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

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42

Abstract

43 Human cognitive abilities are extraordinary. Our large brains are significantly modified from
44 those of our closest relatives, suggesting a history of intense natural selection. The conditions
45 favoring the evolution of human cognitive adaptations, however, remain an enigma. Hypotheses
46 based on traditional ecological demands such as hunting or climatic variability have not provided
47 satisfying explanations. Recent models based on social problem solving linked with ecological
48 conditions offer more convincing scenarios. But it has proven difficult to identify a set of
49 selective pressures that would have been sufficiently unique to the hominin lineage. What was so
50 special about the evolutionary environments of our ancestors that caused them, and them alone,
51 to diverge in such astonishing ways from their close relatives and all other life forms?

52 Richard Alexander (1989, 1990a) proposed a comprehensive integrated explanation. He
53 argued that as our hominin ancestors became increasing able to master the traditional ‘hostile
54 forces of nature’, selective pressures resulting from competition among conspecifics became
55 increasingly important, particularly in regard to social competencies. Given the precondition of
56 competition among kin- and reciprocity-based coalitions (shared with chimpanzees), an
57 autocatalytic social arms race was initiated that eventually resulted in the unusual collection of
58 traits characteristic of the human species, such as concealed ovulation, extensive bi-parental care,
59 complex sociality, and an extraordinary collection of cognitive abilities. We term this scenario
60 the “ecological dominance – social competition” model, and assess the feasibility of this model
61 in light of recent developments in paleoanthropology, cognitive psychology, and neurobiology.
62 We conclude that although strong or direct tests are difficult with current data, Alexander’s
63 model provides a far-reaching and integrative explanation for the evolution of human cognitive
64 abilities that is consistent with evidence from a wide range of disciplines.

65 1. Introduction

66 Humans have an unusual array of characteristics that distinguish us from other species. Our
67 cognitive abilities are perhaps the most remarkable. Hominin brain size increased more than
68 250% in less than 3 million years. Much of this increase occurred in the past 500 thousand years
69 and disproportionately affected the size (Ruff *et al.*, 1997), and perhaps the organization, of the
70 neocortex (Adolphs, 2003; Deacon, 1997a; Holloway, 1996; Rilling & Insel, 1999; Semendeferi
71 *et al.*, 2001). The behavioral changes were even more impressive, especially in the last few
72 thousand generations (e.g., Klein, 1999; Mithin, 1996). The Upper Paleolithic/Late Stone Age
73 “creative explosion”, continuing a long tradition, has generated an unparalleled expansion of
74 information and individual expression, albeit within the restraints of collective meaning (Caspari
75 & Lee, 2004; Henshilwood & Marean, 2003; McBrearty & Brooks 2000). Notwithstanding the
76 impressive cognitive adaptations of other species such as chimpanzees and dolphins (e.g., de
77 Waal & Tyack, 2003; Mann & Sergeant, 2003; Premack & Woodruff 1978), the products of
78 human minds stand out as one of life’s most impressive features.

79 Many hypotheses have been proposed concerning the selective advantages of cognitive
80 change during human evolutionary history. Most explanations involve ecological problem-
81 solving, such as tool use (e.g. Darwin, 1871; Gibson & Ingold, 1993; Washburn 1959; Wynn
82 1988), hunting (e.g., Dart, 1926; Hill, 1982; Washburn & Lancaster, 1968), scavenging (e.g.
83 Blumenschine & Cavallo, 1992), foraging (e.g., Issac, 1978; Kaplan *et al.*, 2000), extended life
84 history (e.g. van Schaik, 2000), food processing (e.g., Wrangham *et al.*, 1999), and savanna (e.g.,
85 Laporte & Zihlman, 1983) or unstable (Potts, 1998; Vrba, 1995) environments. None has
86 achieved complete or general acceptance, even when combined in synthetic models and causally
87 linked to social dynamics.

88 Common problems for these models include difficulties with explaining why humans
89 evolved such extraordinary cognitive competencies (e.g., awareness of the self as a unique and
90 social being; Tulving, 2002), considering that many other species hunt, occupy savanna habitats,
91 have long lifetimes, endured the same climatic fluctuations, and so forth. Additional problems
92 arise from the lack of clear domain-specific adaptations for the above scenarios, with the
93 possible exception of tool construction (Hodges et al., 1999) and folk biology (e.g., mentally
94 representing the ‘essence’ of hunted species; Atran, 1998). Even these adaptations, however, pale
95 in comparison to the human cognitive abilities of consciousness, language, self-awareness, and
96 theory of mind. These competencies do not appear to be adaptations for tracking prey or
97 collecting fruit, nor spurious outcomes of neurogenesis or other developmental processes (but
98 see Finlay et al., 2001; Williams, 1966). All these models, moreover, have difficulties accounting
99 for the diversity of culture into seemingly non-utilitarian areas such as art (Coe, 2003) and
100 religion (Boyer, 2001).

101 One possibility is that an advance in linguistic abilities, such as abstract symbolic
102 representation, was the Rubicon for a dramatic origin of cultural abilities (e.g., Washburn, 1978;
103 White, 1959). Some have suggested that a sudden genetic change might underlie this transition
104 (e.g., Calvin & Bickerton, 2000; Klein & Edgar, 2002; cf. Enard et al., 2002). It is uncertain what
105 benefit such a saltational mutation event might have for the initial individual in which it
106 occurred, for there would not be anyone else to talk or ‘culture’ with. Complex adaptations, and
107 cultural abilities surely qualify as such, are products of long, directional selection with successful
108 intermediary stages (Dawkins, 1986; Mayr, 1982), including language (Nowak et al., 2001). Our
109 close relatives, great apes, exhibit behavioral variations and traditions involving social learning
110 that suggest a more gradual transition (de Waal, 2001; McGrew, 2003; Stanford, 2001; van

111 Schaik, 2003; Wrangham et al., 1994; Whiten et al., 1999). The fossil record indicates a
112 continuous, albeit rapid, pattern of increase in cranial capacity among hominins (e.g., Lee &
113 Wolpoff, 2003; Lewin & Foley, 2004; Ruff et al., 1997). Although apparently abrupt artifact
114 changes are suggestive of significant transitions, the hypothesis that the Upper Paleolithic
115 “creative explosion” was caused by a neurological “hopeful monster” remains implausible.

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

129 A different approach to the problem of the evolution of human cognition involves
130 consideration of the brain as a “social tool” (Alexander, 1971, 1989; Brothers, 1990; Byrne &
131 Whiten, 1988; Dunbar, 1998; Humphrey, 1976; Jolly, 1966, 1999). This hypothesis suggests that
132 many human psychological adaptations function primarily to contend with social relationships,
133 with ecological constraints (e.g., hunting or extractive foraging) being a more secondary source

134 of recent evolutionary change. It appears that some human cognitive competencies, such as
135 theory of mind and language, are most readily understood in terms of social selection pressures,
136 although cognitive competencies for interacting with the physical (e.g., navigating) and
137 biological world are evident as well (Geary & Huffman, 2002). The primary mental chess game,
138 however, was with other intelligent hominin competitors and cooperators, not with fruits, tools,
139 prey, or snow. Human social relationships are complex and variable. Predicting future moves of
140 a social competitor-cooperator, and appropriate countermoves, amplified by networks of multiple
141 relationships, shifting coalitions, and deception, make social success a difficult undertaking
142 (Alexander, 1987, 1990b; Axelrod & Hamilton, 1981; Byrne & Corp, 2004; Daly & Wilson,
143 1988a,b; Stanford, 2001; de Waal, 1982, 2002).

144 Indeed, the potential variety of human social puzzles is apparently infinite; no two social
145 situations are precisely identical, nor are any two individuals ever in exactly the same social
146 environment. Moreover, social relationships can change rapidly, requiring quick modification of
147 strategy. Variability in these dynamics creates conditions that should favor the evolution of brain
148 and cognitive systems above and beyond more traditional modular systems (Fodor, 1983; Tooby
149 & Cosmides, 1995). These systems have been cast in terms of general intelligence, domain-
150 general abilities, or executive functions that are capable of integrating and co-opting information
151 processed by more restricted, domain-specific mechanisms (Adolphs, 2003; Blakemore et al,
152 2004; Geary, 2005; Preuss, 2004) and using mental simulations, or “scenario-building”
153 (Alexander, 1989) to construct and rehearse potential responses to changing social conditions.
154 These complex cognitive processes would be more capable of contending with, and producing,
155 novelties of cultural change and individual-specific differences (Flinn, 1997, 2004; Tomasello,
156 1999).

