with parents, siblings, grandparents, cousins and other kin, peers, teachers, bus drivers, neighbors, shop owners, and so forth. Foraging for mangos and guavas, hunting birds with catapults, or even fishing in the sea from rock cliffs are relatively simple cognitive enterprises, complicated by conflicts with property owners and decisions about which companions to garner and share calories with. The mind seems more involved with the social chess game than with the utilitarian concerns of the ecological.

I pose these questions as an introduction to the broader issue of the biology-culture gap that pervades anthropology, psychology, and other social and behavioral sciences. The relation between biology and culture is the nexus of anthropology and child development. It is arguably one of our most important scientific and philosophical problems; it underpins mind, thought, and action. It is the keystone of anthropology's holistic approach. And yet it is a perennial source of rancor and disagreement. For many, anthropology "has become polarized into two tribes—one oriented toward biology, the other toward culture—who seem unable or unwilling to understand one another" (Holden, 1993, p. 1641). This "biology-culture gap" has a history and a potential solution.

A Brief History of Culture

In 1900, the President of the Royal Society (London) suggested that everything of great importance had already been discovered by science. Perhaps he overlooked anthropology and its problem of culture—at least we were in good company, alongside black holes and the like. Certainly Taung, "Argonauts," Gombe, DNA, and the many other jewels of the past 100 years challenge his speculation.

In hindsight, the 20th century began with formidable empirical, theoretical, and ideological obstacles to understanding the biological significance of culture. The hominid fossil record was sparse and crudely interpreted. Ethnography was slapdash. Archeology was still engaged in treasure hunts. Primatology was limited to circus and zoo anecdotes. Genetics and psychology were just getting started. Linguistics lacked integration with neurobiology. Evolutionary theory had not yet benefited from the insights of the new synthesis and subsequent refinements. Religious and spiritual beliefs of "human uniqueness" were pervasive. Ethnocentrism clouded analysis of cultural diversity. Racism, sexism, and socioeconomic inequalities called for a politically active as well as a scientific anthropology. Even the term *culture* was contentious.

I hope that it is not complacent to observe that anthropology has made significant inroads against these obstacles. We have learned a great deal about human biology and culture; however, we still have not been able to put the two together satisfactorily. We need a comprehensive explanation for the evolution of the extraordinary aptitudes of humans for abstract mental representation and social learning.

Traditional culture theory, however, did not seek answers to the riddles of culture in the evolution of the brain. The "symbol" was posited as a miracle that uncoupled the human mind from biology (Boas, 1911). The physical mechanisms and functional reasons for the origin(s) of culture were considered speculative details lost to prehistory; the important thing was that symbolic representation had sparked a new informational universe with its own set of open rules (Washburn, 1978). The diversity of culture would not be explicable by reference to neurons and synapses. The preconditions were not supposed to constrain or direct culture.

The recent works of behavioral ecologists, evolutionary psychologists, primatologists, and others inspired by the new developments in evolutionary biology, however, suggest otherwise. The biology-culture gap was widened for some by the sociobiology confrontation, but new bridges were built. Although it is difficult to generalize about theoretical positions in anthropology, I think it is fair to summarize that while most anthropologists were

comfortable with the idea that the human brain was a product of natural selection, many were uncomfortable relating this truism to direct connections to informational content, that is, to cultural specifics. The conceptual dichotomy of "nature and nurture" persisted.

Current Ideas

There seems a growing dissatisfaction with the old concepts of culture. A self-reflective anthropology has begun turning over some interesting academic stones. "Culture" was many cherished things: our discipline's authoritative domain, our explanation of our species' uniqueness, and the source of our political influence. It seems surprising that something we had so much difficulty agreeing upon what it was nevertheless could be so important. Let me reiterate the casual definition that I dangled at the beginning of this paper: Culture is shorthand for the information acquired and used by minds in social ways. This definition is undoubtedly problematic. It does not justify territoriality of theory. It does not support a view of our species as qualitatively unique. It does not scientifically privilege the information acquired and processed by humans.

