

Brain Evolution and the Human Adaptive Complex

An Ecological and Social Theory

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This essay considers human brain evolution in terms of a larger set of coevolved traits, which we refer to as *the human adaptive complex* (HAC). The *embodied capital theory of human life-history evolution* explains the evolution of human brain size, development, and function as components of a coadapted complex of traits, including (1) the life history of development, aging, and longevity; (2) diet and dietary physiology; (3) energetics of reproduction; (4) social relationships among men and women; (5) intergenerational resource transfers; and (6) cooperation among related and unrelated individuals (Gurven & Kaplan, 2006; Gurven, Kaplan, & Gutierrez, 2006; Gurven & Walker, 2006; Kaplan, 1997; Kaplan, Gangestad, Lancaster, Gurven, & Robson, in press; Kaplan & Gurven, 2005; Kaplan, Hill, Hurtado, & Lancaster, 2001; Kaplan, Hill, Lancaster, & Hurtado, 2000; Kaplan, Mueller, Gangestad, & Lancaster, 2003; Kaplan & Robson, 2002; Robson & Kaplan, 2003).

According to the theory, the HAC is a very specialized niche, characterized by (1) the highest-quality, most nutrient-dense, and largest-package-size food resources; (2) learning-intensive, sometimes technology-intensive, and often cooperative food acquisition techniques; (3) a large brain to learn and store a great deal of context-dependent environmental information and to develop creative food acquisition techniques; (4) a long period of juvenile dependence to support brain development and learning; (5) low juvenile and even lower adult mortality rates, generating a long productive lifespan and population age structure with a high ratio of adult producers to juvenile dependents; (6) a three-generational system of downward resource flowing from grandparents to parents to children; (7) biparental investment, with men specializing in energetic support, and women combining energetic support with direct care of children; (8) marriage and long-term reproductive unions; and (9) cooperative arrangements among kin and unrelated individuals to reduce variance in food availability through sharing, and to acquire resources in group pursuits more effectively.

In the publications cited earlier, we have shown that the majority of the foods consumed by contemporary hunter-gatherers worldwide are calorically dense hunted and extracted resources taken from a protected substrate (e.g., underground, in shells), accounting for 35–60% of calories. Extractive foraging and hunting proficiency generally does not peak until the mid-30s because they are learning- and technique-intensive. Hunting, in particular, demands great skills and knowledge that takes years to learn, with the amount of meat acquired per unit time more than doubling from age 20 to 40, even though strength peaks in the early 20s. This learning-intensive foraging niche generates large calorie deficits until age 20, followed by great calorie surpluses later in life. This life-history profile of hunter-gatherer productivity is only economically viable with a long adult lifespan. Among hunter-gatherers without access to Western medicine, people can expect to live about 40 more years if they survive age 15, and an additional two decades if they survive to age 45. Chimpanzees, our closest living relative, can expect to live only to age 27 if they survive to age 15. Parents and grandparents often finance the juvenile learning phase through food transfers.

These data, as well as cross-species analyses of primate brain size and life history (e.g., Kaplan et al., 2003, in press), provide substantial support for learning-based, dietary (ecological) theories of primate brain expansion and for the coevolution of age of first reproduction, longevity, and brain size. There are, however, alternative *social* models of brain expansion. The social brain hypothesis (e.g., Byrne, 1995; Dunbar, 1998) is

generally formulated as the evolution of *Machiavellian intelligence* in response to a social arms race of political maneuvering and information manipulation in large groups. Recently, in a proposed signaling version of the social hypothesis, selection for intelligence derives from its ability to signal mutational load in mating competition (Miller, Chapter 30, this volume).

In this chapter, we develop embodied capital theory to include social capital. In doing so, our goal is to incorporate both social and ecological forces in brain evolution in a unified theory of the HAC.