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

194 Taking another example, although part of ecological dominance involves diminished
195 intensity of selection from biotic interactions including predation, this is not sufficient. Top
196 predators, such as eagles, lions, and orcas, and large animals with effective protection, such as
197 elephants and sperm whales (e.g., see Weilgart et al, 1996), are relatively free from predation.
198 But resource scarcity (e.g., getting food) and pathogens may still be significant selective
199 pressures relative to contending with conspecifics, particularly in regard to the evolution of the
200 brain. The critical factor in ecological dominance is the extent to which a species has become
201 its own selective pressure, its own principal hostile force of nature. For dolphins, elephants,
202 lions, and orcas, interactions with conspecifics involving coalitions appear to have major effects
203 on survival and reproduction (e.g., see Tyack & de Waal, 2003). The evolution of social skills is
204 enabled by ecological dominance.

205 Sexual selection is related to ecological dominance because it involves selection arising
206 from competition among conspecifics rather than from the traditional extrinsic pressures.
207 Antlers, for example, reflect ecological dominance to the extent that they were designed to defeat

208 rival males rather than protection from predators. These examples suggest that the relation
209 between ecological dominance and mental abilities is not simple or straightforward.

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

216 The key to Alexander's model of human evolution, however, is not simply the recognition
217 that the evolving hominins seem to have been increasingly successful at dealing with a wide
218 variety of environmental challenges. It is the linkage of ecological dominance with the
219 escalating significance of interactions with conspecifics, wherein hominins increasingly became
220 their own principal hostile force of nature. All species face competition among conspecifics,
221 such as contending for mates and resources, but what is special and extraordinary about humans
222 (and, to a lesser extent, chimpanzees, dolphins, elephants, and orcas) is the importance of social
223 relationships -- more specifically: negotiated, dynamic, multi-level coalitions -- for succeeding in
224 this type of competition. In this evolutionary scenario, the primary selective pressures acting on
225 hominins -- particularly in regard to the brain -- came from their dealings with other hominins,
226 rather than with climate, predators, and food directly. The nature of this within-species
227 competition appears to have involved an evolutionary arms race among ever more effective
228 coalitions. Both the success of one's coalitions, and the success of an individual within her/his
229 coalitions, depended in part on socio-cognitive competencies such as empathy and theory of
230 mind that required new and expanded neurological structures (see *Brain* below).

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

243 Evidence that humans evolved into ecologically dominant predators and foragers comes
244 from patterns of human migration and demography, as well as our variable and flexible
245 subsistence strategies. Darwin's and Wallace's (1858, p. 54) conceptualization of natural
246 selection as a "struggle for existence" becomes in addition a special kind of *struggle with other*
247 *human beings for control* of the resources that support life and allow one to reproduce. In this
248 situation, the stage is set for a form of runaway selection, whereby the more cognitively, socially,
249 and behaviorally sophisticated individuals are able to out maneuver and manipulate other
250 individuals in order to gain control of resources in the local ecology, and to gain control of the
251 behavior of other people. To the extent that access to these resources covaries with survival and
252 reproductive outcomes – and it does in many contexts (Betzig, 1986; Chagnon, 1988; Hed, 1987;

253 Irons, 1979; Malthus, 1798) – the associated sociocognitive competencies, and supporting brain
254 systems, will necessarily evolve.

255 To the extent that ecological dominance was achieved, humans became "their own
256 principal hostile force of nature" (Alexander, 1989:469) via inter- and intra-group competition
257 and cooperation. Increasing linguistic and sociocognitive capacities were favored because such
258 skills allowed individuals to better anticipate and influence social interactions with other
259 increasingly intelligent humans. This "runaway" directional selection produced greater and
260 greater modular (e.g., language, theory of mind) and more general cognitive competencies,
261 because success was based on relative (rather than absolute) levels of ability. Unlike static
262 ecological challenges, the hominin social environment became an autocatalytic process,
263 ratcheting up the selective advantage associated with the ability to anticipate the social strategies
264 of other hominins and to mentally simulate and evaluate potential counter strategies (Alexander,
265 1989). Modular competencies allowed hominins to quickly and efficiently process social
266 information that was static, or invariant, across generations and contexts (e.g., the ability to read
267 basic human facial expressions), whereas the more variable and thus less predictable features of
268 one-on-one and coalitional social relationships favored the ability to mentally construct and
269 manipulate a range of potential social scenarios. These more general competencies are known as
270 working memory, attentional control, and executive functions (e.g., Baddeley, 1986; Engle,
271 2002; for review see Geary, 2005).

272 Although many models of human evolution involve syntheses of multiple factors, the
273 "ecological dominance – social competition" (hereafter EDSC) model is unusual in the
274 comprehensive range of traits that are apposite. Increased sophistication in social cognition
275 (Adolphs, 2003; Geary & Huffman, 2002; Seigel & Varley, 2002) and the components of general

276 intelligence, specifically, working memory and attentional control (Engle, 2002; Engle et al.,
277 1995), are posited to co-evolve with a suite of other characteristics, including altricial infants,
278 lengthy childhood, intensive parenting, concealed ovulation, complex coalitions, and menopause.

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

294 The advantages of intensive parenting, including paternal protection and other care, require
295 unusual mating relationships: moderately exclusive pair bonding in multiple-male groups. No
296 other primate that lives in large, cooperative multiple-reproductive-male groups has extensive
297 male parental care, although some male protection is evident in *Papio* (Buchan et al., 2003).
298 Competition for females in multiple-male groups usually results in low confidence of paternity

299 (e.g., chimpanzees). Males forming exclusive pair-bonds with females within multiple-male
300 groups would provide cues of non-paternity for other males, and hence place their offspring in
301 great danger of infanticide (Hrdy, 1999). Paternal care is most likely to be favored by natural
302 selection in conditions where males can identify their offspring with sufficient probability to
303 offset the costs of investment, although reciprocity with mates is also likely to be involved (B.
304 Smuts, 1986; R. Smuts, 1994). Humans exhibit a unique nested family social structure, involving
305 complex reciprocity among males and females to restrict direct competition for mates among
306 group members. It is difficult to imagine how this system could be maintained in the absence of
307 another unusual human trait: concealed (or cryptic) ovulation (Alexander & Noonan, 1979).

308 Human groups also tend to be male philopatric, resulting in extensive male kin alliances,
309 useful for competing against other groups of male kin (Chagnon, 1988; Wrangham & Peterson,
310 1996; LeBlanc, 2003). Females have complex alliances as well, but usually are not involved
311 directly in the overt physical aggression characteristic of inter-group relations (Campbell, 2002;
312 Geary & Flinn, 2002). Menopause reduces mortality risks for older women, and allows them to
313 concentrate effort on dependent children and other relatives (e.g., grandchildren) with high
314 reproductive value.

315 Alexander's model requires the integrated co-evolution of all these factors to explain how
316 and why humans came to possess their extraordinary cognitive abilities. Evaluating scenarios of
317 human evolution is necessarily speculative to varying degrees (e.g., Holloway, 1996; McHenry
318 & Coffing, 2000; Marks, 2002), but Alexander's model integrates a wide range of interrelated
319 phenomena, thereby generating a large number of ways to potentially falsify it. Full discussion of
320 the EDSC model is beyond the scope of this review, but can be found in the original works:
321 Alexander (1987, 1989, 1990a; see also Geary & Flinn, 2001). Our objective here is to provide

322 the strongest possible tests of the model based on recent advances in neurobiology, paleontology,
323 and other areas that provide useful evidence.

324 Insert Table 1 Here

325 Here we evaluate the ECSD model in terms of how it explains the improbable collection of
326 unusual human characteristics (Table 1). Evaluation of the significance of each of these features
327 would exceed the scope of this paper, so here we concentrate on those we think most significant
328 and most readily testable. The model requires an integrated co-evolution of all of the proposed
329 key factors. This is its main strength: if any single component fails, the whole model is falsified.
330 We emphasize two empirical sources: (1) the hominin fossil record, and (2) human neurobiology
331 and cognition. The main weakness of the model is that data are not available in many cases to
332 provide simple strong or direct tests. Nonetheless, analysis of the temporal patterns indicated by
333 the fossil record, the specific design features of the human brain, and the life history and
334 reproductive characteristics of humans *in combination* provides powerful opportunities to
335 evaluate the model against competing hypotheses.

