

Ecological dominance, social competition, and coalitionary arms races: Why humans evolved extraordinary intelligence

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Abstract

Human cognitive abilities are extraordinary. Our large brains are significantly modified from those of our closest relatives, suggesting a history of intense natural selection. The conditions favoring the evolution of human cognitive adaptations, however, remain an enigma. Hypotheses based on traditional ecological demands, such as hunting or climatic variability, have not provided satisfying explanations. Recent models based on social problem solving linked with ecological conditions offer more convincing scenarios. But it has proven difficult to identify a set of selective pressures that would have been sufficiently unique to the hominin lineage. What was so special about the evolutionary environments of our ancestors that caused them, and them alone, to diverge in such astonishing ways from their close relatives and all other life forms? Richard Alexander proposed a comprehensive integrated explanation. He argued that as our hominin ancestors became increasingly able to master the traditional “hostile forces of nature,” selective pressures resulting from competition among conspecifics became increasingly important, particularly in regard to social competencies. Given the precondition of competition among kin- and reciprocity-based coalitions (shared with

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chimpanzees), an autocatalytic social arms race was initiated, which eventually resulted in the unusual collection of traits characteristic of the human species, such as concealed ovulation, extensive biparental care, complex sociality, and an extraordinary collection of cognitive abilities. We term this scenario the “ecological dominance–social competition” (EDSC) model and assess the feasibility of this model in light of recent developments in paleoanthropology, cognitive psychology, and neurobiology. We conclude that although strong or direct tests are difficult with current data, Alexander’s model provides a far-reaching and integrative explanation for the evolution of human cognitive abilities that is consistent with evidence from a wide range of disciplines.

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1. Introduction

Humans have an unusual array of characteristics that distinguish us from other species. Our cognitive abilities are most remarkable. Hominin brain size increased more than 250% in less than 3 million years. Much of this increase occurred in the past 500 thousand years and disproportionately affected the size (Ruff, Trinkaus, & Holliday, 1997) and the organization of the neocortex (Adolphs, 2003; Deacon, 1997a; Holloway, 1996; Rilling & Insel, 1999; Semendeferi, Armstrong, Schleicher, Zilles, & van Hoesen, 2001). The behavioral changes were even more impressive, especially in the last few thousand generations (e.g., Klein, 1999; Mithin, 1996). The Upper Paleolithic/Late Stone Age “creative explosion,” continuing a long tradition, has generated an unparalleled expansion of information and individual expression, albeit within the restraints of collective meaning (Caspari & Lee, 2004; Henshilwood & Marean, 2003; McBrearty & Brooks, 2000). Notwithstanding the impressive cognitive adaptations of other species such as chimpanzees and dolphins (e.g., de Waal & Tyack, 2003; Mann & Sergeant, 2003; Premack & Woodruff, 1978), the products of human minds stand out as one of life’s most impressive features.

Many hypotheses have been proposed concerning the selective advantages of cognitive change during human evolutionary history. Most explanations involve ecological problem solving, such as tool use (e.g., Darwin, 1871; Gibson & Ingold, 1993; Washburn, 1959; Wynn, 1988), hunting (e.g., Dart, 1925; Hill, 1982; Washburn & Lancaster, 1968), scavenging (e.g., Blumenschine & Cavallo, 1992), foraging (e.g., Isaac, 1978; Kaplan, Hill, Lancaster, & Hurtado, 2000), extended life history (e.g., van Schaik & Deaner, 2003), food processing (e.g., Wrangham, Jones, Laden, Pilbeam, & Conklin-Brittain, 1999), and savanna (e.g., Laporte & Zihlman, 1983) or unstable (Potts, 1998; Vrba, 1995) 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 evolved such extraordinary cognitive competencies (e.g., awareness of the self as a unique and social being; Tulving, 2002), considering that many other species hunt, occupy savanna

habitats, have long lifetimes, endured the same climatic fluctuations, and so forth. Additional problems arise from the lack of clear domain-specific adaptations for the above scenarios, with the possible exception of tool construction (Hodges, Spatt, & Patterson, 1999) and folk biology (e.g., mentally representing the essence of hunted species; Atran, 1998). Even these adaptations, however, pale in comparison with the human cognitive abilities of consciousness, language, self-awareness, and theory of mind (TOM). These competencies do not appear to be adaptations for tracking prey or collecting fruit, nor spurious outcomes of neurogenesis or other developmental processes (but see Finlay, Darlington, & Nicastro, 2001; Williams, 1966). All these models, moreover, have difficulties accounting for the diversity of culture into seemingly nonutilitarian areas, such as art (Coe, 2003) and religion (Boyer, 2001).

One possibility is that an advance in linguistic abilities, such as abstract symbolic representation, was the Rubicon for a dramatic origin of cultural abilities (e.g., Washburn, 1978; White, 1959). Some have suggested that a sudden genetic change might underlie this transition (e.g., Calvin & Bickerton, 2000; Klein & Edgar, 2002; cf. Enard et al., 2002). It is uncertain what benefit such a saltational mutation event 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, are products of long directional selection with successful intermediary stages (Dawkins, 1986; Mayr, 1982), including language (Nowak, Komarova, & Niyogi, 2001). Our close relatives, great apes, exhibit behavioral variations and traditions involving social learning that suggests a more gradual transition (de Waal, 2001; McGrew, 2003; Stanford, 2001; van Schaik et al., 2003; Whiten et al., 1999; Wrangham, McGrew, de Waal, & Heltne, 1994). The fossil record indicates a continuous, albeit rapid, pattern of increase in cranial capacity among hominins (e.g., Lee & Wolpoff, 2003; Lewin & Foley, 2004; Ruff et al., 1997). Although apparently abrupt artifact changes are suggestive of significant transitions, the hypothesis that the Upper Paleolithic creative explosion was caused by a neurological “hopeful monster” remains implausible.

Sexual selection is another recent explanation consistent with several characteristics of hominin cognitive evolution (Darwin, 1871; Miller, 2000). The main idea is that mate choice by hominin females for increasingly intelligent males was an important selective pressure acting on cognitive abilities. As Darwin (1871) speculated, “mental endowment” of the human was analogous to the “ornamental plumage” of the peacock. Although we agree that mate choice is likely to have been a significant force, it is unclear why hominins were the only taxon in which sexual selection favored such elaborate mental displays. The finding that men and women have a different pattern of specific cognitive abilities suggests that different features of sexual selection, including female–female competition, might have contributed to human cognitive evolution, but the lack of sex differences in overall levels of general intelligence is inconsistent with the female choice hypothesis (Geary, 1998). Although a chance genetic event is possible, “perhaps there was a mutation affecting their sexual preferences” (Miller, 2000, p. 71); there are additional factors associated with hominin evolution that suggest that a more comprehensive scenario is likely.

A different approach to the problem of the evolution of human cognition involves the consideration of the brain as a “social tool” (Alexander, 1971, 1989; Brothers, 1990; Byrne & Whiten, 1988; Dunbar, 1998; Humphrey, 1976; Jolly, 1966, 1999). This hypothesis suggests that many human psychological adaptations function primarily to contend with social relationships, with ecological constraints (e.g., hunting or extractive foraging) being a more secondary source of recent evolutionary change. It appears that some human cognitive competencies, such as TOM and language, are most readily understood in terms of social selection pressures, although cognitive competencies for interacting with the physical (e.g., navigating) and biological worlds are evident as well (Geary & Huffman, 2002). The primary mental chess game, however, was with other intelligent hominin competitors and cooperators, not with fruits, tools, prey, or snow. Human social relationships are complex and variable. Predicting future moves of a social competitor–cooperator, and appropriate countermoves, amplified by networks of multiple relationships, shifting coalitions, and deception, make social success a difficult undertaking (Alexander, 1987, 1990b, *in press*; Axelrod & Hamilton, 1981; Byrne & Corp, 2004; Daly & Wilson, 1988a, 1988b; de Waal, 1982, 2002).

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. Variability in these dynamics creates conditions that should favor the evolution of brain and cognitive systems above and beyond more traditional modular systems (Fodor, 1983; Tooby & Cosmides, 1995). These systems have been cast in terms of general intelligence, domain-general abilities, or executive functions that are capable of integrating and co-opting information processed by more restricted, domain-specific mechanisms (Adolphs, 2003; Blakemore et al., 2004; Geary, 2005; Preuss, 2004) and using mental simulations, or “scenario building” (Alexander, 1989), to construct and rehearse potential responses to changing social conditions. These complex cognitive processes would be more capable of contending with, and producing, novelties of cultural change and individual-specific differences (Flinn, 1997, 2004; Tomasello, 1999).

The social tool hypothesis initially encountered the same problems as the physical environment hypotheses did. The uniqueness issue was especially difficult. Comparative analyses indicated that group size and proxy measures for brain size (e.g., cranial capacity, neocortex ratios) were associated in a wide range of taxa, including primates (e.g., Kudo & Dunbar, 2001; Pawlowski, Lowen, & Dunbar, 1998; van Schaik & Deaner, 2003). A major problem, however, remained unresolved: Given that hominin group size was unlikely to have been larger than that of their close relatives (the other hominoids), what was qualitatively different about the hominin social environment? Why did hominins, in particular, form more socially complex groups, hence creating an environment in which more sophisticated forms of social cognition (e.g., TOM) and general intelligence would have been more strongly favored by natural selection than in related species? Why were coalitions more important, and more cognitively taxing, for our hominin ancestors than for any other species in the history of life? Why did hominins evolve special abilities such as “understanding other persons as intentional agents” (Tomasello, 1999, p. 526)? The

critical missing pieces of the puzzle were provided by Alexander (1989, 1990a) in two seminal essays.