COOPERATION AND THE HUMAN ADAPTIVE COMPLEX

Human food acquisition is inherently social in a number of ways. First, the mix of hunting and gathering in which people engage to maximize the rate of nutrient gain per unit effort results in a division of labor by sex (and, to some extent, by age). The human commitment to carrying, rather than caching, children and to providing high-quality child care (a trait shared throughout the primate order) is incompatible with hunting, because it involves long-distance walking and often dangerous pursuits. As a result, in all foraging groups, women allocate the majority of their time to gathering and child care, and men, to hunting (although the exact mix depends on ecology). Associated with this division of labor is the practice of marriage and family formation. All human groups recognize marriage as a bond that regulates sexual activity (especially of women), in which a man and a woman form a cooperative bond in raising children. This bond is generally characterized by intensive food sharing within the family and a division of labor in the organization of other household tasks and child care. Moreover, in foraging groups, the reproductive careers of men and women are highly linked. Although divorce is common in many foraging groups, most couples have the majority of their children together, and men often have their last child when their wives reach menopause. The relationship between men and women in foraging societies is arguably the most intense and multifaceted cooperative relationship in which they engage.

Second, social learning plays a critical role in the intergenerational transmission of knowledge and practices. Moreover, social learning probably increases the rate at which human children, adolescents, and adults learn how to hunt and gather efficiently (Blurton Jones & Marlowe, 2002). Forager children and adolescents have years of experience listening to others

tell stories and anecdotes about different foraging activities, before ever engaging in these activities themselves. In nonhuman primates, the frequency of social transmission of information strongly predicts wide-ranging variation in primate brain size, and most of this information pertains to foraging (Reader & Laland, 2002).

A third characteristic is that human diets are inherently risky, and food sharing is a fundamental component of the HAC. At the individual level, foraging luck is often highly variable. Hunting, in particular, can produce highly variable returns, especially in the case of large game. Food sharing among families is practiced by foragers to even out the daily food supply and buffer against the risks associated with large, mobile packages of food. A social brain also becomes increasingly important in the context of strategic sharing of game (Stanford, 1999). For example, efficient sharing requires the monitoring of meat and other contributions made by other group members.

Fourth, human foraging, especially hunting, is often more effectively done in cooperative groups. Many species can be prevented from escaping predation by groups of cooperating hunters. In cooperative foraging activities, individual roles are often well specified, and the coordination is intentional and consciously understood by all members of the cooperative party.

When all of this is put together, the complexity and intensity of human cooperative relationships, especially among nonkin relationships such as spouses and friends, is unparalleled. Cooperation is risky and fragile given that the possibility of defection always looms in the background. As a result, choice of partners in contexts where cooperation can have profound effects on people's lives puts a large premium on intelligence.

SOCIAL CAPITAL AND THE COMPETITIVE MARKET FOR COOPERATORS

We now introduce the concept of *social capital*, borrowed from sociology and economics, to evolutionary discourse as applied to HAC. Whereas social capital has been traditionally thought of as the web of connections that one attains through family and friends (Coleman, 1988; Putnam, 2000), Lin (1999) provides an individually based definition of "social capital" as investment in social relations with expected returns. We offer a modified definition: "Social capital" is *information or perceptions embodied in other individuals with expected fitness returns through its effects on social interactions*.

In the case of nonhuman primates, social capital is mainly in the form of information about dominance relations and sexual/reproductive states or

qualities. For example, the social capital for dominant individuals is information stored in the brains of subordinates, based on a history of previous interactions. Dominants can expect a return on this capital to the extent that this information affects the behavior of subordinates. As a result, dominants can often obtain priority access to a feeding site or sexual partner with a simple facial or bodily gesture.

The Human Case: Social Capital and Access to Resources

We propose that in traditional human groups, social capital investment is very significant and cognitively demanding, exerting considerable selective force on human psychology and intelligence. Social capital, however, plays a different role in people's lives than in those of nonhuman primates, given the special features of the HAC described earlier.

There is increasing evidence that food is not shared equally with all band members in most hunting and gathering societies, except under specific circumstances (Gurven, 2004). People have preferred partners with whom reciprocal exchange is greatest. The most common social arrangement appears to be one of variably sized food distribution networks, depending on the food resource and its means of obtainment. In many groups, there is significant producer control over sharing and limited scope of partners. For example, among Hiwi foragers, hunters tend to exercise control over how much and with whom they share meat, restricting those who receive shares to some 15–20% of potential recipients in large groups (Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000). Thus, there is a potential market for cooperative partners. The ability to engage in profitable partnerships may require a great deal of social intelligence, particularly the ability to understand how one's actions will affect future access to food and food exchange.