336 **3. The hominin fossil record**

337 The temporal sequence of change in hominin anatomy as documented in the fossil record is
338 the single source of data on the order of acquisition of key human traits. For example, the first
339 substantial increases in hominin brain size, and perhaps reorganization, occurred with the
340 appearance of the genus *Homo* roughly 2 mya (see Lee & Wolpoff, 2003). The fossil record
341 reveals that encephalization is not causally linked with bipedality or stone tool use (Darwin,
342 1871), because encephalization postdates the appearance of bipedal locomotion in the fossil
343 record by at least two million years (Leakey et al., 1995; White et al., 1994), and postdates the
344 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 three-fold 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 et al., 1979; Clutton-Brock, 1977; Dunbar, 2004; Foley, 1999; Plavcan et al., 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 pre- condition 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-

368 male coalitions within multi-male groups in which males and females maintain stable mating
369 relationships greatly enhance social complexity, they should not precede increases in cognitive
370 abilities either.

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

381 Cognitive abilities are broadly indicated by overall brain size and/or encephalization (brain
382 size relative to body size) (Falk, 1987; Holloway, 1968, 1996; Martin, 1983). Evidence of
383 significant brain expansion appears with earliest *Homo*, with the advent of regular meat eating
384 and apparent increase in dietary quality. Improved dietary quality may have reduced constraints
385 on brain size (Aiello & Wheeler, 1995), facilitating increases in brain size and intelligence. Early
386 Pleistocene *H. erectus* (*Homo ergaster*) was characterized by brain sizes of 600-1057 cc (Lee &
387 Wolpoff, 2003), as compared with 343-560 in *Australopithecus* sp. (Brown et al., 1993; Conroy
388 et al., 1998; Falk, 1987; Holloway, 1996; Kimbel et al., 1994) and 510-740 in *H. habilis* (*sensu*
389 *lato*; Wood, 1992) (Figure 1) (Falk, 1987). Body size also increased with *H. erectus*, with
390 individuals increasing in stature from 3.5 to 5 to roughly 5 to 6 feet tall (McHenry, 1992), so the

391 encephalization increase is not as large as raw endocranial size numbers would indicate. Reliable
392 values for encephalization are difficult to compute because body mass estimates for isolated
393 crania cannot be accurately computed (see Elton et al., 2001). Still, there is evidence that
394 absolute, not relative, brain size is more closely related to intelligence (Deacon, 1997a).
395 Regardless, throughout the Pleistocene, brain size increased steadily over time until 50 kya (Lee
396 & Wolpoff, 2003) (see Figure 1.).

397 Figure 1 Here

398 **3.1. Ecological dominance**

399 Although difficult to quantify, the fossil record indicates that significant increases in
400 ecological dominance roughly coincided with the appearance of *Homo erectus*, 1.8 mya (Figure
401 1.). The hypertrophied dentognathic structures typical of australopithecines became greatly
402 reduced, with jaws, teeth and muscles of mastication decreasing in size. These changes indicate a
403 shift to a higher quality diet that required less oral processing. A further indication of
404 improvement in dietary quality is seen in the apparent increased dependence on meat from large
405 mammals in the diet around this time (Walker et al., 1982), whether hunted or scavenged (review
406 in Klein, 1999). Tools were regularly used to process meat and plant foods (Keeley, 1977; Klein,
407 1999). Although we do not know the antiquity of the dependence on stone or other types of tools,
408 tool use appears more systematic and ubiquitous at this time period than ever before (Foley &
409 Lahr, 1997). Use of tools would also have afforded greater protection from predators and
410 carnivorous competitors, although the antiquity of tool use for defense is unknown.

411 Projectile weapons may be of particular importance for dealing with conspecifics
412 (Bingham, 1999; Dunsworth et al., 2003) as well as other species (Calvin, 1983). Evidence that
413 humans have special cognitive facilities for tracking and dodging incoming projectiles (Watson

414 & Kimura, 1991) in addition to the mental aptitudes necessary for aiming projectiles at moving
415 targets suggests that hunting is unlikely to have been the sole selective pressure responsible for
416 the evolution of throwing skills. Chimpanzees throw objects at conspecifics, but never do so
417 while hunting (Goodall 1986). It may also be that by 1.5 mya, hominins were controlling and
418 using fire for cooking or protection (Bellomo, 1994; Brain, 1993; Gowlett et al., 1981; Rowlett,
419 2000; Wrangham et al., 1999), although evidence for controlled fire prior to about 500 kya has
420 been debated (Isaac, 1982, 1984; James, 1989).

421 Another indicator of increased ecological dominance is that by just under 1 mya (de Vos et
422 al., 1994; Pope, 1995), but possibly by 1.8 mya (Swisher et al., 1994), hominins are found in
423 Java, and by 1.7 mya are found in Georgia (Gabunia et al., 2000), as well as persisting in east
424 and south Africa. While some of this dramatic expansion in geographic range may be attributable
425 to ecological stress as a consequence of increased carnivory (Shipman & Walker, 1989), the
426 extent of the expansion must have involved overall population expansion resulting from
427 improved fertility and/or decreased mortality. This population expansion also reflects the ability
428 of hominins to contend with a wide variety of habitats, ecological circumstances, and resources
429 (see also Potts, 1998). Clearly, hominins experienced a significant increase in ecological
430 dominance during the beginning of the Pleistocene.

431 With the increase in ecological dominance accompanying the origin of *Homo erectus*, there
432 was some brain size increase. Brain size continued to increase after this time, as did ecological
433 dominance. Human problem-solving abilities that may have evolved primarily for negotiation of
434 intraspecific interactions could be applied to solving ecological and foraging problems, so the
435 EDSC model would predict a reciprocal and mutually reinforcing relationship between cognition
436 and ecological dominance. Ecological dominance increases result in increasing social pressures –

437 due to reduced mortality and population expansion – that select for enhanced cognitive abilities,
438 which in turn allowed hominins to become even more ecologically dominant, and so forth.

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

451 Similarly, over this time, hominins had expanded into a variety of habitats and regions.
452 Local resources and ecological challenges would have varied across the species' range. Some
453 regions have much colder and more variable climates, some hotter and drier, some are more
454 seasonal (see Potts, 1998). If ecological pressures posed the strongest selection on intelligence,
455 we would expect the most climatically extreme or variable environments to be the loci of
456 increases in cognitive abilities. There is no substantive geographic variation in brain size
457 apparent in hominins, however, nor any obvious association between climate and brain size. In
458 addition, cultural and behavioral innovations, in particular the origin of the Acheulean industry
459 and the creative explosion accompanying the Late Stone Age and Upper Paleolithic periods,

460 appeared first in Africa, most of which would have had relatively stable, rich environments. In
461 general, richer environments where ecological dominance would have been highest experienced
462 the greatest changes in cultural innovation, consistent with the EDSC model. In addition, the
463 EDSC model would predict that populations in regions with high ecological dominance would
464 increase, with population expansion and gene flow moving outwards. This is the pattern seen
465 with the origin of *Homo*, and with the appearance and spread of anatomically modern *Homo*
466 *sapiens* between 100 and 50 kya. If environmental stress were the strongest selective factor, the
467 opposite pattern of population expansion and gene flow should have occurred. It is certainly
468 possible that populations could have expanded without special increases in intelligence;
469 however, the EDSC model would not predict greater increases in intelligence in poor
470 environments than in richer ones.

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

483 biological and ecological resources as early humans. The human niche evidently can only be
484 occupied by one species.

485 **3.2. Sexual dimorphism**

486 The EDSC model predicts that changes in hominin social structure related to increasing
487 stability of male-female pair bonds and male coalitionary behavior should accompany brain size
488 increase, not precede it. The best indicator of these behaviors in the fossil record is sexual
489 dimorphism. Reduced body mass dimorphism is associated with both monogamy (Plavcan, 2000,
490 2001) and male coalitionary behavior (Pawłowski et al., 1998; Plavcan et al., 1995) in extant
491 primates. Although the large canine crown height dimorphism that characterizes all living and
492 fossil great apes had greatly diminished in *Australopithecus* (Ward et al., 2001), the reduced
493 body mass dimorphism typical of modern humans did not occur until sometime during the
494 evolution of *Homo erectus* (McHenry, 1992, 1994a; cf. Reno et al., 2003). The body mass
495 increase accompanying the origin of *H. erectus* suggests that female body size increased from
496 the australopithecine condition more than did male body size. Body mass dimorphism in early *H.*
497 *erectus* is difficult to estimate accurately, but disparities in size and robusticity among even early
498 *H. erectus* crania are less than in australopithecine species, signaling a reduction in body size
499 sexual dimorphism. By the early mid-Pleistocene body mass dimorphism was similar to that
500 found in modern humans (McHenry, 1994a; Ruff et al., 1997).