2. The ecological dominance–social competition model

“... humans had in some unique fashion become so ecologically dominant that they in effect became their own principal hostile force of nature, explicitly in regard to evolutionary changes in the human psyche and social behavior... the real challenge in the human environment throughout history that affected the evolution of the intellect was not climate, weather, food shortages, or parasites—not even predators. Rather, it was the necessity of dealing continually with our fellow humans in social circumstances that became ever more complex and unpredictable as the human line evolved. Social cleverness, especially through success in competition achieved by cooperation, becomes paramount... nothing would select more potently for increased social intelligence... than a within-species co-evolutionary arms race in which success depended on effectiveness in social competition.”

(Alexander, 1990a, pp. 4–7)

Alexander’s scenario posits that hominins increasingly became an “ecologically dominant” species. We interpret Alexander’s concept of “ecological dominance” to mean the diminished intensity of selection from extrinsic causes compared with the relative importance of selection from interactions with conspecifics. From this perspective, the term does more than indicate a species’ success in contending directly with Darwin’s hostile forces of climate, predation, and resource scarcity. Although rhinoviruses and kudzu are successful in their respective ecologies, they are not ecologically dominant in this sense. Their phenotypes have been, and continue to be, primarily designed by selection involving extrinsic forces rather than by interactions with members of their own species.

Taking another example, although part of ecological dominance involves diminished intensity of selection from biotic interactions, including predation, this is not sufficient. Top predators, such as eagles, lions, and orcas, and large animals with effective protection, such as elephants, are relatively free from predation. But resource scarcity (e.g., getting food) and pathogens may still be significant selective pressures relative to contending with conspecifics, particularly in regard to the evolution of the brain. The critical factor in ecological dominance is the extent to which a species has become its own selective pressure, its own principal hostile force of nature. For dolphins, elephants, lions, and orcas, interactions with conspecifics involving coalitions appear to have major effects on survival and reproduction (e.g., see de Waal & Tyack, 2003). The evolution of social skills is enabled by ecological dominance.

Sexual selection is related to ecological dominance because it involves selection arising from competition among conspecifics rather than from the traditional extrinsic pressures. Antlers, for example, reflect ecological dominance to the extent that they were designed to defeat rival males rather than protection from predators. These examples suggest that the relation between ecological dominance and mental abilities is not simple or straightforward.

Although our hominin ancestors were not equipped with exceptional teeth, horns, strength, armor, speed, or size, at some point, they nonetheless may have begun achieving relative freedom from the traditional hostile forces of nature, perhaps even more so than our hominoid relatives, the gorillas and chimpanzees. The means by which hominins increased ecological dominance probably involved behavioral adaptations (e.g., tool use and projectile weapons; see *Hominin fossil record* below).

The key to Alexander's model of human evolution, however, is not simply the recognition that the evolving hominins seem to have been increasingly successful at dealing with a wide variety of environmental challenges. It is the linkage of ecological dominance with the escalating significance of interactions with conspecifics, wherein hominins increasingly became their own principal hostile force of nature. All species face competition among conspecifics, such as contending for mates and resources, but what is special and extraordinary about humans (and, to a lesser extent, chimpanzees, dolphins, elephants, and orcas) is the importance of social relationships—more specifically, negotiated, dynamic, multilevel coalitions—for succeeding in this type of competition. In this evolutionary scenario, the primary selective pressures acting on hominins—particularly in regard to the brain—came from their dealings with other hominins rather than with climate, predators, and food directly. The nature of this within-species competition appears to have involved an evolutionary arms race among ever-more effective coalitions. Both the successes of one's coalitions and of individuals within their coalitions depended, in part, on sociocognitive competencies such as empathy and TOM, which required new and expanded neurological structures (see *Brain* below).

The diminished intensity of constraints on this autocatalytic process of a coalitionary arms race is perhaps unique. Other evolutionary arms races are slowed or stalled by outside constraints. For example, the mate choice advantage of a larger and more colorful tail for male guppies is subject to increasing predation pressures (Endler, 1986; for general review, see Andersson, 1994). Similarly, coalitions for cooperative hunting or foraging are constrained by diminishing returns at relatively small group sizes (Hames, 1992; Hill & Hurtado, 1996). But there are no inherent limits on increasingly complex hominin sociality. Groups whose size is constrained by the economics of foraging or horticulture can nonetheless form larger alliances to meet challenges from other coalitions. The increasing coherence and organization of hominid groups and accompanying sophisticated cognitive abilities were likely to convey ecological advantages rather than costs, resulting in a further coevolutionary synergy of ecological dominance and social complexity.

Evidence that humans evolved into ecologically dominant predators and foragers comes from patterns of human migration and demography, as well as our variable and flexible subsistence strategies. The conceptualization of natural selection as a “struggle for existence” of Darwin and Wallace (1858, p. 54) becomes, in addition, a special kind of *struggle with other human beings for control* of the resources that support life and allow one to reproduce. In this situation, the stage is set for a form of runaway selection, whereby the more cognitively, socially, and behaviorally sophisticated individuals are able to out maneuver and manipulate other individuals to gain control of resources in the local

ecology and to gain control of the behavior of other people. To the extent that access to these resources covaries with survival and reproductive outcomes—and it does in many contexts (Betzig, 1986; Chagnon, 1988; Hed, 1987; Irons, 1979; Malthus, 1798)—the associated sociocognitive competencies, and supporting brain systems, will necessarily evolve.

To the extent that ecological dominance was achieved, humans became “their own principal hostile force of nature” (Alexander, 1989, p. 469) via inter- and intragroup competition and cooperation. Increasing linguistic and sociocognitive 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 modular (e.g., language and TOM) and more general cognitive competencies, because success was based on relative (rather than absolute) levels of ability. Unlike static ecological challenges, the hominin social environment became an autocatalytic process, ratcheting up the selective advantage associated with the ability to anticipate the social strategies of other hominins and to mentally simulate and evaluate potential counterstrategies (Alexander, 1989). Modular competencies allowed hominins to quickly and efficiently process social information that was static, or invariant, across generations and contexts (e.g., the ability to read basic human facial expressions), whereas the more variable and thus less predictable features of one-on-one and coalitional social relationships favored the ability to mentally construct and manipulate a range of potential social scenarios. These more general competencies involve working memory, attentional control, and executive functions (e.g., Baddeley, 1986; Engle, 2002; for review, see Geary, 2005).

Although many models of human evolution involve syntheses of multiple factors, the ecological dominance–social competition (EDSC) model is unusual in the comprehensive range of traits that are apposite. Increased sophistication in social cognition (Adolphs, 2003; Geary & Huffman, 2002; Siegel & Varley, 2002) and the components of general intelligence, are posited to coevolve with a suite of other characteristics, including altricial infants, lengthy childhood, intensive parenting, concealed ovulation, complex coalitions, and menopause.

The altricial (helpless) infant is indicative of a protective environment provided by intense parenting and alloparenting in the context of kin groups. The human baby does not need to be physically precocial. The brain continues rapid growth, and the corresponding cognitive competencies largely direct attention toward the social environment and result in an adaptation of inherent, but plastic, systems sensitive to the nuances of the local community, such as its language (Alexander, 1990b; Bloom, 2000; Small, 2001). A related competency is the extraordinary information-transfer abilities enabled by linguistic competency (Pinker, 1994). An extended childhood is useful for acquiring the knowledge and practice to hone social skills and to build coalitional relationships necessary for successful negotiation of the increasingly intense social competition of adolescence and adulthood, although ecologically related play and activities (e.g., exploration of the physical environment) occur as well. The latter follow from the EDSC model, as activities enhancing the competencies associated with ecological dominance. The unusual scheduling of human reproductive maturity, including an

“adrenarche” and a delay in direct mate competition among males (Herdt & McClintock, 2000), appears to further extend social ontogeny.

The advantages of intensive parenting, including paternal protection and other care, require unusual mating relationships: moderately exclusive pair bonding in multiple-male groups. No other primate that lives in large, cooperative multiple-reproductive-male groups has extensive male parental care, although some male protection is evident in *Papio* (Buchan et al., 2003). Competition for females in multiple-male groups usually results in low confidence of paternity (e.g., chimpanzees). Males forming exclusive pair bonds with females within multiple-male groups would provide cues of nonpaternity for other males and hence place their offspring in great danger of infanticide (Hrdy, 1999). Paternal care is most likely to be favored by natural selection in conditions where males can identify their offspring with sufficient probability to offset the costs of investment, although reciprocity with mates is also likely to be involved (Smuts, 1985, Smuts & Smuts, 1993). Humans exhibit a unique nested family social structure, involving complex reciprocity among males and females to restrict direct competition for mates among group members. It is difficult to imagine how this system could be maintained in the absence of another unusual human trait: concealed (or cryptic) ovulation (Alexander & Noonan, 1979).