Considering the alternatives, "culture as information" is too simple: It neglects the evident emergent properties of psychological development and social and historical process. And yet "culture as that complex whole" is vague and imprecise (but see Cronk, 1999). Even the middle ground is shaky. The goals of our definition of culture have changed. The superorganic concept of culture has crumbled under the scrutiny of individual variability (Barth, 2002). The species-centric perspective has been challenged by primatology (McGrew, 2003; Stanford, 2001; de Waal, 2001; Whiten et al., 1999; Wrangham, McGrew, de Waal, & Heltne, 1994) and ethology (Mann & Sargeant, 2003; de Waal & Tyack, 2003). Perhaps most important, a much more powerful understanding of ontogeny is beginning to emerge from developmental biology (West-Eberhard, 2003) that places culture into a different relation with biology: one that requires an evolutionary theory of phenotype that meshes mind with social and historical process.

A Potential Solution

The culture side of the gap has traditionally identified a number of important and unique characteristics distinguishing human culture. These include:

- 1. Culture content is *transmitted by learning processes* (i.e., cognitive information transfer) and not by the transfer of genetic materials. Hence, culture appears to be a separate inheritance system, uncoupled from genetics.
- 2. Culture (or its effects) is partly *extrasomatic*. Cultural traits (e.g., stone points, political monuments) exist outside the soma (physical body) of the culture-bearing organism.
- 3. Human culture, by most definitions, involves *mental phenomena*, including conscious thought.
- 4. Human culture involves the *use of arbitrary symbols* to form mental representations and to communicate information.
- 5. Culture appears to have *emergent properties at the group level*, such as shared values and beliefs resulting in political and religious institutions.
- 6. Culture involves *historical processes*. History constrains the options (cultural traits) available for individual choice and modification, and culture can change rapidly, apparently outracing genetic evolution.
- 7. Complex culture is uniquely human.

These characteristics of human culture make it a most challenging and difficult aspect of life to understand in scientific terms. However, they do not necessarily cause culture to become a "nonevolutionary" or "separate evolutionary" phenomenon, independent of biological adaptation. Two of the above characteristics stand out as especially important for resolution of the biology-culture gap: (1) the biological basis of social learning and (2) the evolution of human cognitive abilities and associated cultural aptitudes. We need to understand what the mind was designed to do by the selective pressures of hominid evolutionary history. What tasks were accomplished by Woody Allen's second favorite organ that resulted in the survival and reproduction of our ancestors?

The Mechanisms: Biology and Social Learning

It is difficult to conceive of a process responsible for systematic, incremental development of the human brain over several million years that did not involve differential replication of genes (i.e., natural selection), and yet, this is what a "blank-slate" model of the central nervous system requires. If cultural learning is uncoupled from natural selection, then once culture developed, the brain (more specifically, those parts of the brain involved with cultural information) would no longer evolve. Increasingly refined aptitudes

for social learning via symbolic communication would not have evolved if the information obtained did not result in adaptive behavior.

Organic or Darwinian evolution is usually defined as a change in gene or allele frequencies over time. Cultural evolution is usually defined as a change in cultural trait frequencies (or mental information) over time. Because cultural transmission (e.g., imitating a song or adopting a technique for making stone tools) occurs without concomitant genetic transmission, it has been argued that cultural evolution is independent of genes. This leads to the conclusion that cultural evolution is independent of organic evolution. If biology = genetics, and culture = learning, then if learning? genetics, culture? biology.

The logic underlying the above conclusion is an important aspect of the biology-culture gap. It distinguishes learning from other flexible responses (e.g., physiological changes) to environmental influences in the production of the phenotype. This is a critical assumption underlying the view that culture is an autonomous inheritance system. "Cultural" evolution is distinguished from "biological" evolution on the basis that cultural evolution involves a distinct mode of information transmission (learning on one hand, genetics on the other). The analogy between cultural evolution and organic evolution, however, may be inappropriate if cultural information is mediated via organically evolved mental faculties, including social learning processes (Flinn, 1997).

Phenotypes are generally accepted to be the products of genes + environment. The directions and degrees to which organisms modify their phenotypes in response to environmental conditions result from a past history of natural selection on abilities to modify phenotypes in response to environmental changes (Alexander, 1979; Stearns, 1992; West-Eberhard, 2003). Arctic hares have seasonal changes in fur color, humans develop calluses on their hands and feet, fig wasps alter the sex-ratios of their broods, sweat bees learn by association and similarity whom to let into the nest, chimps observe and imitate termiting with sticks, and so forth.