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

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

508 One approach to interpreting hominin social behavior evolution would be to assume that
509 the behavioral characteristics of the ancestor common to the australopithecine species and
510 humans were similar to those observed in modern chimpanzees or bonobos (de Waal & Lanting,
511 1997; Kano, 1992; Wrangham, 1999; Wrangham & Peterson, 1996; Zihlman et al., 1978). This is
512 a reasonable assumption in some respects. The encephalization quotient of chimpanzees,
513 bonobos, australopithecines, and presumably the common ancestor are very similar (McHenry,
514 1994a,b). However, sexual dimorphism in body weight is about 20% for chimpanzees and
515 bonobos (Goodall, 1986; Kano, 1992). Although bonobo males are not known to show consistent
516 coalitional aggression, male-on-male physical aggression is common and presumably a feature of
517 the ancestor common to chimpanzees and bonobos (Wrangham, 1999). In any case, the degree of
518 body mass dimorphism in chimpanzees and bonobos is considerably lower than that estimated
519 for *A. anamensis* (Ward et al., 2001) and *A. afarensis* (McHenry, 1992; but see Reno et al.,
520 2003), in which males were much larger than females. The contrast suggests that the
521 reproductive strategies of australopithecines may have differed in some respects from those of
522 male chimpanzees or bonobos, and thus the social patterns found with chimpanzees and bonobos
523 might not fully capture the social dynamics in australopithecines, or the selective pressures that
524 favored larger females in the transition to *Homo*. *Australopithecus* body mass dimorphism
525 suggests that these early hominins were polygynous, as significant mass dimorphism is not
526 associated with monogamy in any extant primate (Plavcan, 2001).

527 **3.3. Extended childhood**

528 One factor that should closely track increases in cognitive abilities is a prolongation of
529 childhood, which would provide more time for social learning prior to adulthood (Bogin, 1991,
530 1999; Joffe, 1997). The first hominin to have had relatively altricial infants was probably *Homo*
531 *erectus*, roughly 1.8 mya. Female pelvic dimensions are constrained by mechanical-locomotor as
532 well as thermoregulatory constraints, so birth canal size was not greatly expanded over
533 australopithecine levels (Begun & Walker, 1993), yet adult brain sizes were nearly doubled
534 (Figure 1). This means that in order to have appropriate neonatal proportions relative to the size
535 of the mother's pelvic inlet, infants must have been born at a relatively small size. The rapid rate
536 of brain growth seen in human infants, and presumably that of early *Homo*, suggests that in order
537 for infant heads to pass through the birth canal, hominin babies would have been relatively
538 altricial (Portman, 1941). To achieve their ultimate size, these rapid fetal rates of brain growth
539 continued after birth as in humans (Martin, 1983). It is notable that human brains achieve adult
540 size relatively early in life, suggesting a strong selective advantage for neural processing
541 hardware to be in place early in ontogeny, probably to facilitate learning throughout childhood
542 (Bjorklund & Pellegrini, 2002; Leigh, 2001; Flinn & Ward, 2004; but see Bogin, 1991). Even
543 early hominins do not appear to have attained adult brain size simply by prolonging growth
544 (Deacon, 1997a; Dean et al., 2001; Leigh 2001). Having more altricial infants would have
545 required more intensive mothering, and given the decrease in sexual dimorphism occurring at
546 this time, which may indicate pair-bonding, perhaps also by the father and/or alloparents.

547 Despite these ontogenetic shifts, delayed maturation does not appear to have occurred until
548 later in human evolution. Dental development is coupled to life history variables such as age at
549 sexual maturity, and so can be used to infer the timing of important life history stages. Early
550 *Homo erectus* appears to have had relatively rapid development, similar in rate to

551 *Australopithecus* and great apes, whereas that of modern humans is much slower (Dean et al.,
552 2001). Coincident with its apparent rapid rate of development, early *H. erectus* is predicted to
553 have lacked a human-like adolescent growth spurt, based on the fact that the single known
554 juvenile skeleton, KNM-WT 15000, appears to have had a more rapid rate of dental development
555 compared to that of his postcranial skeleton than modern humans (Smith, 1993). There are no
556 comprehensive data on rates of child development for hominins between 1.6 mya and 60 kya, but
557 the single neandertal specimen examined by Dean and colleagues (2001) was modern in its
558 developmental trajectory, indicating that a human-like extended childhood had occurred by this
559 time. A modern human pattern of dental development was present by 800 kya (Bermudez de
560 Castro et al., 1999), but this may not imply a similar rate (Dean et al., 2001). If it does, it might
561 be reasonable to hypothesize that the human adolescent growth spurt was already in place by this
562 time as well. Longevity appears to have gradually increased from *Australopithecus* to modern
563 humans with a higher proportion of individuals living to old age, although definitive evidence is
564 lacking. If ecological dominance reduced mortality from extrinsic causes, this would allow for
565 selection for delayed reproduction and extended life histories (Williams, 1957). Taking all the
566 data together, it appears that the evolution of altriciality may have begun with brain expansion,
567 but that delayed maturation and an adolescent growth spurt may have evolved later in human
568 evolution, perhaps as brain size increase continued throughout the Pleistocene.

569 In summary, the fossil and archeological evidence does not falsify the EDSC model, and
570 indeed supports it more strongly than models favoring subsistence behaviors or material
571 ecological factors as the driving force behind human intelligence. Many of the inferences we can
572 make about hominin behavior based on fossil and archeological data are fairly general; linking

573 this evidence with data from other sources such as comparative neurobiology can provide
574 additional, and in some cases stronger, tests.

575 **4. Design of the Human Brain and Mind**

576 **4.1. Brain**

577 The human brain is roughly two to three times larger than that of both our closest relatives
578 and the earliest fossil hominins, and comes at a cost of 20% of our metabolic resources
579 (Armstrong, 1990). Given this, it is unlikely that the human brain would have evolved without an
580 extraordinary functional payoff (Dunbar, 1998). But the differences between human and non-
581 human brains are not in size and calorie consumption alone. In addition to the much more
582 complex patterns of cerebral convolutions (Zilles et al., 1988), there are many unusual and
583 unique aspects of the human brain. For example, humans have relatively dense connections
584 between those parts of the brain that are involved with emotion and higher cognitive skills, and
585 at least one of these brain regions, the anterior cingulate cortex (ACC; area 24 in Figure 2),
586 contains one type of spindle cell found only in large hominoids, and these are double the
587 frequency in humans than in great apes (Nimchinsky et al., 1999). These changes and changes in
588 the extent of interconnections and possible reorganization of some areas of the prefrontal cortex
589 appear to provide the neurobiological bases for many of the human abilities predicted by the
590 EDSC model, including self-awareness, theory of mind (TOM), and social empathy (e.g.,
591 Adolphs, 2003; Siegel & Varley, 2002; Tulving, 2002). More precisely, the EDSC model
592 predicts that the greatest changes in human neurobiology and cognition involve those areas of the
593 brain associated with solving social problems. In the following sections, we highlight some of
594 the potential evolutionary changes in the corresponding brain systems.

595 Figure 2 Here

596 4.1.1 *Expansion of Prefrontal Cortex*

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

607 Nonetheless, modest proportional expansion, along with organizational changes (next
608 section), and the increase in absolute size of the human prefrontal cortex is consistent with
609 important evolutionary changes. Increases in absolute size result in increases in the degree of
610 interconnections among these regions and with other regions of the brain (Hofman, 2001;
611 Holloway, 1968). Basically, as absolute volume increases, the degree of interconnections among
612 neurons (i.e., axons, white matter) increases much more rapidly than does the increase in the
613 absolute number of neurons (i.e., cell bodies, grey matter) (Zhang & Sejnowski, 2000). The
614 human neocortex is thus less densely packed per volume with neurons, but much more highly
615 interconnected (Miller & Cohen, 2001), which suggests that humans may have a greater ability
616 to integrate information across modalities than other primates (Hofman, 2001; Holloway, 1968).
617 This is an important evolutionary change that would seem necessary to support the domain
618 general cognitive competencies, such as working memory (see below), needed to construct

619 mental simulations of social dynamics and to mentally rehearse behavioral responses to variation
620 in these dynamics (Geary, 2005). These simulations are an important feature of the ‘scenario
621 building’ aspect of social competition and the EDSC model (Alexander, 1989), a point that we
622 will elaborate in the *Mind* section (4.2).

