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*The origin of mind: Evolution of brain, cognition, and general intelligence*

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## Chapter 3

### Hominid Evolution and the Motivation to Control

My goals of for this chapter is to apply the principles of natural and sexual selection to questions related to brain and cognitive evolution in humans and our ancestors. In the first section, I focus on Hominid evolution – hominids are bipedal apes – and the rapid expansion of brain size with the emergence of Homo ergaster/erectus and H. sapiens (Ruff et al., 1997). In the second section, I provide an analysis and synthesis of the various theories regarding the selection pressures that drove this rapid increase in brain size, and outline the basic thesis of the book. Specifically, building on the work of Alexander (1989), Humphrey (1976) and others, it is proposed that the rapid expansion of brain size can be understood in terms of the emergence of ecological dominance, possibly with H. ergaster/erectus, and a resulting shift from a primacy of ecological selection pressures (e.g., food) to social selection pressures. I close the chapter with a motivation-to-control theory that provides a framework for integrating issues related to brain and cognitive evolution with basic motivational, affective, and psychological systems.

#### Hominid Evolution

##### Origins

Although much is known about many of the species comprising the genus Homo and the apparent predecessor genus Australopithecus, there is controversy with respect to the classification of these species (McHenry, 1994; B. Wood & Collard, 1999). The debates include whether variation in fossils presumed to represent a single species in fact represent two or more species, and the evolutionary relatedness of various species (Aiello, 1994; Aiello & Collard, 2001; White, 2003; B. Wood, 1992), debates fueled by the continual discovery of new fossils and potentially new hominid species (Asfaw et al., 1999; Haile-Selassie, 2001; Leakey et al., 2001; T. White et al., 2003; Zhu et al., 2001). There is, nonetheless, a general consensus with respect to major hominid species and their likely evolutionary relationships, as shown in Figure 3.1. The relations shown in the figure are simplified and do not include all species, but still capture the essential pattern of hominid evolution, at least as it is currently understood (B. Wood & Collard, 1999). Of course the ancestor common to modern humans and our closest living relatives, that is, chimpanzees (Pan troglodytes) and bonobos (Pan paniscus), existed before the emergence of these species. Genetic analyses and the fossil record suggest that this common ancestor existed between 5 and 6 MYA (e.g., Haile-Selassie, 2001; Horai, Hayasaka, Kondo, Tsugane, & Takahata, 1995).

Radiometric dating of sediments and other materials found with fossils allows for estimations of when the species represented in Figure 3.1 existed. The results of such studies are represented in Figure 3.2 and suggest that A. anamensis existed about 4.0 millions years ago (MYA) and A. afarensis from about 4.0 to 2.8 MYA (M. Leakey, Feibel, McDougall, & Walker, 1995; M. Leakey, Feibel, McDougall, Ward, & Walker, 1998; McHenry, 1994). It was long thought that A. africanus was the likely link between A. afarensis and the line that eventually led to the

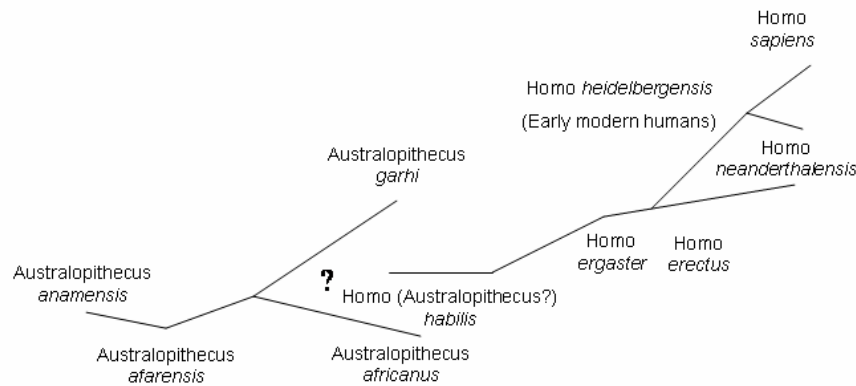


Figure 3.1: Simplified hominid family tree. The ? means that it is not known if the ancestor of *H. habilis* was *A. garhi* or *A. africanus*.