The point here is that phenotypic modification, whether achieved via learning or physiological change, is not random. The environment is a causal factor during the development of the phenotype in the context of an evolutionary history of selection for modifications in response to environmental changes (West-Eberhard, 2003; Williams, 1966). Environments do not have random effects on phenotypes. Among Arctic hares, winter conditions result in white coats, summer in brown coats. Other species of rabbit lack this capability; they do not have genetic materials that allow for this adaptive response. Similarly, chimpanzees lack aptitudes for most aspects of human culture, presumably because chimps do not have genetic materials necessary for development of the requisite central nervous system—especially

an expanded prefrontal cortex—and associated psychological mechanisms. Regardless of environment, chimpanzees cannot acquire and transmit knowledge of black holes, despite their remarkable cognitive abilities (Tomasello, Kruger, & Ratner, 1993). Clearly, there are evolved differences between chimps and humans in regard to mental processes that underlie human culture (e.g., de Waal & Tyack, 2003; Wrangham, Jones, Laden, Pilbeam, & Conklin-Brittain, 1999). These differences involve the underlying neural architecture.

Humans have brains that are roughly 2 to 3 times larger than that of our clever phylogenetic cousins, the chimpanzees (Pan troglodytes and Pan paniscus), the gorilla (Gorilla gorilla), and the orangutan (Pongo pygmaeus), and our distant ancestors, the australopithecines (e.g., Australopithecus afarensis). Our enormous neural structures are not cheap: they consume 20% of our metabolic resources and are energetically and developmentally expensive to build as well. Hence, the evolution of the human brain requires an extraordinary functional payoff (Dunbar, 1996). But the differences are not in size and calories alone. In addition to the much more complex patterns of cerebral convolutions, there are many unusual and unique aspects of the human brain. For example, humans have relatively dense connections between parts of the brain that are involved with emotion and higher cognitive skills. The anterior cingulate cortex (ACC) receives strong projections from the amygdala, providing higher-order cognitive regulation of fear and anxiety. Like our close hominoid relatives, albeit in much greater numbers, humans possess a unique type of neuron, the spindle cell, found in layer 5B of Brodmann's area 24 (Nimchinsky et al., 1999). These spindle cells potentially link distinct components of the brain, providing a mechanism for monitoring performance and rewarding success via the rich dopaminergic cells of the ACC (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001). These and other structures provide the neurobiological bases for the remarkable human abilities of self-awareness, theory of mind, empathy, and consciousness (Adolphs, 2003; Seigal & Varley, 2002).

What are the functions of all this magnificent neural hardware? The simple answer is increased abilities to process information, providing enhanced response to environmental contingencies. The brain provides a means for phenotypic flexibility via adjustable behaviors. Genes evolved to produce phenotypes, including capabilities for learning, because phenotypes provide a means of responding to changing environments:

The whole reason for phenotypes having evolved is that they provide flexibility in meeting environmental contingencies that are only predictable on short-term bases. Learned behavior is the ultimate of all such flexibilities. Not just humans and higher mammals but animals in general develop their behavior, or "learn" to do what is appropriate in their particular life circumstances. Even the remarkably distinctive castes of the social insects are in nearly all cases determined *not* by genetic differences, but by variations in experiences with food or chemicals while they are growing up. The ranges of variation, and the adaptive "peaks" along the axes of such variations (in the case of the social insects, the actual worker and soldier castes), are finite and predictable (e.g., Oster & Wilson, 1978). I believe that we will eventually discover that exactly the same is true for the range and relative likelihoods of composites of learned behavior (or "learning phenotypes") in humans. (Alexander, 1979, p. 14)

Learning capabilities (and neuropsychological mechanisms that use information acquired by learning) would not have evolved if they produced behaviors that were random with respect to biological adaptation. Organisms have evolved to learn in ways that enhance fitness; they have evolved to learn nothing else. This is not to deny that learning can result in maladaptive behavioral modifications; imperfection is the bedfellow of unpredictable environments and novelties that favor learning capabilities in the first place. Hence, perhaps, our evolved abilities to analyze and learn from mistakes and successes of others (Flinn & Alexander, 1982). The degree of skepticism with which we view teachings of others, particularly nonrelatives or others whose interests do not coincide with our own, suggests that deception and manipulation are additional concerns.

Learning is a type of phenotypic modification, one way that environmental conditions are used to adjust responses of the organism:

The alternative to cultural behavior is not "genetically transmitted" behavior: the environment always participates in ontogenesis, even when it is invariable. Plasticity is the rule rather than the exception for all aspects of phenotypes, and imitation and other learning are not restricted to human culture. (Flinn & Alexander, 1982, p. 384)

Cultural differences are due not to genetic differences, but to a *history* of learned responses to different environmental conditions. To take a simple example, just as the white coat is advantageous for the Arctic hare in winter, knowledge of seal hunting is advantageous for the Eskimo. In both cases, there is an evolved ability to respond in a flexible way to varying environmental conditions. In both cases, the phenotype is adjusting itself in a way that is consistent with adaptation. In the case of seal hunting, psychological mechanisms using social transmission of information are involved.