623 *4.1.2 Reorganization of the Anterior Cingulate Cortex and Prefrontal Cortex*

624 In addition to enhanced neural interconnections, the human prefrontal cortex has greater
625 gyrification than that of great apes; specifically, there are more folds and thus more surface area
626 in this part of the neocortex (Rilling & Insel, 1999; Zilles et al., 1988). The expanded surface
627 area creates the potential for greater modularity and differentiation of functions within more
628 specific areas of the prefrontal cortex, and the potential for the evolution of species-specific
629 specializations in these regions (Deacon, 1990; Preuss, 2001). With regard to the predictions of
630 the EDSC model, there is evidence for evolutionary change in prefrontal regions that support
631 competencies described in Table 1 and predicted by the model, such as self awareness (right
632 prefrontal cortex: Tulving 2002), theory of mind (ventromedial region, area 11 in Figure 2:
633 Baron-Cohen, 2000), and attachment (Bartels & Zeki, 2004). We focus on only a few of these
634 regions to illustrate how research in cognitive neuroscience can be used to test predictions of the
635 EDSC model.

636 *4.1.2.1 Anterior cingulate cortex.*

637 The human ACC appears to have undergone important evolutionary reorganization and
638 changes in absolute size (Preuss & Kaas, 1999). The ACC is larger in primates than in other
639 mammals and, as noted earlier, Nimchinsky et al. (1999) found a form of neuron that is only
640 found in the ACC of great apes and humans. These cells appear to be involved in integrating the
641 ACC with the prefrontal cortex and with other brain regions (Allman et al., 2001). Functionally,

642 the ACC is involved in various forms of social cognition, and appears to be involved in the
643 integration of activity in regions of the prefrontal cortex with activity in brain regions such as the
644 amygdala that respond to emotion-laden and social information (Bartels & Zeki, 2004; Damasio,
645 2003; Nimchinsky et al., 1999; Taketoshi & Nishijo, 2000). The ACC is also involved in
646 attentional control and shifting of attention when non-routine information is encountered (Cohen
647 & Miller, 2001), and is thus important for detecting variation in social and other conditions.

648 4.1.2.2 Prefrontal cortex.

649 There is mounting evidence suggesting the human prefrontal cortex has undergone
650 substantive evolutionary reorganization. Semendeferi et al. (1998) found that for humans, area
651 13 – which appears to be a subdivision of area 11 (Figure 2) – is about one-half the size expected
652 based on overall brain size. They speculated that area 13 is comparatively small because adjacent
653 areas, specifically other regions of area 11 and regions of area 47 may be composed of a large
654 number of specialized subdivisions, each of which would process specific but related forms of
655 information, most likely social information. Using endocasts, Holloway and de la Coste-
656 Lareymondie (1982; Holloway, 1996) found evidence for a very specific hemispheric asymmetry
657 in *Homo erectus* and modern humans. The left occipital area (e.g., areas 17 and 18 in Figure 2) is
658 smaller and the left parietal area and the right frontal cortex are larger than the corresponding
659 regions in the opposite hemisphere. Zilles and colleagues (1996) confirmed this pattern for
660 human right-handers, noting that the dorsolateral prefrontal cortex (area 46) and the frontal pole
661 (area 10) were larger in the right than the left hemisphere, but found no such asymmetry in
662 chimpanzees. The size of the frontal pole is especially large in the right hemisphere, and is
663 estimated to be composed of nearly three times as many neurons as the corresponding area in
664 great apes (Semendeferi et al., 2001).

665 The disproportionate expansion of the right prefrontal cortex in general and the frontal pole
666 in particular, as well as the potential reorganization of area 11, are relevant to the EDSC model.
667 These areas appear to be involved in self awareness, social problem solving, the ability to recall
668 personal experiences, and the ability to mentally project oneself into the future (Tulving, 2002).
669 Although projecting oneself into the future might facilitate hunting and anticipation of seasonal
670 climatic change, this ability is heavily integrated with a sense of self. The latter is not needed for
671 hunting or coping with climatic change, but would be essential in a social world in which
672 competitors have a theory of mind, that is, an ability to make inferences about others' thoughts,
673 feelings, intentions, and likely future behavior. In other words, a sense of self may have co-
674 evolved with theory of mind in that it enables people to understand which aspects of their
675 behavior or personality other people are focusing on in their competitive interactions. As
676 Alexander stated, the human brain – areas of the right prefrontal cortex – has evolved to allow us
677 to "...see ourselves as others see us so that we may cause competitive others to see us as we wish
678 them to" (Alexander 1990a: 7). Other regions of the prefrontal cortex also appear to be engaged
679 in social cognition. For instance, recent brain imaging studies suggest that areas 32 and 9 (Figure
680 2) are particularly active in tasks that require people to mentally simulate the behavior of other
681 people or to simulate future social or other scenarios (Gallagher & Frith, 2003). These
682 simulations correspond to Alexander's (1989) scenario building.

683 **4.2. Mind**

684 Cognition is composed of the mechanisms that allow organisms to attend to, process, store
685 in memory, and retrieve from memory information patterns that have tended to covary with
686 survival and reproduction during the species' evolutionary history. Some of these information
687 patterns will vary across generations and within lifetimes (Geary, 2005). Variation in turn creates

688 conditions that will favor the evolution of phenotypic plasticity, that is, mechanisms that are
689 modifiable in response to the type of information that can change during the organisms' lifetime.
690 For example, phenotypic plasticity can accommodate individual differences in significant
691 modular domains, such as facial recognition: There are inherently constrained mechanisms that
692 draw attention to and process the basic features of a human face and complementary plastic
693 mechanisms that enable recognition of individual faces. Other forms of plasticity have evolved to
694 cope with variation in more macro-level conditions (e.g., social discourse) and support the ability
695 to form conscious representations of past, present, and potential future states, specifically, to
696 form mental models of these states and then manipulate the models in ways that enable the
697 simulation of behavioral strategies to cope with variable conditions (Geary, 2005; Wheeler et al.,
698 1997). These forms of plasticity are needed to support Alexander's (1989) social scenario
699 building.

700 *4.2.1. Cognition*

701 *4.2.1.1. Scenario building.*

702 There are two basic classes of conscious, explicit knowledge, semantic and episodic
703 (Tulving, 1983). This knowledge is typically assessed using memory tests, and thus the systems
704 are referred to as semantic memory and episodic memory, respectively. Semantic memory refers
705 to the retrieval of decontextualized facts and information (e.g., *Homo erectus* appeared before *H.*
706 *sapiens*), and episodic memory refers to the retrieval of time-based, contextualized memories of
707 one's life history. A conscious representation of facts and decontextualized information is known
708 as noetic awareness, and a conscious time-based representation of the self and personal
709 experiences is auto-noetic awareness (Tulving, 2002; Wheeler et al., 1997). The latter is the
710 ability to consciously consider the self across time, that is, to recall past personal experiences,

711 relate these experiences to current situations, and project oneself into the future. As argued by
712 Levine (1999, p. 200), auto-noetic awareness includes the ability to “cast oneself as a player in
713 scenarios emerging from various choices available at any given moment ... this capacity
714 facilitates the self-regulation of behavior necessary for the achievement of personally-relevant
715 goals.” These scenarios can be understood as a form of mental model (Johnson-Laird, 1983) in
716 which not only is the self the primary actor in the situation, but the individual is aware that the
717 self is the primary actor.

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

726 4.2.1.2. *Working memory.*

727 Auto-noetic mental models and scenario building are supported by working memory
728 systems. These entail a central executive function that controls attentional resources and
729 maintains cognitive representations in an active and conscious state (Baddeley, 1986). More
730 precisely, the central executive function and working memory are defined by the ability to use
731 attentional resources to amplify and maintain goal-relevant internal representations – such as a
732 pattern of neural activity associated with external information (e.g., a sentence uttered by
733 someone else) – and to inhibit irrelevant information patterns from entering conscious awareness

734 (Engle, 2002). The temporal dynamics of how these systems operate suggest that the evolved
735 function is to cope with rapid variation in external conditions and information patterns. The
736 details are beyond the scope of the current treatment, but this degree of variation is more
737 consistent with social dynamics than hunting, climatic change, or other ecological factors (see
738 Geary, 2005). In other words, there are many features of human cognition that are most readily
739 understandable in terms of selection for coping with considerable variation in social conditions
740 and dynamics within the lifespan, in keeping with predictions of the EDSC model. Still,
741 arguments that the working memory system is designed to cope with variation in ecological
742 conditions, such as those generated during hunting, cannot be ruled out. Cognitive
743 anthropological research that focuses on the demands of hunting will be needed before more
744 definitive conclusions can be drawn.

745 *4.2.2. Brain Systems*

746 The prefrontal cortex and the ACC are of particular interest because of above noted
747 changes in these regions during human evolution, and because these brain regions are implicated
748 in the competencies that define working memory, executive functions, attentional control,
749 episodic memory, and self awareness; specifically those competencies listed in Table 1 as having
750 been uniquely elaborated during human evolution.