evolution of humans, but recent discovery of a contemporaneous species, *A. garhi*, makes this less certain (Asfaw et al., 1999). In any case, these species existed about 2.5 MYA, and *A. africanus* from about 3.0 to 2.3 MYA. The place of *H. habilis* in the evolutionary tree is also uncertain. In fact, this species has many features that are more similar to *Australopithecus* than to *Homo* (Dean, et al., 2001; B. Wood & Collard, 1999), but in any case it existed from about 2.5 to 1.5 MYA (Wood, 1992). The evolutionary relation of *H. ergaster* and *H. erectus* is debated, with the central issue being whether the associated fossils represent two distinct species or primitive and more advanced specimens of the same species, respectively. Recent evidence suggests that the fossils represent microevolutionary change in the same species, that is, earlier and later forms of the same evolving species (Asfaw et al., 2002).

Either way, *H. ergaster*/*H. erectus*, hereafter *H. erectus*, emerged in eastern Africa about 1.8 MYA and began to move into Asia and possibly parts of southern Europe (Gabunia et al., 2000; Stringer, 1992; Stringer, 1992). Evidence to date suggests that populations of *H. erectus* evolved into several species, including *H. neanderthalensis* and *H. sapiens* (McHenry, 1994). Although we must await more definitive results, the most recent common ancestor of *H. neanderthalensis* and *H. sapiens* may have existed more 500,000 years ago (Ovchinnikov et al., 2000; Pääbo, 1999), but this is debated (Wolpoff, Frayer, & Hunley, 2001). Genetic analyses suggest that modern humans evolved between 150,000 (Ke et al., 2001; R. Thomson, Pritchard, Shen, Oefner, & Feldman, 2000; Underhill et al., 2001) and roughly 50,000 years ago (Horai, Hayasaka, Kondo, Tsugane, & Takahata, 1995; Karafet et al., 1999). Early forms of the species (sometimes designated as *H. heidelbergensis*) appear to have emerged in eastern Africa, migrated into Asia, and later into Europe (Cavalli-Sforza, 1998; Semino et al., 2000; Stringer, 1992; see

also T. White et al., 2003), although an initial migration by means of a sea route from southern Africa to India and east Asia is also possible (Underhill et al., 2001).

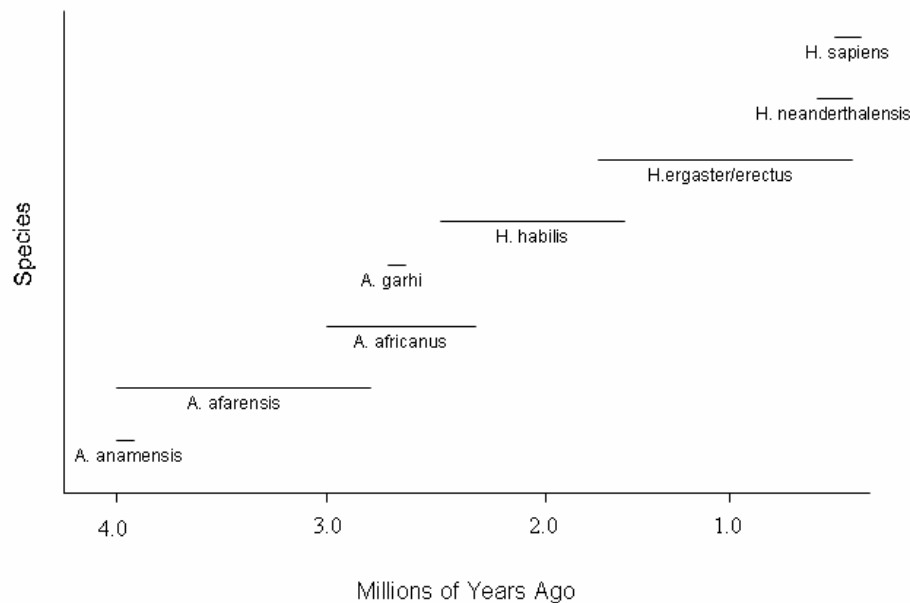


Figure 3.2: Estimated age of first appearance and extinction of various hominid species. There are only a limited number of fossils for *A. anamensis* and *A. garhi* and thus the age of first appearance and extinction are not currently known for these species.