Learning capabilities involve specific propensities and constraints (e.g., Gould & Marler, 1987; Heyes & Galef, 1996). Cognitive capacities, including

complex features such as personality development, are influenced by genetic factors (e.g., Plomin, 1990; Scarr, 1992). The important questions here are whether learning propensities and constraints are adaptations produced by natural selection and whether they influence transmission of cultural information.

Learning allows modification of behavior based on experience. Behavioral modifications are no less "biological" than physiological modifications; both involve chemical-neurological mechanisms, and both are products of evolution. There are several general "methods" or pathways by which adaptive learning can occur (e.g., Shettleworth, 1998). The simplest method is behavior modification based on the "trial and error" of individual experience within specific domains (e.g., rats develop aversions to foods that result in nausea; Garcia, 1974).

More complex learning methods use information transfer from one individual to another via "imitation" (for more specific use of the term, see Heyes, 1994; Galef, 1996; Tomasello, 1999; Tomasello & Call 1995). The ability to (a) observe behavior (of parents, etc.), (b) produce a mental image, and (c) reproduce the behavior (imitate or copy) can have tremendous advantages over trial and error (e.g., Heyes & Galef, 1996). Social learning allows one to benefit from the experiences of others and to provide coresident offspring with a "head start." Aversions to poisonous mushrooms can be developed by following the example set by others rather than by direct experience. Problems with imitative learning arise if inappropriate (maladaptive) behaviors are acquired. For example, it would not suit nest parasitic species such as European cuckoos to learn their mating songs from their hosts. Imitative learning requires learning "templates" or "innately tuned sensory systems" that may be time and/or situation restricted (e.g., kin recognition; Alexander, 1990a).

Imitative learning need not be "blind." Evaluation of the relative success and failure of one's peers may allow for more sophisticated behavioral modification. For example, in some species of birds, selective imitation of songs of males that are successful in attracting females can be more advantageous than random imitation of a singing male (Baker & Cunningham, 1985). Learning via selective imitation can lead to cumulative directional change if successful innovations are passed along to the next generation (e.g., Maestripieri, 1996). Intergenerational social learning with cumulative modifications can result in "progressive" historical development of information. Because the current information pool is based on experiences of past generations, this type of learning involves historical constraints. Most definitions of "culture" involve learned information of this sort and the behavior it produces (McGrew, 2003).

A further modification of learning involves selective imitation of behavior based on an individual's specific microenvironment and life history stage. Abilities to "custom-fit" acquisition of information to an individual's specific life history circumstances are advantageous if there are significant differences in individual strategies. What is best for one individual to learn at a certain time in life may be inappropriate for another. Ideally, one would learn the right thing at the right time from the right role model (e.g., MacDonald, 1988). Specialized learning of this sort requires the ability to analyze the individual's position in current social-environmental conditions (perhaps involving self-awareness and consciousness; see Adolphs, 2003; Alexander, 1989; Dennett, 1995; Povinelli, 1993, 1994; Tomasello, 1999). Such analysis probably requires extensive information storage (memory) in order to have a basis for comparison and perhaps for delayed usage (e.g., young chimps observing an alpha male may store images of his behavior for imitation later in their lives).

Humans (and perhaps other hominoids, especially chimpanzees) have developed complex forms of learning that involve behavior modification based on mental representation and scenario building. We use mental "games" to predict possible outcomes of alternatives. Should I get Aunt Leila the red sweater or the blue? Which color would she prefer? What will my other relatives think? Such decisions are based on a "theory of mind" including foresight and comprehension of thought processes (and likely behavioral strategies) of others (Adolphs, 2003; Seigal & Varley, 2002; Tomasello, 1999). Decision making based on mental scenarios allows for experience without the cost. In addition to the task-specific modular capacities (e.g., ability to recognize facial expressions), such enhanced psychological mechanisms require expanded neural capacity for increased general competencies of working memory, attentional control, and executive functions (allowing for more extensive analysis, framing, categorization, etc.; see Engle, 2002).