This logic may explain why humans commonly cooperate in experimental games and punish defectors (Henrich et al., 2001). The tendency to cooperate on the first move allows people to experience greater gains from cooperation and to demonstrate their quality as potential cooperators in future interactions. People have a moral approach to these problems, because a more Machiavellian approach, which would take advantage of all opportunities for defection in one-shot games, is outcompeted by a moral psychology when there is uncertainty about the possibility of being detected as a defector and the costs of being labeled as a cheater have great long-term consequences. Runaway selection on the ability to detect signs of a Machiavellian strategy in the context of a food acquisition strategy that depends on

cooperation and sharing may have been of great importance in the evolution of social intelligence and moral reasoning.

Human psychological traits and social norms of sharing are likely to reflect the relative strengths of two opposing forces: gains from cooperation and possibilities for free-riding (Tooby, Cosmides, & Price, 2006). These opposing forces may have led to the evolution of general moral sentiments, supported by both the emotional–motivational psychology of individuals and common cultural norms. This reasoning predicts that natural selection has shaped our psychology to possess the following traits: (1) perceptual sensitivity to potential gains from cooperation; (2) motivation to take advantage of those gains; (3) perceptual sensitivity to opportunities for free-riding; (4) motivation to avoid being free-ridden; (5) motivation to take advantage of opportunities for free-riding; (6) perceptual sensitivity to the short- and long-term personal costs and benefits of social norms regarding cooperative behavior (from the perspectives of both self and others); (7) motivation to negotiate social norms, so that personal benefits from cooperation and free-riding are maximized; and (8) motivation to obey and enforce social norms, so that punishment is avoided and those who disobey norms or fail to enforce them are punished.

Social Capital, Mating, and Marriage

Human marriage is probably the most complex cooperative relationship in which we engage. It involves the production and processing of resources for familial consumption, the distribution of those resources, the provision of child care, the production and maintenance of belongings and residential amenities, and sexual rights and responsibilities. The ability to coordinate the allocation and execution of those responsibilities (i.e., the ability to “get along”) is fundamental to successful marriage, and it appears to play a role in mate choice. In traditional societies, it is common to hear remarks about success and failure in coordinating and getting along as reasons for why marriages succeed or fail.

One problem that people face in mate choice is that long-term dependency and multiple dependency make mate switching more costly for humans. Once one has reproduced with a given partner, a change in partners can entail reduced investment in those previous children. Moreover, most mate choice occurs before economic abilities are proven. For example, at marriage age (around 20), Aché and Tsimane men are only 25 and 50% proficient as hunters (respectively) as they will be at their peak in their mid-to-late 30s.

Thus, from the perspective of both men and women, there are great gains from choosing a good partner, and there are also great risks of economic and sexual defection. For the most part, it is a long-term choice with direct consequences for fitness. It is further complicated by the fact that partners contribute to fitness not only through behavior but also through genetic inputs, which can lead to either further complementarities or to conflicts of interest. Marriages redirect social interaction and cooperation not only within the pair bond but also across members of respective extended families.

Social capital is likely to play an important role in mate choice. Capital affecting perceptions about fairness, industriousness, loyalty, promiscuity, and economic abilities is likely to influence mate choice decisions by both men and women. Some of the same factors affecting the choice of production and sharing partners may also affect the choice of marriage partners.

Such considerations leave ample room for display behavior. Whereas over the long run the primary motivation for economic production may be the raising of a family, symbolic forms of production and sharing may be important investments in social capital. Some proportion of food-sharing behavior is likely to be symbolic investments in social capital affecting future cooperative interactions. Importantly, as emphasized by others (Bird, 1999; Hawkes, 1990; Smith, 2004), displays of hunting competence and generosity may play an important role in mating success. In fact, many foraging and forager-horticulturalist societies, such as the !Kung and the Tsimane, practice bride service, in which young men hunt to feed their future father-in-law's family before having full marital rights.