Whatever the migration route, it is important to note that many of our predecessor species, such as *A. afarensis* and *H. erectus*, existed for hundreds of thousands of years (McHenry, 1994), suggesting that these species were well adapted to the ecologies in which they were situated. In fact, *H. erectus* may have survived in some parts of the world until about 26,000 years ago, and Neanderthals survived in portions of Europe until about 30,000 years ago (Stringer, 1992; Swisher et al., 1996). Fossils for both of these species have been found in the same geographical areas as fossils of early modern humans, although it cannot be stated with certainty whether these species had contact with early humans. Contact, however, is plausible. At least with respect to the relation between *H. erectus* and modern humans it is vigorously debated as to whether this contact resulted in interbreeding or aggressive replacement of *H. erectus* by early modern humans (e.g., Wolpoff, Hawks, & Caspari, 2000; Wolpoff et al., 2001). Genetic patterns for populations of modern humans are consistent with waves of migrations, within and between geographic regions, and suggest a combination of interbreeding and replacement (Templeton, 2002; Underhill et al., 2001), as discussed in a later section (Sexual Selection and Population Genetics section).

### Brain Evolution

My goal here is to provide an overview of gross changes in brain size over the past five million years of hominid evolution. Although it is almost certain that brain and cognitive

specializations occurred independent of changes in brain volume during hominid evolution (Holloway, 1968, 1996), the relation between size of the neocortex and performance on measures of general intelligence make it important to also consider evolutionary changes in brain volume (Rushton & Ankney, 1996; see also Gibson, Rumbaugh, & Beran, 2001). In the first section, I review research on changes in brain volume and potential changes in brain organization, and the second changes in the encephalization quotient (defined below).

### Brain Volume and Organization

A variety of techniques are available to estimate the brain volume of extinct hominids. One method involves reconstructing the fossilized cranium and then making a plaster cast of the inside of the cranium (e.g., Holloway, 1973a). These endocasts can be used to estimate cranial volume and thus brain volume and in some cases provide an impression of the architecture of the outer surface of the neocortex (e.g., Falk, 1983; Holloway & de la Coste-Lareymondie, 1982; Tobias, 1987). A representation of the outer surface of the left hemisphere of a human neocortex is shown in Figure 3.3. The gyri (folds) and sulci (valleys) leave impressions on the inner surface of the skull, impressions that can sometimes be recaptured in the endocast (for discussion see Holloway, 1996).

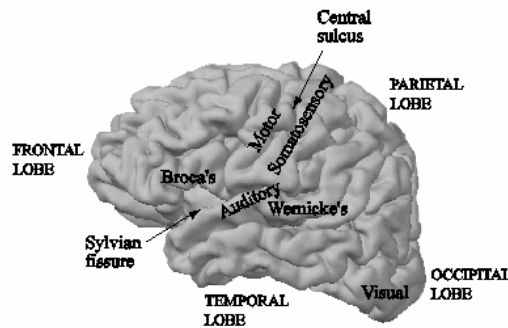


Figure 3.3: Outer surface of the left hemisphere of the neocortex of *H. sapiens*. From Words and rules: The ingredients of language (p. 244), by S. Pinker, 1999, New York: Basic Books. Copyright 1999 by Steven Pinker. Reprinted with permission.