Humans use a combination of learning methods in day-to-day living. We obtain information from direct observation and symbolic communication. We "think over" acquired information (consciously or unconsciously) and evaluate whether it is useful (e.g., Chibnik, 1981). We modify our behavior accordingly. Unfortunately, quantitative models of cultural transmission do not yet include complex learning and information manipulation that exemplify human culture and behavior. Humans appear "smart"; we do not randomly imitate cultural traits, even from apparently successful role models. Nor are cultural traits employed randomly; individuals strategically use different behaviors to suit particular contexts.

The complexity of social learning processes is a key issue for resolving the biology-culture gap. Theories based on evolved psychological mechanisms

emphasize adaptive decision making, whereas traditional theories focus on nonpsychological aspects of information transmission, such as structure of diffusion (vertical via parents, horizontal via peers, etc.). The issue involves whether learning "rules of thumb" are simple or sophisticated, and the importance of "other forces" besides evolutionary design of cognitive processes that affect culture content.

The ubiquity of apparently nonadaptive or maladaptive behaviors such as tattoos, arbitrary food taboos, religious beliefs, celibacy, ethnic markers, dress style, and so on, may be interpreted as evidence that forces besides evolved psychological mechanisms influence culture choice. Cultural traits that are maladaptive nonetheless become common by virtue of "cultural" processes such as society level functions, conformity, or blind imitation, because human psychological mechanisms are not sophisticated enough to discriminate among cultural options. There are, however, alternative explanations for the existence of nonadaptive and maladaptive behaviors, including historical lag, deception and manipulation by competitors (Krebs & Dawkins, 1984), experimentation, selective conformity, and chance (see Alexander, 1979; Dawkins, 1982, pp. 33-54, for discussion of "constraints on perfection"). Perhaps the most difficult aspect of evaluating the utility of cultural traits is determining social and historical context. Conformity, imitation of success, and other aspects of human sociality may generate complex dynamics that do not fit with simplistic utilitarian models of culture.

Evolved psychological mechanisms theory emphasizes that learning capabilities are evolved aspects of the phenotype, and, as such, have been designed by natural selection. The information bits in human minds are generated by processing of observations of the behaviors of others, and are not independent replicators (for debate, see Flinn, 1997; Laland & Brown, 2002; Sperber, 1996). Detailed descriptions of psychological mechanisms (and their ontogenetic development) are important research objectives. Social learning may involve numerous distinct processes, such as social facilitation, local enhancement, mimicking, emulation, and imitation (Heyes, 1994; Tomasello, 1999), perhaps further specialized in different functional domains (Hirschfeld & Gelman, 1994), including language (Pinker, 1997). As summarized by Leda Cosmides and John Tooby (1989),

The study of culture is the study of how different kinds of information from each individual's environment, especially from his or her social environment, can be expected to affect that individual's behavior. The behavior elicited by this information reverberates throughout the individual's social group, as information that other individuals may act on in turn. The ongoing cycle that results is the generation of culture. By directly regulating individual learning and

behavior, those psychological mechanisms that select and process information from the individual's social environment govern the resulting cultural dynamics. (pp. 51-52)

Information, or culture, thus involves not only social interaction but also an endless history of social interaction, filtered and analyzed at each step by psychological mechanisms that are themselves developed during ontogeny in response to the particular subset of information to which each individual is exposed. This approach parallels studies of human motivation in cultural anthropology (e.g., D'Andrade & Strauss, 1992).

No one has argued that culture content can be explained by reference to evolved psychological mechanisms alone. How could we predict and explain the directions and pace of cultural changes, given that all humans have roughly the same psychological mechanisms? Environmental differences appear insufficient to account for cultural differences without including some type of interaction with historical context. A complete model of culture must include the effects of (a) social integration and shared information, "reverberation throughout the individual's social group"; (b) history, "the ongoing cycle"; (c) individual psychological and informational development (ontogeny); (d) the noncultural environment (e.g., flora and fauna, geography, and demography); (e) chance or accidental events; and (f) evolved psychological mechanisms that underlie mental representation and communication. The devil is in the details; for evolutionary psychologists such as Cosmides and Tooby, the emphasis is on the "psychological mechanisms that select and process information" because they "directly regulat[e] individual learning and behavior." Direct regulation, however, may not be the optimal strategy if the game is constantly being reinvented and is contingent upon specific social and historical context. The empirical focus on "universals" is similarly problematic in some domains: The human social environment generates conditions under which individuals may benefit from innovation and behavioral diversity.