Human groups also tend to be male philopatric, resulting in extensive male kin alliances, useful for competing against other groups of male kin (Chagnon, 1988; LeBlanc, 2003; Wrangham & Peterson, 1996). Females have complex alliances as well, but usually are not involved directly in the overt physical aggression characteristic of intergroup relations (Campbell, 2002; Geary & Flinn, 2002). Menopause reduces mortality risks for older women and allows them to concentrate effort on dependent children and other relatives (e.g., grandchildren) with high reproductive value.

Alexander’s model requires the integrated coevolution of all these factors to explain how and why humans came to possess their extraordinary cognitive abilities. Evaluating scenarios of human evolution is necessarily speculative to varying degrees (e.g., Holloway, 1996; Marks, 2002; McHenry & Coffing, 2000), but Alexander’s model integrates a wide range of interrelated phenomena, thereby generating a large number of ways to potentially falsify it. Our objective here is to provide the strongest possible tests of the model based on recent advances in neurobiology, paleontology, and other areas that provide useful evidence.

Here, we evaluate the EDSC model in terms of how it explains the improbable collection of unusual human characteristics (Table 1). The evaluation of the significance of each of these features would exceed the scope of this paper, thus, here, we concentrate on those we think most significant and most readily testable. The model requires an integrated coevolution of all of the proposed key factors. This is its main strength: If any single component fails, the whole model is falsified. We emphasize two empirical sources: (1) the hominin fossil record and (2) human neurobiology and cognition. The main weakness of the model is that the data are not available in many cases to provide simple strong or direct tests. Nonetheless, the analysis of the temporal patterns indicated by the fossil record, the specific design features of the human brain, and the life history and reproductive

Table 1

Attributes of humans that may provide clues to our evolution

I. Unusual speciation and extinction pattern

- A. No remaining ancestral species or side branches; absence of adaptive radiation in Homo** (White, 2003)
despite rapid evolutionary change.

II. Rapid reduction of sexual dimorphisms

- A. Canine SD reduced early (Australopithecus: Ward et al., 2001)**
B. Body size SD reduced later (Homo erectus)

III. Unusual dentition

- A. Reduced canine size
B. Small incisors
C. Thick enamel on teeth
D. Overall dental reduction
E. Orthognathic face
F. Protruding nose

IV. Dietary niche

- A. Omnivorous catholic diet
B. Variable environments
C. Meat eating
D. Hunting
E. Extractive foraging of tubers, nuts, and other high quality foods
F. An array of corresponding cognitive and brain specializations, including those that support tool use (Hodges et al. 1999), and the development of folk biological knowledge (Atran, 1998)

V. Habitual bipedal locomotion

- A. Lumbar curve, pelvis, bicondylar angle, knees
B. Foot, arch, no grasping big toe
C. Loss of climbing abilities

VI. Unusual upper limbs

- A. Shortened, modified
B. Accurate and powerful throwing of projectiles, and dodging, especially in males (Cannell, 2002; Dunsworth et al., 2003; Watson & Kimura, 1991)
C. Fine manipulation with hands, digit proportions, innervation

VII. Extraordinary mental capabilities

- A. Large brains, high metabolic cost**
B. Unique aspects of gene and protein expression, transcription in brain cells
C. Neuroanatomy; expanded neocortex (Jerison, 1973, prefrontal cortex), class of large and clustered spindle cells in anterior cingulate cortex (Nimchinsky et al., 1999), possible expansion of language-related neocortical areas (Rilling & Insel, 1999), expansion, controlling for overall increase in brain size, and possible reorganization of some regions of the prefrontal cortex (Semendeferi et al., 1998, 2001), development of Broca's area, and other unique brain features. Increased lateralization (Holloway & de la Coste-Lareymondie, 1982) and increased gyrification (Zilles et al., 1988, 1989).

- D. Consciousness and awareness of the self as a social being** (Tulving, 1985, 2002)
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Table 1 (continued)

Attributes of humans that may provide clues to our evolution

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- E. Theory of mind** (Baron-Cohen, 1999; Leslie, 1987; Seigel & Varley, 2002), **and a complimentary set of sociocognitive competencies** (Adolphs, 2003; see Geary, 2005; Geary & Huffman, 2002, for a taxonomy)
 - F. Foresight, planning, scenario building, ability to mentally time travel** (Johnson-Laird, 1983; Tulving, 2002); **related to functioning of areas of the prefrontal cortex** (Gallagher & Frith, 2003)
 - G. Complex psyche, integrated cognitive aptitudes, flexible and relatively open learning
 - H. Social emotions, guilt, embarrassment, pride, restraint and concealment** (Damasio, 2003; Damasio et al., 2000)
 - I. Humor (Alexander, 1987)
 - J. Complex deception and deception-detection**
 - K. Multiple order reasoning**
 - L. Imagination, fantasy
 - M. Creativity**
 - N. Senses (vision, hearing) similar to other hominoids, some olfactory reduction
 - O. Complex facial expressions
 - P. Specific psychopathologies, e.g., autism (Baron-Cohen, 1999)

VIII. Language, specific linguistic abilities

- A. Precocial language acquisition** (Brown, 1973)
- B. Open syntax, infinite combinations and creativity (Nowak et al., 2001)

IX. Culture

- A. Traditions, cumulative information building (Coe, 2003)
- B. Technology stemming from evolution of tool use and ecological dominance
- C. Social learning, complex imitation, emulation, teaching. The working memory and attentional control systems that support scenario building can also be used for the teaching and learning of culturally specific academic abilities, such as reading and writing (Geary, 2002)

X. Complex social groups

- A. Male kin- and nonkin coalitions** (e.g., Boehm, 1999; Chagnon, 1968)
- B. Complex systems of reciprocity (indirect and direct; e.g., Alexander, 1987)
- C. Friendships (Hartup & Stevens, 1997)
- D. Laws
- E. Ethics and moral systems (Alexander, 1987; Bowles & Gintis, 1998)
- F. Pervasive intra- and intergroup conflict, raiding, war** (Alexander, 1971; Daly & Wilson, 1988; LeBlanc, 2003; Manson & Wrangham, 1991; Wrangham, 1999; Wrangham & Peterson, 1996)
- G. Complex social play, team sports (Lever, 1978; Wagner, Flinn, & England, 2002)

XI. Unusual patterns of kinship, parenting, and grandparenting

- A. Extensive kin networks
- B. Male philopatry** (Murdock, 1949; Seielstad, Minch, & Cavalli-Sforza, 1998; Wells et al., 2001)
- C. Extensive parental care, including protection by males** (Geary, 2000)
- D. Complex bonding, attachment, grief
- E. Long-term mating relationships, pair bonds
- F. Variable mating systems
- G. Parental and kin influence on mate choice
- H. Age- and sex-based division of labor, activity differences

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Table 1 (continued)

*XII. Unusual life history***A. Altricial young**

- B. Rapid early brain growth, but continued throughout childhood (Deacon, 1997a, 1997b)
- C. Unusual patterning of growth and development, e.g., pubertal growth spurt (Bogin, 1999)

D. Menopause**E. Precocial communication skills****F. Extended “childhood”** (Bogin, 1999; Low, 2000)**G. Adrenarche** (Herdt & McClintock, 2000)*XIII. Unusual sexual characteristics***A. Concealed ovulation** (Alexander & Noonan, 1979; Strassmann, 1981)

- B. Postreproductive sexual behavior
- C. Frontal copulation, kissing, foreplay
- D. Female orgasm
- E. Permanently enlarged breasts
- F. Large penis, lack of penis bone (baculum)
- G. Moderate testes
- H. Hymen

XIV. Other unusual physical characteristics

- A. Variation in skin, hair, facial appearance
- B. Melanin skin pigmentation
- C. Pale sclera
- D. Unusual importance of facial appearance for mate choice
- E. General hairlessness, but with sex-specific patterning, ever-growing hair on head

XV. Unusual demographic and population traits

- A. Wide geographic distribution, large population size, rapid potential population growth (Blurton Jones, Hawkes, & O’Connell, 2002)

Traits that are especially relevant to testing the EDSC model are marked in bold. Note that most of these traits are identified and discussed in Alexander, 1979, 1987, 1989; Daly & Wilson, 1983; Low, 2000.

characteristics of humans *in combination* provides powerful opportunities to evaluate the model against competing hypotheses.

3. The hominin fossil record

The temporal sequence of change in hominin anatomy, as documented in the fossil record, is the single source of data on the order of acquisition of key human traits. For example, the first substantial increases in hominin brain size, and perhaps reorganization, occurred with the appearance of the genus *Homo* roughly 2 mya (see Lee & Wolpoff, 2003). The fossil record reveals that encephalization is not causally linked with bipedality or stone tool use (Darwin, 1871) because encephalization postdates the appearance of bipedal locomotion in the fossil record by at least two million years (Leakey et al., 1995; White, Suwa, & Asfaw, 1994) and postdates the earliest evidence of tool use and manufacture by more than half a million years

(Asfaw et al., 1999; Semaw et al., 2003). Similarly, encephalization is not directly associated with cooperative hunting, as meat eating precedes significant brain size increases (Klein, 1999). Tool use and hunting are also common among chimpanzees (Mitani & Watts, 2001; Stanford, 2001). The paleontological and archeological records thus provide critical clues useful for testing hypotheses about the selective pressures that shaped human evolution, by allowing us to evaluate what characters appeared in concert and which were independent.