The use of these and other methods has provided considerable information on the general pattern of evolutionary change in brain volume since and including *A. afarensis*. Figure 3.4 shows the mean values estimated from multiple sources for all species (Falk, Redmond, Guyer, Conroy, Recheis, Weber, & Seidler, 2000; Holloway, 1973a, 1973b; McHenry, 1994; Tobias, 1987; B. Wood & Collard, 1999), with the exception of *A. garhi* which is estimated from a single source (Asfaw et al., 1999). Although there is disagreement regarding the brain volume of some

individual species, the overall pattern is clear. The australopithecines (A. afarensis, A. africanus, and A. garhi) show a significantly but modestly larger brain volume than extant chimpanzees and thus presumably a larger brain volume than the ancestor common to australopithecines, chimpanzees, and humans (McHenry, 1994; Tobias, 1987). There also appears to have been further but still modest increases in brain volume from A. afarensis to A. africanus and A. garhi.

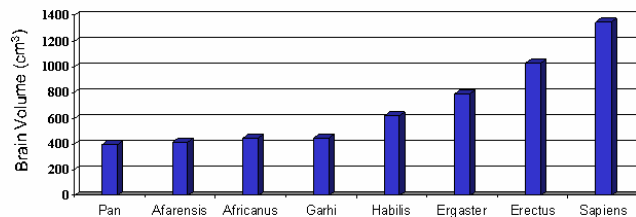


Figure 3.4: Estimated brain volume for chimpanzees (e.g., Pan troglodytes) and various species of hominid.

Inferences about the brain morphology of the outer portion of the neocortex can only be made with caution, but are nonetheless potentially instructive. Falk (1983) found that the brain morphology – inferred from endocast patterns – of a likely australopithecine skull was more similar to that of a chimpanzee and other great apes than to that of a human, in terms of gyri and sulci patterns. However, Holloway and Kimbel (1986) questioned this interpretation and suggested that the brain morphology associated with this skull was in fact more human like. In any event, one pattern that is not found in great apes but is consistently found in australopithecines and other hominids, including humans, is a difference in the shape of the posterior portions of the left hemisphere and anterior portions of the right hemisphere. The visual area of the left hemisphere is smaller than expected based on body and brain size (see next section), whereas portions of the left parietal area and right frontal area are larger than expected (Holloway & de la Coste-Lareymondie, 1982).

Further increases in brain volume and added changes in the morphology of the outer surface of the neocortex are evident in H. habilis (Falk, 1983; Tobias, 1987). Included among the potential changes in the neocortex of H. habilis are expansions, albeit modest (see Problem Solving and Human Evolution section of chapter 7), of the frontal and parietal lobes and extensive remodeling, specifically, evidence for more folding and thus more surface area of the frontal lobes relative to A. africanus. As an example, one area of the frontal lobe that is implicated in human speech and gesture, specifically, Broca's area, appeared to have been expanded and had an architecture (e.g., pattern of sulcal and gyral folds) similar to that of modern humans. The increase in the size of the parietal cortex is interesting as well (Holloway, 1996), because it is coincident with increasingly sophisticated tool use with and after the emergence of H. habilis (see Ecological Pressures section below), and because areas of the parietal cortex are engaged during tool use in modern humans (see Ecological Modules section of chapter 5), and are involved in some components of controlled attention as related to working

memory (see Cognitive and Brain Systems section of chapter 7). I discuss potential functional correlates of changes in the right frontal cortex, among other areas, in the Problem Solving and Human Evolution section of chapter 7.

As shown in Figure 3.4, further increases in brain volume, as well as morphology, are evident with the emergence of H. erectus and continuing to modern humans (McHenry, 1994; Ruff et al., 1997; B. Wood & Collard, 1999). The threefold increase in brain volume comparing A. afarensis to modern humans belies another important pattern, that is, relative stasis for very long periods of time. Although there was a modest increase in brain volume from A. afarensis to A. africanus and A. garhi, the changes evolved over the course of 1.5 million years. In other words, there was comparatively little change in brain volume from about 4 MYA until the emergence of H. habilis about 2.5 MYA (McHenry, 1994; B. Wood & Collard, 1999). As described in the next section, another period of relative stasis occurred from about 1.8 MYA until about 500,000 years ago (Ruff et al., 1997). Stasis in size, however, does not mean there were no changes in the specialized functions of one or more brain regions (Holloway, 1996).