Moreover, because intelligence and cognitive ability are likely to be important in food production, social access to shared food, and efficient child care, we might expect young men and women to invest in social capital through displays of social and ecological intelligence. We might also expect people to be very discriminating in their appreciation of those displays. In addition, as discussed by Miller (Chapter 30, this volume), to the extent that such displays are honest advertisements of genetic fitness and mutational load, there would be another incentive to engage in and discriminate among displays.

CONCLUSION

Our proposal is that ecological and social intelligence, coupled with specific psychological characteristics, are fundamental components of the

HAC. This psychology, the complex analytical brain, and the extended life history coevolved in the hominid line, all because of the dietary shift toward large, high-quality food packages and division of labor in food production and child care. It is this feeding adaptation that generates gains from cooperation. In this sense, both social and foraging intelligence are ecologically determined.

Cooperative strategies, however, also entail gains from, and risks of, defections. This places a premium on decisions about when and with whom to cooperate. Behaviors that facilitate being selected as a cooperative partner may have played a great role in individual and family food consumption patterns. Given that marriage is a fragile and complex human social relationship, it may have played an important role in shaping both our intelligence and our psychological characteristics.

In addition, some of the cognitive substrates for solving economic and social problems are probably shared. For example, inferences about animal behavior, such as likely escape strategies if the hunter's presence is detected, are critical for hunting success. Animal "mind-reading" and human mind-reading may involve similar cognitive abilities, including the ability to discriminate among types of minds (deer, child, adult friend, adult enemy, etc.). To the extent that such substrates are shared, selection would act on the total effects of increased abilities, summed over all routes through which those abilities affect fitness. In a recent review of the comparative anatomy of primate brains, Rilling (2006) notes that natural selection uniquely modified the human brain to deviate from the rules of brain design that obtain among other primates. He points to a unique evolutionary modification in the prefrontal cortex associated with symbolic thinking, knowledge of appropriate social behavior, decision making, planning, cognitive control, and working memory. Bering and Povenilli (2003; Povenilli, 2003) propose that the critical divide between the minds of apes and humans is not just the difference of 1000 cc of volume in order to do the same things much better, but an entirely unique feature of cognition, an ability to think about things that cannot be directly observed by the senses. Humans can think about the hidden world of causation—the world of forces and causes that lie beneath the surface appearance of things such as emotions and thoughts of others or perceptions and beliefs about forces impinging on inanimate objects such as gravity, force, mass, and physical connection. This is the world of *why* and *how*. We can take for an example the classic behavior of chimpanzee termite fishing. The naive chimpanzee sees the association of a probe and the acquisition of termites and can quickly emulate what he sees but without any attention to the qualities of a successful tool

in terms of flexibility, length, and diameter. The association of probe and outcome can be learned rapidly but the critical intervening variables must be learned through trial and error. Similarly, the simplest level of a theory of the mind might be tested through the interpretation of gaze. A chimpanzee clearly makes use of information about whether an individual faces or has the back turned toward him but cannot discriminate between a blindfolded or gagged demonstrator in terms of what the person might see and hence know.

In contrast to the chimpanzee's unquestioned skill at extracting statistical regularities about what objects do and how they behave, the world of why and how is one that humans never stop thinking about, whether the issue is what others are thinking, how a tool works, or why people get sick (Bering & Povenilli, 2003). Humans crave insight and are so committed to knowing causation that they will confabulate if necessary or attribute minds and emotions to trees and weather. This desire to command the unseen world of causation links social and foraging intelligence as well as all other human endeavors through a single process of insight and understanding, a shared cognitive substrate for the unique performances of the human mind.

In this sense, embodied capital in the form of social and foraging skills are inevitably linked and probably coevolved since they utilize the same brain mechanisms. The abilities to scenario-build in solving both foraging and social problems, to engage in high-level abstract logical reasoning, and to think insightfully about the hidden world of causation appear to have evolved in one lineage only. Perhaps our species is an outlier, precisely because the human adaptive complex demands both *ecological* and *social* intelligence.

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