The theoretical logic and evidence for the evolved mind are compelling. Hence the firm stance on the biology side of the gap. The view from the other side is a bit different. Many cultural anthropologists look at the situation and do not see the relevance of biology, regardless of the evolutionary basis for the mind. The nearly infinite diversity of cultural detail does not appear to be reducible to a set of biological universals. Culture does not adhere to a strict utilitarian scheme. If the evolved psychological mechanisms are so influential, why the cacophony of information? Why the riot of individual expression and yet the restraint of collective meaning? From the culture side of the gap, one can only conclude that whatever our minds might

have evolved to do, it is not a collection of simple biological routines (Mithen, 1996). Getting calories and breathing air are great, but what would life be without friends, art, sports, religion, music, sex, quarks, status, and the stars and the moon?

Hence the quandary of the biology-culture gap. One side is convinced that the mind is a product of organic evolution, designed by natural selection for specific functions and yet capable of considerable "cognitive fluidity." The other side sees little relevance of that obvious fact for understanding the diversity of culture; we spin our webs of meaning far from the apparent constraints of our DNA heritage. Both positions are backed by logical theories and mountains of empirical evidence.

The Missing Link: Why Did Human Intelligence Evolve?

Anthropology has considered many hypotheses concerning the selective advantages of human intelligence. Most explanations involve ecological problem solving, such as tool use (e.g., Byrne, 1997; Darwin, 1871; Gibson & Ingold, 1993; Washburn, 1959; Wynn, 1988, 2002), hunting (e.g., Dart, 1925; Stanford, 2001), scavenging, foraging (e.g., Isaac, 1978; Kaplan, Hill, Lancaster, & Hurtado, 2000), projectile weapons (e.g., Bingham, 1999), extended life history (e.g., van Schaik & Deaner, 2003), food processing (e.g., Wrangham et al., 1999), and savanna, aquatic (e.g., Morgan, 1995), or unstable (Potts, 1996) environments. None has achieved complete or general acceptance, even when combined in synthetic models and causally linked to social dynamics.

Common problems for these models include difficulties with explaining why humans uniquely evolved such extraordinary cognitive abilities, considering that many other species hunt, occupy savanna habitats, have long lifetimes, and so forth. Given the very high metabolic costs of evolving, building, and maintaining a human brain (20% of total caloric intake), the ecological gains required are difficult to imagine (Dunbar, 1996). Additional problems arise from the lack of clear domain-specific adaptations for the above scenarios. The exceptional human cognitive abilities of consciousness, emotions, self-awareness, and theory of mind do not make sense as adaptations for tracking prey or collecting fruit, nor as spurious outcomes of neurogenesis or other developmental processes (cf. Finlay, Darlington, & Nicastro, 2001). All of these models, moreover, have difficulties accounting for the diversity of culture into nonutilitarian areas.

One possibility is that a single genetic event resulted in a dramatic origin of cultural abilities (e.g., Calvin & Bickerton, 2000; Klein & Edgar, 2002;

cf. Enard et al., 2002). It is uncertain what benefit such a saltational mutation might have for the initial individual in which it occurred, for there would not be anyone else to talk or "culture" with. Complex adaptations and cultural abilities surely qualify as such, products of long, directional selection with successful intermediary stages (Dawkins, 1986; Mayr, 1982). The fossil record suggests a gradual, albeit rapid, pattern of increase in cranial capacity (e.g., Lee & Wolpoff, 2003; Lewin, 1998; Ruff, Trinkaus, & Holliday, 1997) among hominids. Although apparently abrupt artifact changes are suggestive of significant transitions, the hypothesis that the "creative explosion" was caused by a neurological "hopeful monster" remains tenuous. Artifacts found by future archeologists at the contemporary sites of New York City and the upper Orinoco might suggest significant differences in mental abilities between the populations, but such an inference would be wrong.

A different approach to the problem of the evolution of human intelligence involves consideration of the brain as a "social tool" (Adolphs, 2003; Alexander, 1971, 1989; Brothers, 1990; Byrne & Whiten, 1988; Dunbar, 1996; Humphrey, 1976, 1983; Jolly, 1999). This hypothesis suggests that the human psyche is designed primarily to contend with social relationships, whereas the physical (nonsocial) environment is relatively less important. Most natural selection in regard to brain evolution was a consequence of interactions with conspecifics, not with food and climate. The primary mental chess game was with other intelligent hominid competitors and cooperators, not with fruits, tools, prey, or snow (although enhanced intelligence surely was useful in dealing with such hostile forces as well).² Human social relationships are complex. Predicting future moves of a social competitorcooperator, and appropriate countermoves, amplified by multiple relationships, shifting coalitions, and deception, makes social success a difficult undertaking (Alexander, 1987, 1990b; Axelrod & Hamilton, 1981; Henrich et al., 2001; de Waal, 1982).