751 *4.2.2.1. Working memory.*

752 A consensus is now emerging that areas of the dorsolateral region of the prefrontal cortex,
753 such as areas 9 and 46 (Figure 2), are involved in the executive functions of working memory, as
754 is the ACC (area 24; Kane & Engle, 2002; Miller & Cohen, 2001). These regions are particularly
755 important for active goal maintenance, and the inhibition of competing and goal-irrelevant
756 distractions. These ends appear to be achieved by biasing, perhaps through attentional

757 amplification (Dehaene & Naccache, 2001), the activation of posterior and subcortical pathways
758 that represent the information needed for goal achievement. However, the dorsolateral areas and
759 the ACC only appear to be heavily involved in coping with novelty and variability in current
760 conditions. Under these conditions, the ACC appears to automatically direct attention to the
761 novel or variable information which results in the explicit and conscious representation of this
762 information in working memory. Our point is that auto-noetic mental models and scenario
763 building are dependent on this form of brain and cognitive system, especially as related to the
764 ability to mentally generate scenarios that involve potential *change* in social conditions and to
765 plan social strategy.

766 4.2.2.2. *Self-awareness.*

767 The brain and cognitive systems that support episodic memory and awareness of the self
768 appear to differ from those that support working memory and executive functions (Tulving,
769 2002). Of particular importance are regions of the right prefrontal cortex (e.g., area 10, Figure 2).
770 Traumatic injuries to these areas result in an array of deficits that differ from the trauma-related
771 deficits in executive functions (Levine, 1999; Tulving, 1985). One patient, KC, who suffered
772 severe injuries to these brain regions as a result of a motorcycle accident, performed normally on
773 IQ tests and on tests of executive functions, but “cannot recollect a single episode of his life from
774 either before or after” the injury (Levine, 1999, p. 207). Nor can KC project himself into the
775 future, that is, when asked to imagine his activities for the following day he draws a blank
776 (Tulving, 1985, 2002). He has since learned facts about himself (e.g., his former job), but is
777 unable to place these facts in the context of memories of his life.

778 The associated deficits also include difficulties in self-regulation and with social activities
779 in general. These patients find it difficult to inhibit previously learned responses, and thus have

780 considerable difficulty on tasks that involve change from one type of response to another. In
781 effect, they cannot problem solve when the task involves novelty, and cannot make effective
782 decisions that involve comparing current choices to future outcomes. Social activities are, of
783 course, very complex and entail subtle and almost constant and concurrent change in multiple
784 sources of information, including facial expression, vocal intonation, body language, and so
785 forth. In addition, social activities are intimately related to one's sense of self. In social
786 situations, an individual with right prefrontal damage had "difficulty knowing how to behave
787 around family members and friends, and had to be taught socially acceptable behaviour" (Levine
788 et al., 1998, p. 1956). The patients recognize social deficits in other people, but have difficulty
789 understanding these same deficits in themselves.

790 4.2.3. *Conscious Psychological Systems*

791 How is the evolution of executive functions, explicit and conscious awareness of the self,
792 mental time travel, and the ability to engage in controlled problem solving related to the EDSC
793 model? The theme that ties all of these together with the proposals of many other scientists (e.g.,
794 Humphrey, 1976; Picton *et al.*, 2002) is the auto-noetic mental model, which can be understood
795 as the core of Alexander's (1989) scenario building. With these models, the individual creates a
796 self-centered mental simulation of the "perfect world" (Flinn & Bluedorn, 2002; Geary, 1998,
797 2005): one in which the individual is able to organize and control social (e.g., social dynamics),
798 ecological (e.g., access to food), and physical (e.g., shelter) resources in ways that would have
799 enhanced survival or reproductive options of the individual or his or her kin during human
800 evolution. The mental simulation of a perfect world requires the ability to decouple modular
801 systems from engagement of the actual world and use these systems to either recreate a previous
802 episode or create a more abstracted and decontextualized representation of social dynamics or

803 other aspects of the world. The mental reconstitution of a past episode allows the individual to
804 consciously and explicitly evaluate the dynamics of the episode (e.g., “What did he mean when
805 he said ...”), and to plan and rehearse strategies for anticipated future episodes that involve the
806 same person or theme. Mental simulations can also involve abstractions that are common
807 features or themes across episodes.

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

825 Controlled attention, working memory and other executive functions are necessary
826 components of these conscious simulations. The combination results in the ability to generate an
827 explicit simulation and maintain it in an active and changeable state. Problem solving involves
828 successive and goal related changes in this state that, among other things, allow the individual to
829 generate and simulate strategies to reduce the distance between one's perfect world and one's
830 current circumstances. Simulated behavioral strategies are in effect problem solving exercises
831 focused on ways to gain access to and control social relationships and dynamics and the forms of
832 resources that enhance survival or reproductive options in the current ecology. Emotional
833 systems are necessarily an integral feature of these simulations. If the simulations are built from
834 episodic memories and corresponding abstract representations of common features across
835 episodes, then recreation of episodes should include associated emotional responses (Damasio et
836 al., 2000). Imagined success at achieving a social goal or acquiring riches should result in an
837 emotional response that is similar to the response that would result from actually achieving
838 success in these endeavors. As in navigating life in the actual world, emotional responses that
839 result during simulated activities provide feedback as to the value of the goal and the potential
840 outcomes of control-related behavioral strategies and the counter strategies of others.

841 In summary, empirical and theoretical advances in the cognitive neurosciences are not
842 conclusive, but they are consistent with several key predictions of the EDSC model. Much of the
843 prefrontal cortex is involved in various forms of social cognition, and in the ability to control
844 attention and manipulate information in working memory. These different features of the
845 prefrontal cortex and areas in which it is integrated, such as the ACC, can be combined in a way
846 that allows people to mentally simulate complex social scenarios and generate an array of
847 strategies to cope with these scenarios. When these competencies are fused with a sense of self,

848 the result is an evolutionarily unique neurocognitive system that appears to be well adapted to
849 deal with the forms of social cooperation and competition described by Alexander (1989, 1990a),
850 and others (Dunbar, 2003; Humphrey, 1976). In short, these are the brain and cognitive systems
851 that are needed to support Alexander's (1989) social scenario building and the systems that
852 would have evolved if scenario building were one of the core traits that facilitated social
853 competition in a co-evolutionary arms race.

854 **5. Concluding remarks**

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

865 The model is supported by a unique combination of co-evolved characteristics and their
866 temporal sequencing. (1) Humans have an unusual pattern of speciation. The extinction of all
867 intermediate stages (e.g. gracile Australopithecines and *Homo erectus*) and non-descendent
868 branch species (e.g. robust Australopithecines), and the absence of a pattern of adaptive
869 radiation, suggest that within-taxon competition was highly significant. (2) Humans have an
870 unusual life history pattern, with extended childhood and post-reproductive stages (Bogin, 1997;

871 Leigh, 2001; Mace, 2000). Childhood may be necessary for complex development and
872 experience to acquire social skills (Bjorklund & Pellegrini, 2002; Flinn & Ward, 2004; Joffe,
873 1997); a post-reproductive stage may be useful for caretaking of dependent offspring,
874 grandchildren, and other relatives (Alexander 1979; Hawkes, 2003; Hawkes *et al.*, 1998). (3)
875 Humans have a unique mating system, with extensive male parental care and long term pair-
876 bonding in a context of multi-male/multi-female communities (cf. Flinn & Low, 1986; Geary,
877 2000). Humans have a unique sexuality, with concealed ovulation, menopause, and other
878 characteristics that may facilitate aspects of the unique human mating/parenting system (above).
879 Humans have reduced sexual dimorphism of body size and other traits (e.g., canines).
880 Comparative analyses of hominid fossils and primates suggest that coalitions and fighting
881 techniques other than biting were important during human evolution. (4) The human neocortex is
882 apparently larger than that of other primates in precisely those areas that support social
883 competencies that are unique to humans (Rilling & Insel, 1999), such as theory of mind
884 (Adolphs, 2003; Baron-Cohen, 1999), language (Pinker, 1994), a sense of self (Wheeler et al.,
885 1997), and the ability to mentally simulate social scenarios (Gallagher & Frith, 2003). (5)
886 Humans have unusual aptitudes for use of projectile weapons (throwing and dodging); these are
887 involved in male-male competition – a form of social competition (Geary, 1998) – and hunting
888 and predator avoidance vis-à-vis ecological dominance. (6) Humans have unique aptitudes for
889 communication, including language and specific linguistic abilities. (7) Humans have unique
890 aptitudes for developing large, complex social groups based on kinship and reciprocity. Humans
891 converge with those species that have competition among socially complex coalitions, for
892 example chimpanzees (e.g. Harcourt, 1988; Mitani & Watts, 2001; Watts & Mitani, 2001;
893 Wrangham, 1999) and dolphins (e.g. Mann & Sargeant, 2003; Smolker, 2000). The factor that

894 ties all of the above components – one might consider them “evolutionary clues” – especially the
895 rapid changes associated with the emergence and evolution of *Homo*, is social competition and
896 cooperation in the context of increasing ecological dominance.