### Encephalization Quotient

An understanding of changes in absolute brain volume during hominid evolution is important but can be misleading. This is because the absolute size of the brain increases with increases in overall body size, and thus confounds cross-species comparisons (Harvey & T. Clutton-Brock, 1985). For instance, an adult male A. africanus weighed about 30% less than a modern adult human male. As discussed in chapter 4 (Allometry and size of the neocortex section), one result is that some proportion of the difference in absolute brain volume comparing these two species is due to differences in overall body size and not to selection pressures for increased brain size (McHenry, 1994). One measure used to control for this confound is the encephalization quotient (EQ), which is an index of brain size relative to that of a mammal of the same body weight (Jerison, 1973; for discussion see Holloway, 1996). As an example, McHenry (1994) estimated the EQ of chimpanzees to be 2.0, that is, that the brain volume of chimpanzees is twice that of an average mammal of the same body weight.

EQ values for modern humans range from less than 5.0 (Aiello & Wheeler, 1995) to more than 7.0 (Jerison, 1973; Tobias, 1987), with estimates commonly ranging between 5.0 and 6.0 (McHenry, 1994; Ruff et al., 1997). The values vary from one analysis to the next because of different assumptions regarding the scaling relation between body size and brain size. Despite this variability, the overall evolutionary pattern is clear: EQ has increased dramatically over the past 4 million years of hominid evolution. I estimated EQ values for various hominid species as a percentage of the EQ of modern humans, by taking the brain volumes shown in Figure 3.4 and interpolating these with EQ estimates derived by Tobias (1987). As shown in Figure 3.5, the EQ of chimpanzees, although double that of the typical mammal, is estimated to be 34% that of modern humans. The EQ of australopithecines was less than ½ that of modern humans and the EQ of H. habilis was slightly more than ½ that of modern humans. Substantive increases in EQ are evident with the emergence of H. erectus, with values at the high end close to 80% that of modern humans. Figure 3.6 shows the general EQ trend over the past 1.8 million years, that is, since the emergence of H. erectus (based on tabled data in Ruff et al., 1997). As with absolute brain size, EQ values indicate a long period (about 1.2 million years) of stasis, followed by a modest increase (about 12%) from 500,000 to 400,000 years ago, and then more rapid increases until about 35,000 to 20,000 years ago.

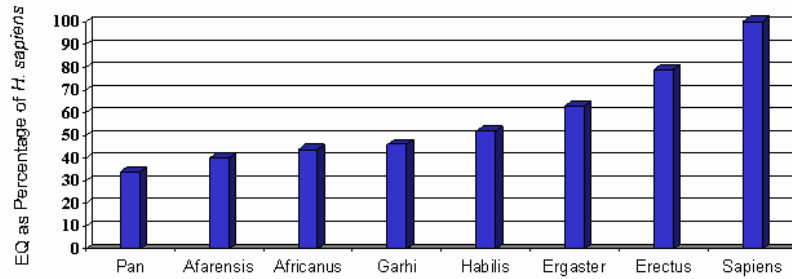


Figure 3.5: Encephalization quotients (EQ) for chimpanzees (e.g., *Pan troglodytes*) and various species of hominid as a percentage of the mean brain volume of modern humans (*H. sapiens*).