The fossil record indicates that, during the past four million years, there has been a significant reduction in the magnitude of the sex difference in physical size, a threefold increase in brain volume, a near-doubling of the length of the developmental period, and a disappearance of related species of hominins. Based on covariation among these factors, and social and ecological differences across living primates, defensible inferences can be drawn about the nature of social dynamics in early hominins (Alexander, Hoogland, Howard, Noonan, & Sherman, 1979; Clutton-Brock, 1977; Dunbar, 2004; Foley, 1999; Plavcan, van Schaik, & Kappeler, 1995), although associated models are not definitive (Plavcan, 2000).

The EDSC model makes certain predictions about the order of acquisition of characters, some of which may be inferred from the paleontological and archeological records. Because ecological dominance is a concurrent or precondition of social arms races in hominoids, improved ecological dominance should arise prior to or along with increases in brain size, extension of childhood, male–female pair bonding, and significant coalitionary behavior. Although the initial primary function of male parenting is likely to have been to provide protection, subsequent elaboration of male parental roles, in concert with extended childhood, were likely to involve social learning (Geary & Flinn, 2001). Hence, extensive male parental effort should not precede significant increases in cognitive abilities. Likewise, because male–male coalitions within multimale groups in which males and females maintain stable mating relationships greatly enhance social complexity, they should not precede increases in cognitive abilities either.

These predictions differ from those based on other models. If hunting or complex foraging were the driving force for increased intelligence, evidence of significant changes in foraging behavior or abilities should be associated with concomitant intelligence and life history changes. If environmental or ecological challenges were the driving force for human intelligence, evidence for increases in cognitive sophistication should be found where and when environments are the harshest, most variable, or otherwise most cognitively challenging. Conversely, the EDSC model predicts that selective pressures for increased cognitive abilities would be most intense in rich environments supporting relatively high population densities and high levels of social competition. Unfortunately, paleontological data for some of these characteristics are notoriously broad brush and hence provide limited, albeit important, tests of these predictions.

Cognitive abilities are broadly indicated by overall brain size and/or encephalization (brain size relative to body size; Falk, 1987; Holloway, 1968, 1996; Martin, 1983). Evidence of significant brain expansion appears with earliest *Homo*, with the advent of regular meat eating and apparent increase in dietary quality. Improved dietary quality may have reduced constraints on brain size (Aiello & Wheeler, 1995), facilitating increases in brain size and intelligence. Early Pleistocene *Homo erectus* (*Homo ergaster*) was characterized by brain

sizes of 600–1057 cc (Lee & Wolpoff, 2003) as compared with 343–560 in the *Australopithecus* sp. (Brown, Walker, Ward, & Leakey, 1993; Conroy et al., 1998; Falk, 1987; Holloway, 1996; Kimbel, Johanson, & Rak, 1994) and 510–740 in *H. habilis* (*sensu lato*; Wood, 1992; Fig. 1; Falk, 1987). Body size also increased with *H. erectus*, with individuals increasing in stature from 3.5 to 5 ft to roughly 5 to 6 ft tall (McHenry, 1992), thus, the encephalization increase is not as large as raw endocranial size numbers would indicate. Reliable values for encephalization are difficult to compute because body mass estimates for isolated crania cannot be accurately computed (see Elton, Bishop, & Wood, 2001). Still, there is evidence that absolute, not relative, brain size is more closely related to intelligence (Deacon, 1997a). Regardless, throughout the Pleistocene, brain size increased steadily over time until 50 kya (Lee & Wolpoff, 2003; see Fig. 1).

3.1. Ecological dominance

Although difficult to quantify, the fossil record indicates that significant increases in ecological dominance roughly coincided with the appearance of *H. erectus*, 1.8 mya (Fig. 1). The hypertrophied dentognathic structures typical of australopithecines became greatly reduced, with jaws, teeth and muscles of mastication decreasing in size. These changes indicate a shift to a higher quality diet that required less oral processing. A further indication of improvement in dietary quality is seen in the apparent increased dependence on meat from large mammals in the diet around this time (Walker, Zimmerman, & Leakey, 1982), whether hunted or scavenged (review in Klein, 1999). Tools were regularly used to process meat and plant foods (Keeley, 1977; Klein, 1999). Although we do not know the antiquity of the dependence on stone or other types of tools, tool use appears more systematic and ubiquitous at this time period than ever before (Foley & Lahr, 1997). The use of tools would also have afforded greater protection from predators and carnivorous competitors, although the antiquity of tool use for defense is unknown.

Projectile weapons may be of particular importance for dealing with conspecifics (Bingham, 1999; Dunsworth, Challis, & Walker, 2003), as well as other species (Calvin, 1983). Evidence that humans have special cognitive facilities for tracking and dodging incoming projectiles (Watson & Kimura, 1991), in addition to the mental aptitudes necessary for aiming projectiles at moving targets, suggests that hunting is unlikely to have been the sole selective pressure responsible for the evolution of throwing skills. Chimpanzees throw objects at conspecifics, but never do so while hunting (Goodall, 1986). It may also be that, by 1.5 mya, hominins were controlling and using fire for cooking or protection (Bellomo, 1994; Brain, 1993; Gowlett, Harris, Walton, & Wood, 1981; Rowlett, 2000; Wrangham et al., 1999), although evidence for controlled fire prior to about 500 kya has been debated (Isaac, 1982, 1984; James, 1989).

Another indicator of increased ecological dominance is that, by just under 1 mya (de Vos, Sondaar, & Swisher, 1994; Pope, 1995), but possibly by 1.8 mya (Swisher, Curtis, Jacob, Getty, & Suprijo, 1994), hominins are found in Java, and by 1.7 mya, are found in Georgia (Gabunia et al., 2000), as well as persisting in east and south Africa. While some of this dramatic expansion in geographic range may be attributable to ecological stress, as a

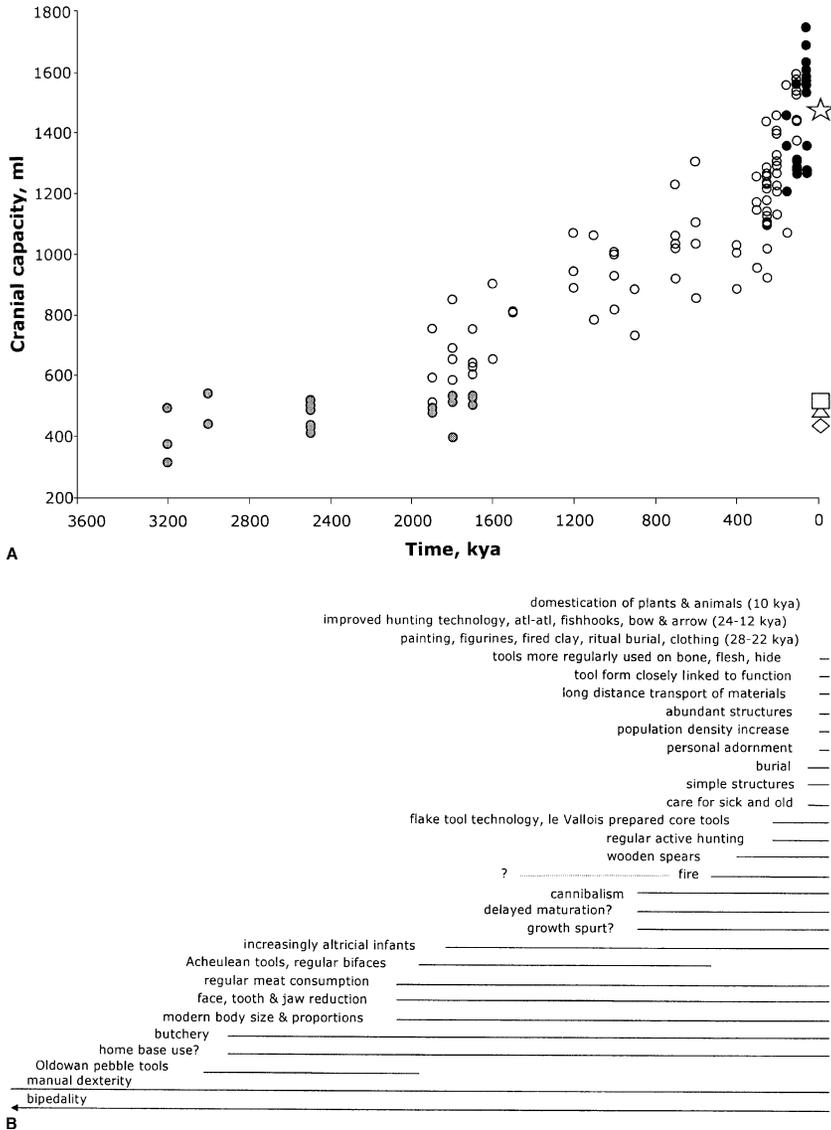


Fig. 1. (A) Cranial capacity and evidence of behavioral evolution over the past 3.4 million years of human evolution. Cranial capacities from Falk (1987), Holloway (1996), Kimbel et al. (1994), and Lee and Wolpoff (2003). Gray circles represent nonhabiline *Australopithecus* (and *Paranthropus*), black circles Neandertals, and open circles all other *Homo* and *H. (Australopithecus) habilis*. Modern hominoid average cranial capacities are also indicated for reference: star=modern *H. sapiens*, square=*Gorilla gorilla*, triangle=*Pongo pygmaeus*, diamond=*Pan troglodytes* (Martin, 1983). Dates of fossil specimens are rounded off to the nearest 50 ky and derive from Brown et al. (1993), Feibel et al. (1989), Kimbel et al. (1994), Lee and Wolpoff (2003), White et al. (2003), and Wood and Collard (1999). (B) The paleontological and archeological indicators of behavior were from Asfaw et al. (1999), Begun and Walker (1993), Bermudez de Castro et al. (1999), Dean et al. (2001), Klein (1999), Smith (1993), and Ward et al. (2001).

consequence of increased carnivory (Shipman & Walker, 1989), the extent of the expansion must have involved overall population expansion resulting from improved fertility and/or decreased mortality. This population expansion also reflects the ability of hominins to contend with a wide variety of habitats, ecological circumstances, and resources (see also Potts, 1998). Clearly, hominins experienced a significant increase in ecological dominance during the beginning of the Pleistocene.