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

904 The use of mental simulations and abstract mental models are necessary for the complex
905 analysis of social relationships and networks (Gallagher & Frith, 2003; Geary, 2005). The
906 diversity of human culture, the extraordinary range of information that we use in comparison
907 with other species, results from the social dynamics of our complex coalitions (Flinn, 2004).
908 Alexander’s model posits that we evolved our aptitudes and predilections for art, dance, theatre,
909 friendship, technology, and so forth, primarily as methods for contending with the social world.
910 Art, dance, and theatre are likely to be supported by the same brain and cognitive systems that
911 enable humans to form mental simulations of social and other scenarios. The advantages such
912 abilities offered for dealing with the ecological demands of drought, food shortages, snow, and
913 the like, are posited to be secondary.

914 The foci and products of human mental processing are unusual. Whereas most species have
915 evolved cognitive specializations that appear designed to solve task-specific ecological problems
916 and some specialized social problems like offspring recognition and optimal mate choice, the

917 human mind possesses uniquely sophisticated social-problem-solving abilities, including theory
 918 of mind, language, consciousness, romantic love, and empathy. The neurological mechanisms for
 919 these abilities are beginning to be identified in detail (Adolphs, 2003; Bartels & Zeki, 2004;
 920 Seigal & Varley, 2002). These social capabilities, moreover, seem to occupy the majority of
 921 human thoughts. The information pool developed and socially transmitted by human minds, what
 922 might be termed “culture”, has resulted in a new domain of competition and adaptation.

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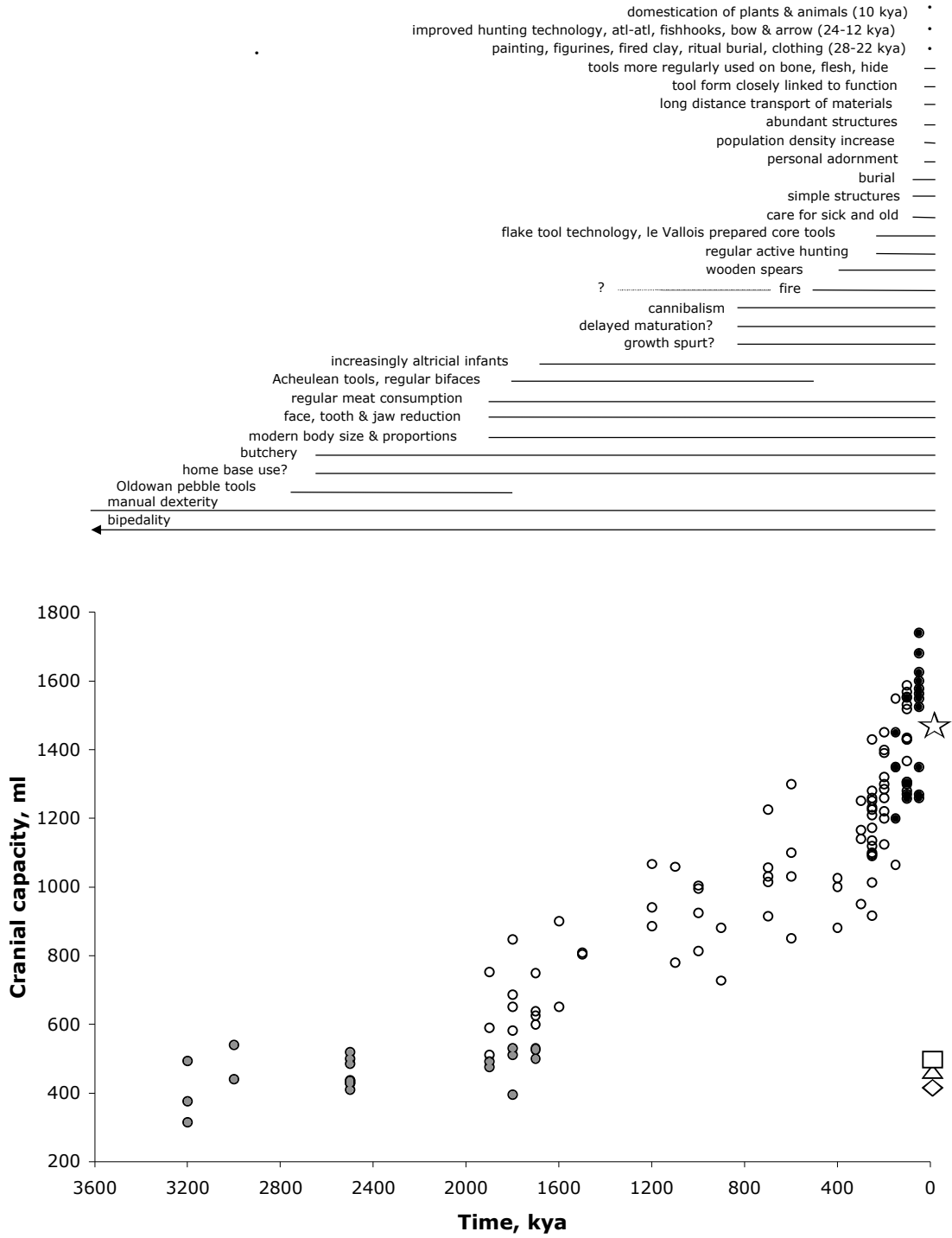
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1398 Table 1: Attributes of humans that may provide clues to our evolution (traits that are especially
 1399 relevant to testing the EDSC model are marked in **bold**; note that most of these traits are
 1400 identified and discussed in Alexander, 1979, 1987, 1989; Daly & Wilson, 1983; Low, 2000).

- 1401
- 1402 I. Unusual speciation and extinction pattern
- 1403 **A. No remaining ancestral species or side-branches; absence of adaptive radiation in *Homo***
 1404 (White, 2003) despite rapid evolutionary change.
- 1405
- 1406 II. Rapid reduction of sexual dimorphisms
- 1407 **A. Canine SD reduced early (*Australopithecus*: Ward *et al.*, 2001)**
 1408 **B. Body size SD reduced later (*Homo erectus*)**
- 1409
- 1410 III. Unusual dentition
- 1411 A. Reduced canine size
- 1412 B. Small incisors
- 1413 C. Thick enamel on teeth
- 1414 D. Overall dental reduction
- 1415 E. Orthognathic face
- 1416 F. Protruding nose
- 1417
- 1418 IV. Dietary niche
- 1419 A. Omnivorous catholic diet
- 1420 B. Variable environments
- 1421 C. Meat eating
- 1422 D. Hunting
- 1423 E. Extractive foraging of tubers, nuts, and other high quality foods
- 1424 F. An array of corresponding cognitive and brain specializations, including those that support
 1425 tool use (Hodges *et al.* 1999), and the development of folk biological knowledge (Atran,
 1426 1998)
- 1427
- 1428 V. Habitual bipedal locomotion
- 1429 A. Lumbar curve, pelvis, bicondylar angle, knees
- 1430 B. Foot, arch, no grasping big toe
- 1431 C. Loss of climbing abilities
- 1432
- 1433 VI. Unusual upper limbs
- 1434 A. Shortened, modified
- 1435 **B. Accurate and powerful throwing of projectiles, and dodging, especially in males (Watson**
 1436 **& Kimura, 1991; Cannell, 2002; Dunsworth *et al.*, 2003)**
- 1437 C. Fine manipulation with hands, digit proportions, innervation