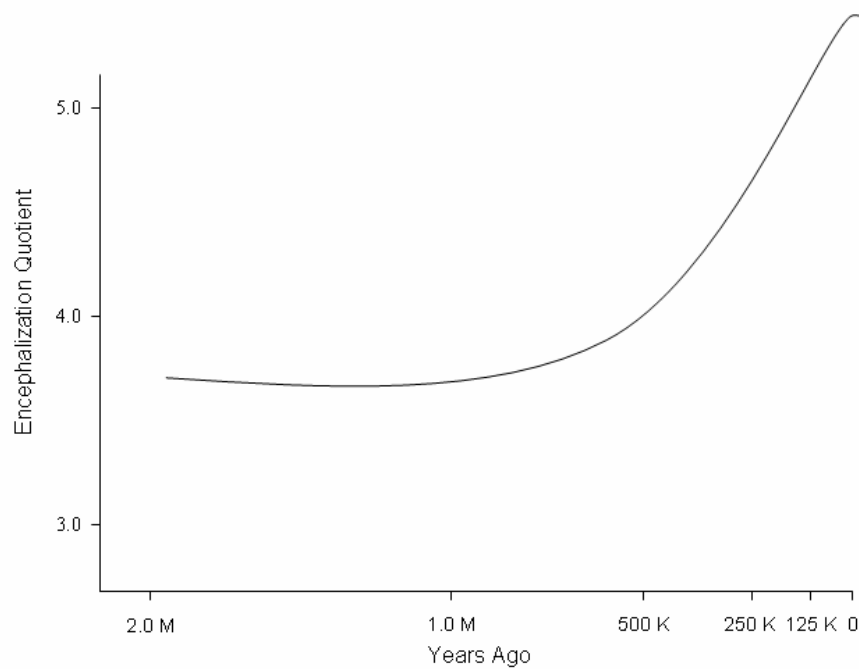


Figure 3.6: Estimated changes in encephalization quotient from *H. erectus* to modern humans. M = million; K = thousand.

On the basis of Ruff et al.'s (1997) estimates and those of Holloway (1996), the EQ of modern humans appears to have peaked between 20,000 and 35,000 years ago and declined 3% to 4% during the past 10,000 to 20,000 years. The gradual decline in EQ values suggests that the selection pressures that resulted in the rapid increase in EQ beginning about 500,000 years ago have been relaxed during the last 10,000 to 20,000 years (Brace, 1995). During this timeframe, agriculture, economic specialization, city-states, and other changes were becoming increasingly central features of human subsistence activities and social organization in many parts of the world (J. Clutton-Brock, 1992; Hole, 1992). The implication is that changes in social organization resulted in a relaxation of the selection pressures that drove the rapid increase in EQ from 400,000 to about 20,000 years ago. In other words, the evolved competencies associated with changes in brain size and organization were not as strongly correlated with survival or reproductive prospects over the past 20,000 years, in comparison to the 450,000 years prior to this epoch. The implications for interpreting research on *g* are discussed in chapter 8.

### Adaptation and Selection

My goal for this section is to review and evaluate models of potential selection pressures and adaptations associated with changes in EQ during hominid evolution. Specifically, I discuss climatic, ecological, and social pressures.

#### Climatic and Ecological Pressures

##### Climatic

Climatic variations and geological changes (e.g., volcanoes) are common and can result in short- and long-term changes in ambient temperature, rainfall, and other ecological conditions. As described for Darwin's finches in chapter 2 (Climatic and Ecological Selection Pressures section), these changes can influence the mix of vegetation, woodland, and so forth that support other species (e.g., deMenocal, 2001; Rutherford & D'Hondt, 2000; Tudhope et al., 2001; Vrba, Denton, Partridge, & Burckle, 1995). The most influential model of climatic and geological influences on the evolution of flora and fauna is that proposed by Vrba, specifically, the turnover-pulse hypothesis (1974, 1975, 1995a, 1995b). The gist of the hypothesis is that large-scale climatic changes, such as those associated with glaciations and global cooling, can result in large-scale changes in habitat (e.g., change in the distribution of food sources) and in physical ecology (e.g., ambient temperature). The result is pulses of speciation and extinction events. Adaptive radiation and speciation occur, in theory, as habitat change results in geographic isolation – due, for instance, to deforestation and resulting pockets of woodlands within savanna – of populations of the same species, and subsequent adaptations of these populations to local conditions. Extinction follows for those species that are unable to adapt to change in habitat or physical conditions (e.g., temperature).