With the increase in ecological dominance accompanying the origin of *H. erectus*, there was some brain size increase. Brain size continued to increase after this time, as did ecological dominance. Human problem-solving abilities that may have evolved primarily for negotiation of intraspecific interactions could be applied to solving ecological and foraging problems; thus, the EDSC model would predict a reciprocal and mutually reinforcing relationship between cognition and ecological dominance. Ecological dominance increases result in increasing social pressures—due to reduced mortality and population expansion—that select for enhanced cognitive abilities, which, in turn, allowed hominins to become even more ecologically dominant, and so forth.

The correspondence between initial encephalization in *Homo* and dietary change also supports hunting and foraging efficiency models. Control of fire at this time would support both models as well. By 400 kya, hominins were using spears; around 250 kya, there is increased evidence for active hunting; by 50 kya, they were hunting large mammals more regularly than ever before; by 12–14 kya, they were using atl–atls, fishhooks, and bows and arrows; and by 10 kya, they had begun to domesticate plants and animals (see Fig. 1). Despite these apparently significant changes in subsistence practices, there are no corresponding jumps in evidence of behavioral complexity outside of foraging behavior, except at 50 kya, and no corresponding jumps in cranial capacity. The EDSC model predicts no necessary close association between foraging and brain size, although they should positively reinforce one another. Admittedly, the paleontological and archeological evidences are not tight, but these data can be interpreted to support EDSC more strongly than models tightly focused on foraging behaviors.

Similarly, over this time, hominins had expanded into a variety of habitats and regions. Local resources and ecological challenges would have varied across the species' range. Some regions have much colder and more variable climates, some hotter and drier, some are more seasonal (see Potts, 1998). If ecological pressures posed the strongest selection on intelligence, we would expect the most climatically extreme or variable environments to be the loci of increases in cognitive abilities. There is no substantive geographic variation in brain size apparent in hominins, however, nor any obvious association between climate and brain size. In addition, cultural and behavioral innovations, in particular, the origin of the Acheulean industry and the creative explosion accompanying the Late Stone Age and Upper Paleolithic periods, appeared first in Africa, most of which would have had relatively stable, rich environments. In general, richer environments where ecological dominance would have been highest experienced the greatest changes in cultural innovation, consistent with the EDSC model. In addition, the EDSC model would predict that populations in regions with high ecological dominance would increase, with population expansion and gene flow moving outwards. This is the pattern seen with the origin of the *Homo* and with the appearance and

spread of anatomically modern *Homo sapiens* between 100 and 50 kya. If environmental stress were the strongest selective factor, the opposite pattern of population expansion and gene flow should have occurred. It is certainly possible that populations could have expanded without special increases in intelligence; however, the EDSC model would not predict greater increases in intelligence in poor environments than in richer ones.

Another related factor is the unusual pattern of extinction among hominins. Significant evolutionary change of the sort exhibited by *Homo* is usually accompanied by adaptive radiation (Mayr, 1982), as with the appearance of australopithecines. In the case of the hominins, the extinction of all intermediate stages and nondescendent branch species (e.g., *Australopithecus*) suggests significant within-taxon competition. The pattern fits with ecological dominance, and competition among hominins for control of resources. A species that is expanding its range, as did *H. erectus* and later humans, and then overexploits a variety of biological niches within this range, will perforce reduce the overall carrying capacity of these ecologies. Reduced carrying capacity may intensify within-species competition (Malthus, 1798), as well as competition with other species that are dependent on the same resources. The competition could involve direct conflict, a disappearance of survival-related resources, or some combination. Whatever the details, the result would be the same: disappearance of species that were dependent on the same biological and ecological resources as early humans. The human niche evidently can only be occupied by one species.

3.2. Sexual dimorphism

The EDSC model predicts that changes in hominin social structure related to the increasing stability of male–female pair bonds and male coalitionary behavior should accompany brain size increase, not precede it. The best indicator of these behaviors in the fossil record is sexual dimorphism. Reduced body mass dimorphism is associated with both monogamy (Plavcan, 2000, 2001) and male coalitionary behavior (Pawłowski et al., 1998; Plavcan et al., 1995) in extant primates. Although the large canine crown height dimorphism that characterizes all living and fossil great apes had greatly diminished in *Australopithecus* (Ward, Leakey, & Walker, 2001), the reduced body mass dimorphism typical of modern humans did not occur until sometime during the evolution of *H. erectus* (McHenry, 1992, 1994a; cf. Reno, Meindl, McCollum, & Lovejoy, 2003). The body mass increase accompanying the origin of *H. erectus* suggests that female body size increased from the australopithecine condition more than did male body size. Body mass dimorphism in early *H. erectus* is difficult to estimate accurately, but disparities in size and robusticity among even early *H. erectus* crania are less than that in australopithecine species, signaling a reduction in body size sexual dimorphism. By the early mid-Pleistocene, body mass dimorphism was similar to that found in modern humans (McHenry, 1994a; Ruff et al., 1997).

The pattern of diminished sexual dimorphism associated with the origin of *Homo*, coupled with greater encephalization, supports the EDSC model. The changes in social behavior accompanying the shift in mating and parenting strategies are likely to have presented novel cognitive challenges involving complex reciprocity among coalition members. Unlike gorillas, with one-male breeding groups, and chimps, with promiscuous mating and little

male parental behavior, the evolving hominids were faced with the difficulties of managing increasingly exclusive pair bonds in the midst of increasingly large coalitions of potential mate competitors.

One approach to interpreting hominin social behavior evolution would be to assume that the behavioral characteristics of the ancestor common to the australopithecine species and humans were similar to those observed in modern chimpanzees or bonobos (de Waal & Lanting, 1997; Kano, 1992; Wrangham, 1999; Wrangham & Peterson, 1996; Zihlman, Cronin, Cramer, & Sarich, 1978). This is a reasonable assumption in some respects. The encephalization quotient (EQ) of chimpanzees, bonobos, australopithecines, and, presumably, the common ancestor are very similar (McHenry, 1994a, 1994b). However, sexual dimorphism in body weight is about 20% for chimpanzees and bonobos (Goodall, 1986; Kano, 1992). Although bonobo males are not known to show consistent coalitional aggression, male-on-male physical aggression is common and is presumably a feature of the ancestor common to chimpanzees and bonobos (Wrangham, 1999). In any case, the degree of body mass dimorphism in chimpanzees and bonobos is considerably lower than that estimated for *A. anamensis* (Ward et al., 2001) and *A. afarensis* (McHenry, 1992; but see Reno et al., 2003), in which males were much larger than females were. The contrast suggests that the reproductive strategies of australopithecines may have differed in some respects from those of male chimpanzees or bonobos, and thus, the social patterns found with chimpanzees and bonobos might not fully capture the social dynamics in australopithecines or the selective pressures that favored larger females in the transition to *Homo*. *Australopithecus* body mass dimorphism suggests that these early hominins were polygynous, as significant mass dimorphism is not associated with monogamy in any extant primate (Plavcan, 2001).

3.3. *Extended childhood*

One factor that should closely track increases in cognitive abilities is a prolongation of childhood, which would provide more time for social learning prior to adulthood (Bogin, 1991, 1999; Joffe, 1997). The first hominin to have had relatively altricial infants was probably *H. erectus*, roughly 1.8 mya. Female pelvic dimensions are constrained by mechanical–locomotor, as well as thermoregulatory, constraints, and thus, birth canal size was not greatly expanded over australopithecine levels (Begun & Walker, 1993), yet, adult brain sizes were nearly doubled (Fig. 1). This means that to have appropriate neonatal proportions relative to the size of the mother's pelvic inlet, infants must have been born at a relatively small size. The rapid rate of brain growth seen in human infants, and presumably that of early *Homo*, suggests that for infant heads to pass through the birth canal, hominin babies would have been relatively altricial (Portman, 1941). To achieve their ultimate size, these rapid fetal rates of brain growth continued after birth, as in humans (Martin, 1983). It is notable that human brains achieve adult size relatively early in life, suggesting a strong selective advantage for neural processing hardware to be in place early in ontogeny, probably to facilitate learning throughout childhood (Bjorklund & Pellegrini, 2002; Flinn & Ward, 2004; Leigh, 2001; but see Bogin, 1991). Even early hominins do not appear to have attained

adult brain size simply by prolonging growth (Deacon, 1997a; Dean et al., 2001; Leigh, 2001). Altricial infants would have required more intensive mothering and, given the decrease in sexual dimorphism during this period that may indicate pair bonding, more intensive paternal and alloparental care.