Indeed, the potential variety of human social puzzles is apparently infinite; no two social situations are precisely identical, nor are any two individuals ever in exactly the same social environment. Moreover, social relationships can change rapidly, requiring quick modification of strategy. This unpredictable, dynamic social hodgepodge would seem to favor flexible, "open," "domain-general," or "executive" psychological mechanisms highly dependent upon social learning and capable of integrating information processed by more restricted, "domain-specific" mechanisms (e.g., Hirschfeld & Gelman, 1994; Shettleworth, 1998). These complex cognitive processes would be more capable of contending with (and producing) novelties created by cultural change and culture- and individual-specific differences. Unfortunately, such chameleonic psychological mechanisms would

be nightmares to document empirically, evidenced perhaps by our meager understanding of the "black box."

The "social tool" hypothesis initially encountered the same common problems as the physical environment hypotheses. The uniqueness issue was especially difficult. Comparative analyses indicated that group size and proxy measures for intelligence (e.g., cranial capacity, neocortex ratios) were associated in a wide range of taxa, including primates (e.g., Kudo & Dunbar, 2001; Pawlowski, Lowen, & Dunbar, 1999). What was missing, however, was the reason(s) why hominids formed larger and/or more socially complex groups, hence creating an environment in which greater intelligence would have been favored by natural selection. That critical part of the puzzle was provided by the biologist Richard Alexander (1989, 1990b) in two seminal essays.

Alexander's scenario posits that hominids increasingly became an "ecologically dominant" species. Humans uniquely evolved sophisticated brains because humans were the only species to become their own "principal hostile force of nature" (Alexander, 1989, p. 469) via inter- and intragroup competition and cooperation. Increasing intellectual and linguistic capacities were favored because such skills allowed individuals to better anticipate and influence social interactions with other increasingly intelligent humans. This "runaway" directional selection produced greater and greater cerebral capabilities because success was based on relative (rather than absolute) levels of intelligence. Unlike static ecological challenges, the hominid social environment became an autocatalytic process, ratcheting up the importance of increased intelligence.

Evaluating scenarios of human evolution is necessarily speculative to varying degrees (e.g., Marks, 2002; McHenry & Coffing, 2000). Alexander's model, however, posits a wide range of interrelated phenomena, thereby generating a large number of ways to falsify it. Full discussion of his model is beyond the scope of this review (see Flinn, Geary, & Ward, in press; Geary & Flinn, 2001), but a synopsis of the key components may suffice:

- Humans have an unusual pattern of speciation. The extinction of all intermediate stages (e.g., gracile australopithecines and *Homo erectus*) and nondescendant branch species (e.g., robust australopithecines) and the absence of a pattern of adaptive radiation suggest that within-taxa competition was highly significant.
- Humans have an unusual life history pattern, with extended childhood and
 postreproductive stages (Bogin, 1997; Leigh, 2001; Mace, 2000). Childhood
 may be necessary for complex development and experience to acquire social
 skills (Hirschfeld, 2002; Joffe, 1997); a postreproductive stage may be useful

for caretaking of dependent offspring, grandchildren, and other relatives (Hawkes, 2003; Hawkes, O'Connell, Jones, Alvarez, & Charnov, 1998).

- Humans have a unique mating system, with extensive male parental care and long-term pair-bonding in a context of multimale/multifemale communities.
- Humans have a unique sexuality, with concealed ovulation, menopause, and other characteristics that may facilitate aspects of the unique human mating/ parenting system (above).
- Humans have reduced sexual dimorphism of body size and other traits (e.g., canines). Comparative analyses of hominid fossils and primates suggest that coalitions and fighting techniques other than biting were important during human evolution.
- The neocortex is larger than that of other primates in areas that support social competencies that are unique to humans (Rilling & Insel, 1999), such as theory of mind (Adolphs, 2003; Baron-Cohen, 1999) and language (Pinker, 1994)
- Humans have unusual aptitudes for use of projectile weapons (throwing *and* dodging, suggesting that competition with conspecifics was important, because prey such as antelope do not pick up spears or stones and throw them back at hunters).
- Humans have unique aptitudes for communication, including language and specific linguistic abilities.
- Humans have unique aptitudes for developing large, complex social groups based on kinship and reciprocity.
- Humans converge with species that have competition among socially complex coalitions, for example, chimpanzees (e.g., Harcourt, 1988; Mitani & Watts, 2000; Watts & Mitani, 2001; Wrangham, 1999) and dolphins (e.g., Mann & Sargeant, 2003; Smolker, 2000).