- 1438
 1439 VII. Extraordinary mental capabilities
 1440 **A. Large brains, high metabolic cost**
 1441 B. Unique aspects of gene and protein expression, transcription in brain cells.
 1442 C. **Neuroanatomy**; expanded neocortex (Jerison 1973, pre-frontal cortex), class of large and
 1443 clustered spindle cells in anterior cingulate cortex (Nimchinsky *et al.*, 1999), possible
 1444 expansion of language-related neocortical areas (Rilling & Insel, 1999), expansion,
 1445 controlling for overall increase in brain size, and possible reorganization of some regions of
 1446 the prefrontal cortex (Semendeferi *et al.*, 1998, 2001) development of Broca's area, and other
 1447 unique brain features. Increased lateralization (Holloway & de la Coste-Lareymondie, 1982)
 1448 and increased gyrification (Zilles *et al.*, 1988, 1989).
 1449 **D. Consciousness and awareness of the self as a social being** (Tulving, 1985, 2002)
 1450 **E. Theory of mind** (Baron-Cohen, 1999; Leslie, 1987; Seigel & Varley, 2002), **and a**
 1451 **complimentary set of sociocognitive competencies** (Adolphs, 2003; see Geary, 2005, Geary
 1452 & Huffman, 2002 for a taxonomy)
 1453 **F. Foresight, planning, scenario-building, ability to mentally time travel** (Johnson-Laird,
 1454 1983; Tulving, 2002); **related to functioning of areas of the prefrontal cortex** (Gallagher
 1455 & Frith, 2003)
 1456 G. Complex psyche, integrated cognitive aptitudes, flexible and relatively open learning
 1457 **H. Social emotions, guilt, embarrassment, pride, restraint and concealment** (Damasio, 2003;
 1458 Damasio *et al.*, 2000)
 1459 I. Humor (Alexander, 1987)
 1460 **J. Complex deception and deception-detection**
 1461 **K. Multiple order reasoning**
 1462 L. Imagination, fantasy
 1463 **M. Creativity**
 1464 N. Senses (vision, hearing) similar to other hominoids, some olfactory reduction
 1465 O. Complex facial expressions
 1466 P. Specific psycho-pathologies, e.g., autism (Baron-Cohen, 1999)
 1467
 1468 VIII. Language, specific linguistic abilities
 1469 **A. Precocious language acquisition** (Brown, 1973)
 1470 B. Open syntax, infinite combinations and creativity (Nowak *et al.*, 2001)
 1471
 1472 IX. Culture
 1473 A. Traditions, cumulative information building (Coe 2003)
 1474 B. Technology stemming from evolution of tool use and ecological dominance
 1475 C. Social learning, complex imitation, emulation, teaching. The working memory and attentional
 1476 control systems that support scenario building can also be used for the teaching and learning
 1477 of culturally specific academic abilities, such as reading and writing (Geary, 2002)
 1478
 1479 X. Complex social groups
 1480 **A. male kin- and non-kin coalitions** (e.g., Boehm 1999; Chagnon, 1968)
 1481 B. Complex systems of reciprocity (indirect and direct; e.g., Alexander 1987)
 1482 C. Friendships (Hartup & Stevens, 1997)
 1483 D. Laws
 1484 E. Ethics and moral systems (Alexander 1987; Gintis 2001)
 1485 **F. Pervasive intra- and inter-group conflict, raiding, war** (Alexander, 1971; Daly & Wilson,
 1486 1988; LeBlanc, 2003; Manson & Wrangham, 1991; Wrangham, 1991; Wrangham &
 1487 Peterson, 1996)
 1488 G. Complex social play, team sports (Lever, 1978; Wagner *et al.*, 2002)

- 1489
- 1490 XI. Unusual patterns of kinship, parenting, and grandparenting
- 1491 A. Extensive kin networks
- 1492 **B. Male philopatry** (Murdock, 1949; Seielstad *et al.*, 1998; Wells *et al.*, 2001)
- 1493 C. **Extensive parental care, including protection by males** (Geary, 2000)
- 1494 D. Complex bonding, attachment, Grief
- 1495 E. Long term mating relationships, pair bonds
- 1496 F. Variable mating systems
- 1497 G. Parental and kin influence on mate choice
- 1498 H. Age and sex based division of labor, activity differences
- 1499
- 1500 XII. Unusual life history
- 1501 **A. Altricial young**
- 1502 B. Rapid early brain growth, but continued throughout childhood (Deacon, 1997a, 1997b)
- 1503 C. Unusual patterning of growth and development, e.g., pubertal growth spurt (Bogin, 1999)
- 1504 **D. Menopause**
- 1505 **E. Precocial communication skills**
- 1506 **F. Extended 'childhood'** (Bogin, 1999; Low, 2000)
- 1507 G. Adrenarche (Herdt & McClintock, 2000)
- 1508
- 1509 XIII. Unusual sexual characteristics
- 1510 **A. Concealed ovulation** (Alexander & Noonan, 1979; Strassmann, 1981)
- 1511 B. Post-reproductive sexual behavior
- 1512 C. Frontal copulation, kissing, foreplay
- 1513 D. Female orgasm
- 1514 E. Permanently enlarged breasts
- 1515 F. Large penis, lack of penis bone (baculum)
- 1516 G. Moderate testes
- 1517 H. Hymen
- 1518
- 1519 XIV. Other unusual physical characteristics
- 1520 A. Variation in skin, hair, facial appearance
- 1521 B. Melanin skin pigmentation
- 1522 C. Pale sclera
- 1523 D. Unusual importance of facial appearance for mate choice
- 1524 E. General hairlessness, but with sex-specific patterning, ever-growing hair on head
- 1525
- 1526 XV. Unusual demographic and population traits
- 1527 A. Wide geographic distribution, large population size, rapid potential population growth
- 1528 (Blurton-Jones *et al.*, 2002).



1530 Figure 2.

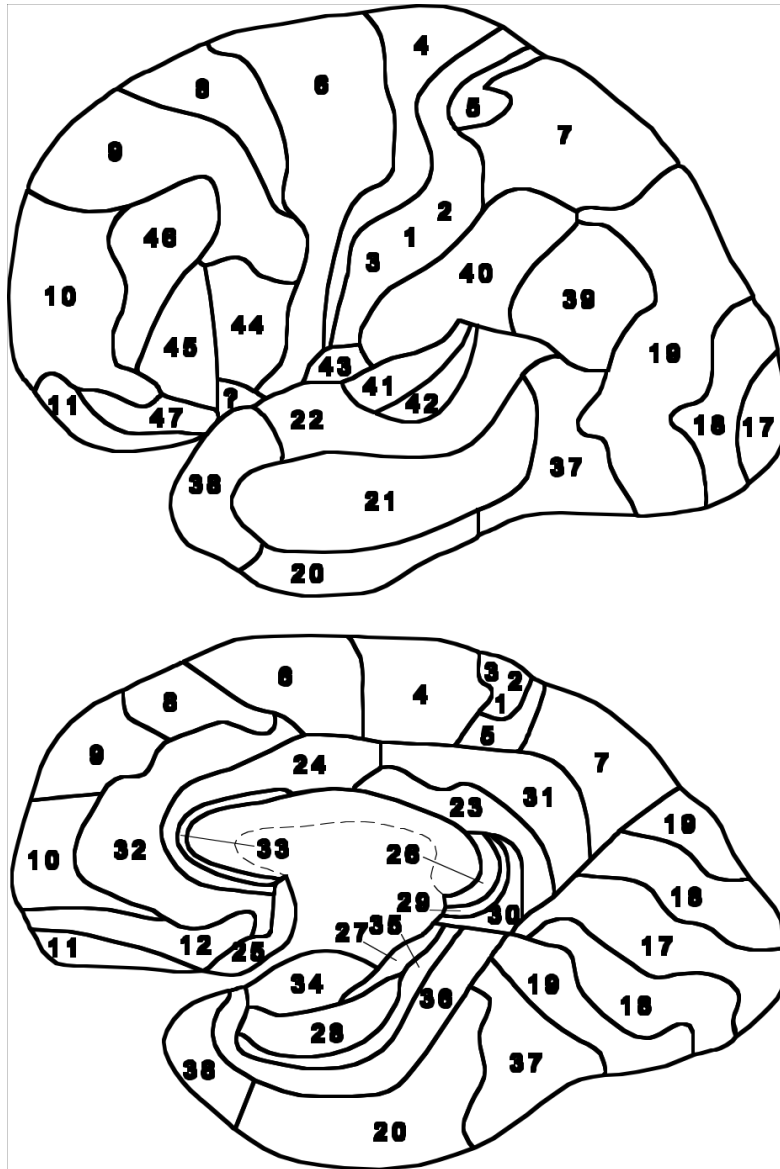


Figure Captions

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Figure 1. Cranial capacity and evidence of behavioral evolution over the past 3.4 million years of human evolution. Cranial capacities from Falk (1987), Kimbel et al. (1994), Holloway (1996) and Lee & Wolpoff (2003). Gray circles represent non-habiline *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 *Homo 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), Kimbel et al. (1994), Feibel et al. (1989), Wood & Collard (1999), White et al. (2003), and Lee & Wolpoff (2003). Paleontological and archeological indicators of behavior from Begun & Walker (1993), Smith (1993), Asfaw et al. (1999), Bermudez de Castro et al. (1999), Klein (1999), Ward et al. (2001), and Dean et al. (2001).

Figure 2. Maps of Brodmann's (1909) areas of the human neocortex. 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 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.