Despite these ontogenetic shifts, delayed maturation does not appear to have occurred until later in human evolution. Dental development is coupled to life history variables, such as age at sexual maturity, and hence can be used to infer the timing of important life history stages. Early *H. erectus* appears to have had relatively rapid development, similar in rate to that of *Australopithecus* and great apes, whereas that of modern humans is much slower (Dean et al., 2001). Coincident with its apparent rapid rate of development, early *H. erectus* is predicted to have lacked a human-like adolescent growth spurt, based on the fact that the single known juvenile skeleton, KNM-WT 15000, appears to have had a more rapid rate of dental development compared with that of his postcranial skeleton than modern humans do (Smith, 1993). There are no comprehensive data on rates of child development for hominins between 1.6 mya and 60 kya, but the single Neandertal specimen examined by Dean et al. (2001) was modern in its developmental trajectory, indicating that a human-like extended childhood had occurred by this time. A modern human pattern of dental development was present by 800 kya (Bermudez de Castro et al., 1999), but this may not imply a similar rate (Dean et al., 2001). If it does, it might be reasonable to hypothesize that the human adolescent growth spurt was already in place by this time as well. Longevity appears to have gradually increased from *Australopithecus* to modern humans, with a higher proportion of individuals living to old age, although definitive evidence is lacking. If ecological dominance reduced mortality from extrinsic causes, this would allow for the selection for delayed reproduction and extended life histories (Williams, 1957). Taking all the data together, it appears that the evolution of altriciality may have begun with brain expansion, but that delayed maturation and an adolescent growth spurt may have evolved later in human evolution, perhaps as brain size increase continued throughout the Pleistocene.

In summary, the fossil and archeological evidence does not falsify the EDSC model and indeed supports it more strongly than it does models favoring subsistence behaviors or material ecological factors as the driving force behind human intelligence. Many of the inferences we can make about hominin behavior based on fossil and archeological data are fairly general; linking this evidence with data from other sources, such as comparative neurobiology, can provide additional and, in some cases, stronger tests.

4. Design of the human brain and mind

4.1. Brain

The human brain is roughly two to three times larger than that of both our closest relatives and the earliest fossil hominins and comes at a cost of 20% of our metabolic resources (Armstrong, 1990). Given this, it is unlikely that the human brain would have evolved without an extraordinary functional payoff (Dunbar, 1998). But the differences between

human and nonhuman brains are not in size and calorie consumption alone. In addition to the much more complex patterns of cerebral convolutions (Zilles, Armstrong, Schleicher, & Kretschmann, 1988), there are many unusual and unique aspects of the human brain. For example, humans have relatively dense connections between those parts of the brain that are involved with emotion and higher cognitive skills, and at least one of these brain regions, the anterior cingulate cortex (ACC; Area 24 in Fig. 2), contains one type of spindle cell found only in large hominoids, and these are double the frequency in humans than in great apes (Nimchinsky et al., 1999). These changes and changes in the extent of interconnections and possible reorganization of some areas of the prefrontal cortex appear to provide the neurobiological bases for many of the human abilities predicted by the EDSC model, including self-awareness, TOM, and social empathy (e.g., Adolphs, 2003; Siegel & Varley, 2002; Tulving, 2002). More precisely, the EDSC model predicts that the greatest changes in human neurobiology and cognition involve those areas of the brain associated with solving social problems. In the following sections, we highlight some of the potential evolutionary changes in the corresponding brain systems.

4.1.1. *Expansion of prefrontal cortex*

There is little doubt that human evolution has been characterized by substantive increases in overall brain size and in EQ. EQ is an index of brain size relative to that of a mammal of the same body weight (Jerison, 1973; for discussion, see Holloway, 1996). It has long been assumed that the EQ of the prefrontal cortex (e.g., Areas 25, 45, 46, and 47, Fig. 2)—that area of the brain most commonly associated with many of social-cognitive competencies predicted by the EDSC model—has shown a proportionally larger increase during human evolution than have other areas of the neocortex (e.g., Deacon, 1990). Recent comparative studies suggest that the proportional increase may be more modest (about 10%) than once assumed, at least in comparison with the prefrontal cortex of great apes (e.g., Holloway, 2002; Semendeferi & Damasio, 2000; Semendeferi, Lu, Schenker, & Damasio, 2002).

Nonetheless, modest proportional expansion, along with organizational changes (next section), and the increase in absolute size of the human prefrontal cortex are consistent with important evolutionary changes. Increases in absolute size result in increases in the degree of interconnections among these regions and with other regions of the brain (Hofman, 2001; Holloway, 1968). Basically, as absolute volume increases, the degree of interconnections among neurons (i.e., axons and white matter) increases much more rapidly than does the increase in the absolute number of neurons (i.e., cell bodies and grey matter; Zhang & Sejnowski, 2000). The human neocortex is thus less densely packed per volume with neurons, but much more highly interconnected (Miller & Cohen, 2001), which suggests that humans may have a greater ability to integrate information across modalities than other primates do (Hofman, 2001; Holloway, 1968). This is an important evolutionary change that would seem necessary to support the domain-general cognitive competencies, such as working memory (see below), needed to construct mental simulations of social dynamics and to mentally rehearse behavioral responses to variation in these dynamics (Geary, 2005). These simulations are an important feature of the scenario-building aspect of social

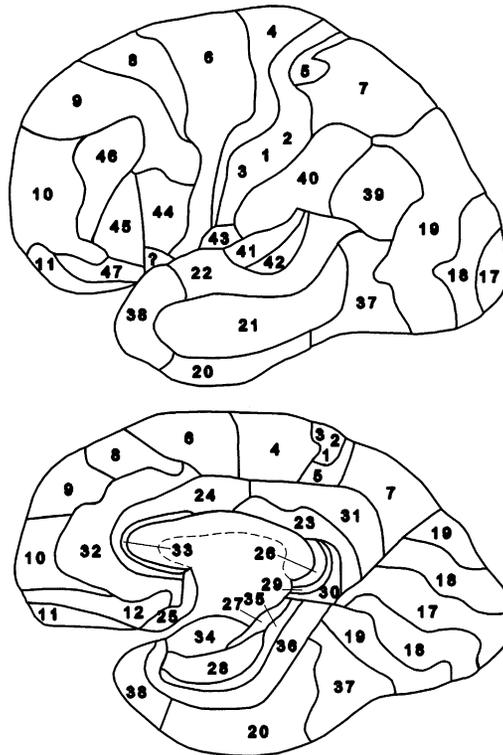


Fig. 2. Maps of the areas of the human neocortex of Brodmann (1909). The top section is a lateral (outer) view of the cortex, whereas the bottom section is a medial (center, between the two hemispheres) view. Many of these areas can be subdivided into specialized subregions that may process different forms of information. Very generally, Areas 1, 2, 3, 5, 31, and 43 are part of the parietal cortex and support a variety of functions, including sense of body position, attention, and spatial competencies. Areas 17, 18, and 19 are part of the occipital cortex and support simple and complex visual perception. Areas 22, 41, 42, and subregions of Areas 40 and 38 are part of the temporal cortex and support simple and complex auditory and speech perception. Areas 20, 21, 26–28, 34–37, and 52 are also part of the temporal lobe, but support a variety of complex visual competencies. Areas 4, 6, and 8 are involved in complex motor movements and are part of the frontal cortex. Area 44 and subregions of Area 45 are involved in speech generation and are part of the frontal cortex. Areas 9, 10, 11, 25, 46, 47, and subregions of Area 45 are part of the prefrontal cortex and support behavioral control, executive functions, and many complex social competencies. Areas 23, 24, 30, (parts of 31), 32, and 33 are part of the cingulate and support attentional and emotional functions. Illustration by Mark Dubin.

competition and the EDSC model (Alexander, 1989), a point that we will elaborate in the Mind section.

4.1.2. Reorganization of the ACC and prefrontal cortex

In addition to enhanced neural interconnections, the human prefrontal cortex has greater gyrification than that of great apes; specifically, there are more folds and, thus, more surface area in this part of the neocortex (Rilling & Insel, 1999; Zilles et al., 1988). The expanded surface area creates the potential for greater modularity and differentiation of functions within

more specific areas of the prefrontal cortex, and the potential for the evolution of species-specific specializations in these regions (Deacon, 1990; Preuss, 2001). With regard to the predictions of the EDSC model, there is evidence for evolutionary change in prefrontal regions that support competencies described in Table 1 and predicted by the model, such as self-awareness (right prefrontal cortex: Tulving, 2002), TOM (ventromedial region, Area 11 in Fig. 2: Baron-Cohen, 2000), and attachment (Bartels & Zeki, 2004). We focus on only a few of these regions to illustrate how research in cognitive neuroscience can be used to test predictions of the EDSC model.