The factor that ties all of the above components—one might consider them "evolutionary clues"—especially the rapid changes associated with the emergence of *H. sapiens*, is social competition and cooperation in the context of ecological dominance:

The ecological dominance of evolving humans diminished the effects of extrinsic forces of natural selection such that within-species competition became the principal "hostile force of nature" guiding the long-term evolution of behavioral capacities, traits, and tendencies, perhaps more than any other species. (Alexander, 1989, p. 458)

As ecological dominance was achieved, the traits that began to strongly covary with individual differences in survival and reproductive outcomes were those that allowed hominids to socially "outmaneuver" other hominids. These traits would include sophisticated social competencies, such as

language, self-awareness, consciousness, and theory of mind; an accompanying increase in brain size; and other adaptations that facilitated kin-based social coalitions. An extended period of childhood with intensive parenting would contribute to the acquisition of social skills.

Abstract mental representation is useful, perhaps even necessary, for the complex analysis of social relationships and networks that most humans conduct with such ease. The diversity of human culture, the extraordinary range of information that we use in comparison with other species, results from the social dynamics of our complex coalitions. Alexander's model posits that we evolved our abilities for art, dance, theatre, friendship, technology, and so forth primarily as methods for contending with the social world of other humans. The advantages such abilities offered for dealing with the ecological demands of drought, food shortages, snow, and the like, are posited to be secondary.

Concluding Remarks: Reconciliation

The success of a theory of culture is not determined by its ability to smooth the ruffled feathers of disgruntled colleagues arguing across the biology-culture gap. Nonetheless, I think it is salient that Alexander's version of the social tool model for the evolution of human intelligence may explain the apparent incongruities that have plagued us for so many years.

Humans are unique in the extraordinary levels of novelty that are generated by the processing of abstract mental representations. Human culture is cumulative; human cognition produces new ideas built upon 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, food, and dialects, 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., Adolphs, 2003; Boyer, 1998; Carruthers, 2002). 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). It also reconciles symbolic and interpretive approaches in cultural anthropology with the biological "evolved-mind" approaches. Deconstruction is a complicated, but necessary, enterprise, for we are all players in the social arena. The twist is that we are evolved participants.

Reconciliation of the biology-culture gap is important for anthropological contributions to child development (Bjorklund & Pellegrini, 2002) and may provide a basic underpinning for the links among the many interrelated fields that anthropologists engage in. Returning to the anecdotal example at the beginning of this essay, consider the relations among stress, health, and culture. People in difficult social environments tend to be less healthy in comparison with their more fortunate peers (e.g., Cohen et al., 2003; Dressler & Bindon, 2000; Flinn, 1999; Wilkinson, 2001). The obvious explanation of a better physical environment-improved housing, work conditions, nutrition, health care, and reduced exposure to pathogens and poisons—is insufficient (Ellis, 1994; Marmot et al., 1991). The specific mechanisms underlying the association between socioeconomic conditions and health are uncertain. Psychosocial stress and associated immunosuppression are possible intermediaries (Adler et al., 1994; Kiecolt-Glaser, Malarkey, Cacioppo, & Glaser, 1994). If the brain evolved as a social tool, then the expenditure of somatic resources via cortisol release to resolve psycho-social problems makes sense (e.g., Beylin & Shors, 2003). Relationships are of paramount importance.

Notes

- 1. Cultural "progress" (e.g., increasing social complexity, technology, and group size) is an incidental effect (Ingold 1986, 2001; Wright 1994). Apparent "intentionality" of human reason is a product of evolution, not the driving force. Competition within a cultural environment, however, may be a zero-sum, "red-queen" game in which "winners" must continually advance their tactics beyond their competitors'. Arms races are a good example.
- 2. This might explain the apparent lack of significant population differences in cognitive abilities: The uniquely common selective force that all humans contend with is competition with other humans, regardless of physical environment. Interpopulational gene flow further reduces potential differences among populations.

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