4.1.2.1. Anterior cingulate cortex. The human ACC appears to have undergone important evolutionary reorganization and changes in absolute size (Preuss & Kaas, 1999). The ACC is larger in primates than in other mammals, and, as noted earlier, Nimchinsky et al. (1999) found a form of neuron that is only found in the ACC of great apes and humans. These cells appear to be involved in integrating the ACC with the prefrontal cortex and with other brain regions (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001). Functionally, the ACC is involved in various forms of social cognition and appears to be involved in the integration of activity in regions of the prefrontal cortex with activity in brain regions, such as the amygdala, that respond to emotion-laden and social information (Bartels & Zeki, 2004; Damasio, 2003; Nimchinsky et al., 1999; Taketoshi & Nishijo, 2000). The ACC is also involved in the attentional control and shifting of attention when nonroutine information is encountered (Miller & Cohen, 2001) and is thus important for detecting variation in social and other conditions.

4.1.2.2. Prefrontal cortex. There is mounting evidence suggesting the human prefrontal cortex has undergone substantive evolutionary reorganization. Semendeferi, Armstrong, Schleicher, Zilles, and van Hoesen (1998) found that, for humans, Area 13—which appears to be a subdivision of Area 11 (Fig. 2)—is about one half the size expected based on overall brain size. They speculated that Area 13 is comparatively small because adjacent areas, specifically other regions of Area 11 and regions of Area 47, may be composed of a large number of specialized subdivisions, each of which would process specific but related forms of information, most likely social information. Using endocasts, Holloway and de la Coste-Lareymondie (1982; Holloway, 1996) found evidence for a very specific hemispheric asymmetry in *H. erectus* and modern humans. The left occipital area (e.g., Areas 17 and 18 in Fig. 2) is smaller, and the left parietal area and the right frontal cortex are larger than the corresponding regions in the opposite hemisphere. Zilles et al. (1996) confirmed this pattern for human right-handers, noting that the dorsolateral prefrontal cortex (Area 46) and the frontal pole (Area 10) were larger in the right than in the left hemisphere, but found no such asymmetry in chimpanzees. The size of the frontal pole is especially large in the right hemisphere and is estimated to be composed of nearly three times as many neurons as the corresponding area in great apes does (Semendeferi et al., 2001).

The disproportionate expansion of the right prefrontal cortex, in general, and the frontal pole, in particular, as well as the potential reorganization of Area 11, is relevant to the EDSC model. These areas appear to be involved in self-awareness, social problem solving, the

ability to recall personal experiences, and the ability to mentally project oneself into the future (Tulving, 2002). Although projecting oneself into the future might facilitate hunting and anticipation of seasonal climatic change, this ability is heavily integrated with a sense of self. The latter is not needed for hunting or coping with climatic change, but would be essential in a social world in which competitors have a TOM, that is, an ability to make inferences about others' thoughts, feelings, intentions, and likely future behavior. In other words, a sense of self may have coevolved with TOM in that it enables people to understand which aspects of their behavior or personality other people are focusing on in their competitive interactions. As Alexander (1990a, p. 7) stated, the human brain—areas of the right prefrontal cortex—has evolved to allow us to "...see ourselves as others see us so that we may cause competitive others to see us as we wish them to." Other regions of the prefrontal cortex also appear to be engaged in social cognition. For instance, recent brain imaging studies suggest that Areas 32 and 9 (Fig. 2) are particularly active in tasks that require people to mentally simulate the behavior of other people or to simulate future social or other scenarios (Gallagher & Frith, 2003). These simulations correspond to the scenario building of Alexander (1989).

4.2. *Mind*

Cognition is composed of the mechanisms that allow organisms to attend to, process, store in memory, and retrieve from memory information patterns that have tended to covary with survival and reproduction during the species' evolutionary history. Some of these information patterns will vary across generations and within lifetimes (Geary, 2005). Variation, in turn, creates conditions that will favor the evolution of phenotypic plasticity, that is, mechanisms that are modifiable in response to the type of information that can change during the organisms' lifetime. For example, phenotypic plasticity can accommodate individual differences in significant modular domains, such as facial recognition: There are inherently constrained mechanisms that draw attention to and process the basic features of a human face and complementary plastic mechanisms that enable the recognition of individual faces. Other forms of plasticity have evolved to cope with variation in more macrolevel conditions (e.g., social discourse) and support the ability to form conscious representations of past, present, and potential future states, specifically, to form mental models of these states, and then manipulate the models in ways that enable the simulation of behavioral strategies to cope with variable conditions (Geary, 2005; Wheeler, Stuss, & Tulving, 1997). These forms of plasticity are needed to support the social scenario building of Alexander (1989).

4.2.1. *Cognition*

4.2.1.1. *Scenario building.* There are two basic classes of conscious, explicit knowledge: semantic and episodic (Tulving, 1983). This knowledge is typically assessed using memory tests, and thus, the systems are referred to as semantic and episodic memories, respectively. Semantic memory refers to the retrieval of decontextualized facts and information (e.g., *H. erectus* appeared before *H. sapiens*), and episodic memory refers to the retrieval of time-

based, contextualized memories of one's life history. A conscious representation of facts and decontextualized information is known as noetic awareness, and a conscious time-based representation of the self and personal experiences is auto-noetic awareness (Tulving, 2002; Wheeler et al., 1997). The latter is the ability to consciously consider the self across time, that is, to recall past personal experiences, relate these experiences to current situations, and project oneself into the future. As argued by Levine (1999, p. 200), auto-noetic awareness includes the ability to "cast oneself as a player in scenarios emerging from various choices available at any given moment...this capacity facilitates the self-regulation of behavior necessary for the achievement of personally-relevant goals." These scenarios can be understood as a form of mental model (Johnson-Laird, 1983) in which not only is the self the primary actor in the situation, but the individual is aware that the self is the primary actor.

Stated more plainly, the auto-noetic mental model is experienced as daydreams and fantasies, but serves the more serious function of allowing individuals to consciously form future-oriented goals, regulate future-directed behavior, and integrate these within a seamless and self-aware knowledge of one's life history. These simulations are only needed in situations that differ from day-to-day routines (Levine, 1999). They allow people to anticipate and mentally simulate potential behavioral strategies to deal with variation in social dynamics or changing ecological contexts. Although the research on auto-noetic mental models emerged independent of the scenario building of Alexander (1989), they clearly capture the same concept.

4.2.1.2. Working memory. Auto-noetic mental models and scenario building are supported by working memory systems. These entail a central executive function that controls attentional resources and maintains cognitive representations in an active and conscious state (Baddeley, 1986). More precisely, the central executive function and working memory are defined by the ability to use attentional resources to amplify and maintain goal-relevant internal representations—such as a pattern of neural activity associated with external information (e.g., a sentence uttered by someone else)—and to inhibit irrelevant information patterns from entering conscious awareness (Engle, 2002). The temporal dynamics of how these systems operate suggest that the evolved function is to cope with rapid variation in external conditions and information patterns. The details are beyond the scope of the current treatment, but this degree of variation is more consistent with social dynamics than hunting, climatic change, or other ecological factors (see Geary, 2005). In other words, there are many features of human cognition that are most readily understandable in terms of selection for coping, with considerable variation in social conditions and dynamics within the life span, in keeping with predictions of the EDSC model. Still, arguments that the working memory system is designed to cope with variation in ecological conditions, such as those generated during hunting, cannot be ruled out. Cognitive anthropological research that focuses on the demands of hunting will be needed before more definitive conclusions can be drawn.

4.2.2. Brain systems

The prefrontal cortex and the ACC are of particular interest because of above-noted changes in these regions during human evolution, and because these brain regions are

implicated in the competencies that define working memory, executive functions, attentional control, episodic memory, and self-awareness, specifically those competencies listed in [Table 1](#) as having been uniquely elaborated during human evolution.

4.2.2.1. Working memory. A consensus is now emerging that areas of the dorsolateral region of the prefrontal cortex, such as Areas 9 and 46 ([Fig. 2](#)), are involved in the executive functions of working memory, as is the ACC (Area 24; [Kane & Engle, 2002](#); [Miller & Cohen, 2001](#)). These regions are particularly important for active goal maintenance and the inhibition of competing and goal-irrelevant distractions. These ends appear to be achieved by biasing, perhaps through attentional amplification ([Dehaene & Naccache, 2001](#)), the activation of posterior and subcortical pathways that represent the information needed for goal achievement. However, the dorsolateral areas and the ACC only appear to be heavily involved in coping with novelty and variability in current conditions. Under these conditions, the ACC appears to automatically direct attention to the novel or variable information, which results in the explicit and conscious representation of this information in working memory. Our point is that autozoetic mental models and scenario building are dependent on this form of brain and cognitive system, especially as related to the ability to mentally generate scenarios that involve potential *change* in social conditions and to plan social strategy.

4.2.2.2. Self-awareness. The brain and cognitive systems that support episodic memory and awareness of the self appear to differ from those that support working memory and executive functions ([Tulving, 2002](#)). Of particular importance are regions of the right prefrontal cortex (e.g., Area 10, [Fig. 2](#)). Traumatic injuries to these areas result in an array of deficits that differ from the trauma-related deficits in executive functions ([Levine, 1999](#); [Tulving, 1985](#)). One patient, KC, who suffered severe injuries to these brain regions as a result of a motorcycle accident, performed normally on IQ tests and on tests of executive functions, but “cannot recollect a single episode of his life from either before or after” the injury ([Levine, 1999](#), p. 207). Nor can KC project himself into the future; that is, when asked to imagine his activities for the following day, he draws a blank ([Tulving, 1985, 2002](#)). He has since learned facts about himself (e.g., his former job) but is unable to place these facts in the context of memories of his life.

The associated deficits also include difficulties in self-regulation and with social activities, in general. These patients find it difficult to inhibit previously learned responses and thus have considerable difficulty on tasks that involve change from one type of response to another. In effect, they cannot problem solve when the task involves novelty and cannot make effective decisions that involve comparing current choices to future outcomes. Social activities are, of course, very complex and entail subtle and almost constant and concurrent change in multiple sources of information, including facial expression, vocal intonation, body language, and so forth. In addition, social activities are intimately related to one’s sense of self. In social situations, an individual with right prefrontal damage had “difficulty knowing how to behave around family members and friends, and had to be taught socially acceptable behaviour” ([Levine et al., 1998](#), p. 1956). The patients recognize social deficits in other people, but have difficulty understanding these same deficits in themselves.

4.2.3. *Conscious psychological systems*

How are the evolution of executive functions, explicit and conscious awareness of the self, mental time travel, and the ability to engage in controlled problem solving related to the EDSC model? The theme that ties all of these together with the proposals of many other scientists (e.g., Humphrey, 1976; Picton, Alain, & McIntosh, 2002) is the auto-noetic mental model, which can be understood as the core of the scenario building of Alexander (1989). With these models, the individual creates a self-centered mental simulation of the “perfect world” (Flinn & Blue-dorn, 2002; Geary, 1998, 2005): one in which the individual is able to organize and control social (e.g., social dynamics), ecological (e.g., access to food), and physical (e.g., shelter) resources in ways that would have enhanced the survival or reproductive options of individuals or of their kin during human evolution. The mental simulation of a perfect world requires the ability to decouple modular systems from engagement of the actual world and use these systems to either recreate a previous episode or create a more abstracted and decontextualized representation of social dynamics or other aspects of the world. The mental reconstitution of a past episode allows the individual to consciously and explicitly evaluate the dynamics of the episode (e.g., “What did he mean when he said . . .”) and to plan and rehearse strategies for anticipated future episodes that involve the same person or theme. Mental simulations can also involve abstractions that are common features or themes across episodes.

The creation of these conscious simulations is likely to be driven by executive control (Baddeley, 1986) and associated brain regions. As noted above, Gallagher and Frith (2003) reviewed evidence consistent with the position that Areas 32 and 9 of the prefrontal cortex (Fig. 2) are integrally involved in the human ability to form mental simulations of social and other changing conditions. The function of these cognitive and brain systems is to reconstitute the activity of the brain regions that were engaged during personal experiences or activate more abstracted representations of common features of these experiences (Damasio, 1989). The reconstitution would, for instance, involve retrieving episodic memories and then explicitly and consciously examining them in working memory. When the ability to create these simulations is fused with the auto-noetic awareness of Tulving (1985, 2002) and integrated with the functioning of associated brain regions, such as the right frontal pole (Area 10), an evolutionarily unique brain, cognitive, and conscious system emerges, as predicted by the EDSC model. The system places the self-aware individual at the center of a simulated construction or reconstruction of the social or ecological world and, more importantly, allows the individual to control outcomes in this world. The use of such a simulation, perforce, requires the ability to mentally time travel, both backward in time to reconstruct an episode and forward in time to simulate behavioral strategies to make changes in the world.

Controlled attention, working memory, and other executive functions are necessary components of these conscious simulations. The combination results in the ability to generate an explicit simulation and maintain it in an active and changeable state. Problem solving involves successive and goal-related changes in this state that, among other things, allow the individual to generate and simulate strategies to reduce the distance between one’s perfect world and one’s current circumstances. Simulated behavioral strategies are, in effect, problem-solving exercises focused on ways to gain access to and control social relationships and dynamics and the forms of resources that enhance survival or reproductive options in the

current ecology. Emotional systems are necessarily an integral feature of these simulations. If the simulations are built from episodic memories and corresponding abstract representations of common features across episodes, then the recreation of episodes should include associated emotional responses (Damasio et al., 2000). Imagined success at achieving a social goal or acquiring riches should result in an emotional response that is similar to the response that would result from actually achieving success in these endeavors. As in navigating life in the actual world, emotional responses that result during simulated activities provide feedback as to the value of the goal and the potential outcomes of control-related behavioral strategies and the counterstrategies of others.

In summary, empirical and theoretical advances in the cognitive neurosciences are nonconclusive, but they are consistent with several key predictions of the EDSC model. Much of the prefrontal cortex is involved in various forms of social cognition and in the ability to control attention and manipulate information in working memory. These different features of the prefrontal cortex and areas in which it is integrated, such as the ACC, can be combined in a way that allows people to mentally simulate complex social scenarios and generate an array of strategies to cope with these scenarios. When these competencies are fused with a sense of self, the result is an evolutionarily unique neurocognitive system that appears to be well adapted to deal with the forms of social cooperation and competition described by Alexander (1989, 1990a) and others (Dunbar, 2003; Humphrey, 1976). In short, these are the brain and cognitive systems that are needed to support the social scenario building of Alexander (1989) and the systems that would have evolved if scenario building were one of the core traits that facilitated social competition in a coevolutionary arms race.

5. Concluding remarks

The EDSC model proposes that hominins uniquely evolved sophisticated brains because they increasingly became “their own principal hostile force of nature” (Alexander, 1989, p. 469) via increased inter- and intragroup competition and cooperation. Sophisticated social-cognitive and linguistic capacities were favored because such skills allowed individuals to better anticipate and influence social interactions with other increasingly sophisticated humans. This “runaway” directional selection produced increasingly large brains and specialized cognitive capabilities because success was based on relative (rather than absolute) levels of ability (e.g., in executive functions, self-awareness). Unlike static ecological challenges, the hominid social environment became an autocatalytic process, ratcheting up the importance of social-cognitive competencies and supporting brain systems.

The model is supported by a unique combination of coevolved characteristics and their temporal sequencing. (1) Humans have an unusual pattern of speciation. The extinction of all intermediate stages (e.g., gracile Australopithecines and *H. erectus*) and nondescendent branch species (e.g., robust Australopithecines), and the absence of a pattern of adaptive radiation, suggest that within-taxon competition was highly significant. (2) 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 (Bjorklund & Pellegrini, 2002; Flinn & Ward, 2004; Joffe, 1997); a postreproductive stage may be useful for the care taking of dependent offspring, grandchildren, and other relatives (Alexander, 1979; Hawkes, 2003; Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998). (3) Humans have a unique mating system, with extensive male parental care and long-term pair bonding in a context of multimale/multifemale communities (cf. Flinn & Low, 1986; Geary, 2000). 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. (4) The human neocortex is apparently larger than that of other primates in precisely those areas that support social competencies that are unique to humans (Rilling & Insel, 1999), such as TOM (Adolphs, 2003; Baron-Cohen, 1999), language (Pinker, 1994), a sense of self (Wheeler et al., 1997), and the ability to mentally simulate social scenarios (Gallagher & Frith, 2003). (5) Humans have unusual aptitudes for the use of projectile weapons (throwing and dodging); these are involved in male–male competition, a form of social competition (Geary, 1998), and hunting and predator avoidance vis-a-vis ecological dominance. (6) Humans have unique aptitudes for communication, including language and specific linguistic abilities. (7) Humans have unique aptitudes for developing large, complex social groups based on kinship and reciprocity. Humans converge with those species that have competition among socially complex coalitions, for example, chimpanzees (e.g., Harcourt, 1988; Mitani & Watts, 2001; 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 and evolution of *Homo*, is social competition and cooperation in the context of increasing ecological dominance.

As ecological dominance increased, the traits that began to strongly covary with individual differences in survival and reproductive outcomes were those that allowed hominins to socially “outmaneuver” other hominins. These traits would include sophisticated social competencies, such as language, self-awareness, and TOM, an accompanying increase in brain size, and other adaptations that facilitated kinship- and reciprocity-based social coalitions. An extended period of childhood with intensive parenting would contribute to the acquisition of social skills and the development of personal social networks.

The use of mental simulations and abstract mental models are necessary for the complex analysis of social relationships and networks (Gallagher & Frith, 2003; Geary, 2005). 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 (Flinn, 2004, Chap. 3). Alexander's model posits that we evolved our aptitudes and predilections for art, dance, theatre, friendship, technology, and so forth, primarily as methods for contending with the social world. Art, dance, and theatre are likely to be supported by the same brain and cognitive systems that enable humans to form mental simulations of social and other scenarios. The advantages that such abilities offered for dealing with the ecological demands of drought, food shortages, snow, and the like, are posited to be secondary.

The foci and products of human mental processing are unusual. Whereas most species have evolved cognitive specializations that appear designed to solve task-specific ecological problems and some specialized social problems, like offspring recognition and optimal mate choice, the human mind possesses uniquely sophisticated social problem-solving abilities, including TOM, language, consciousness, romantic love, and empathy. The neurological mechanisms for these abilities are beginning to be identified in detail (Adolphs, 2003; Bartels & Zeki, 2004; Seigal & Varley, 2002). These social capabilities, moreover, seem to occupy the majority of human thoughts. The information pool developed and socially transmitted by human minds, what might be termed culture, has resulted in a new domain of competition and adaptation.

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