The issue I address here is whether such climatic changes contributed to hominid evolution in general and to the accompanying changes in brain volume and EQ in particular. Vrba (1995b) argued that significant glaciation between 2.8 and 2.5 MYA resulted in decreased temperature and rainfall in Africa and a corresponding turnover pulse of many species of large fauna, including hominids. Evolutionary responses to decreasing temperature often include increases in physical size to enable greater retention of body heat and a prolonged period of



physical development to enable growth of a larger body. Vrba argued that these physical adaptations resulted in an accompanying change in brain volume and EQ: “The conclusion is inescapable that hominine encephalization in the latest Pliocene started a new trend, of higher evolutionary rates than before” (Vrba, 1995b, p. 406). The specific mechanisms driving or at least maintaining the increase in hominid EQ are not detailed, but the implication is that EQ changes were not the direct result of ecological or social pressures but rather an incidental effect of broader physical adaptations (see Allometry and Size of the Neocortex section of chapter 4).

Vrba’s (1974) turnover pulse hypothesis is difficult to test, given the incompleteness of the fossil record, among other issues (see Vrba, 1995a). Nonetheless, the model in general and as related to hominid evolution has attracted much attention and has been vigorously debated (Behrensmeyer, Todd, Potts, McBrinn, 1997; Kimbel, 1995; Kingston, Marino, & Hill, 1994; Potts, 1998; Turner & Wood, 1993; T. White, 1995). Although the 2.8 to 2.5 million year timeframe has been questioned, there is evidence for the emergence of many new species of fauna in Africa between 3.0 and 2.0 MYA, including as many as 4 to 6 new species of hominid, 3 of which are shown in Figure 3.2 (Behrensmeyer et al., 1997; Kimbel, 1995). However, inconsistent with the model is evidence that some groups of species did not show the predicted speciation and extinction pulses (T. White, 1995), and the change in mix of savanna and woodland may not have been as drastic as predicted (Kingston et al., 1994). Moreover, most of the changes in brain volume and EQ in H. habilis and H. erectus occurred less than 2 MYA, and do not appear to have been coupled with periods of rapid climatic change (T. White, 1995).

Another approach that can be used to address this issue involves determining if the increases in brain volume and EQ of early species of Homo were associated with similar increases in other African hominids and primates that lived in the same regions and during the same timeframe. If there is a general relation between climatic changes and changes in body size and brain volume, then these other species should have experienced the same selection pressures and thus experienced a similar change in brain volume and EQ as H. habilis and H. erectus. In one test of this hypothesis, Falk et al. (2000) compared the brain volumes of these early species of Homo to the brain volumes of three sister species of African hominids (Paranthropus robustus, P. boisei, P. aethiopicus) from roughly 2.0 to 1.5 MYA. With the possible exception of P. boisei (see Elton, Bishop, & Wood, 2001), the brain volumes of these species did not change substantively during this timeframe. Elton et al. examined change in the brain volume of a species of now extinct baboon (Theropithecus) that appears to have lived in the same localities as H. habilis and H. erectus. As with the findings of Falk and colleagues, there was no change in the brain volume of this species of baboon during the timeframe when H. habilis and H. erectus were experiencing significant increases in brain volume and EQ.

At this point, Vrba’s (1974) turnover pulse hypothesis and related models (e.g., Potts, 1998) may explain the apparent increase and adaptive radiation of hominid species from 3.0 to 2.0 MYA, including the evolutionary emergence of the line that eventually led to modern humans. Patterns of climatic variation and geological change are not, however, consistent with the pattern of increased brain volume and EQ during hominid evolution, especially the very rapid changes during the past 500,000 years; see Calvin (2002) for an alternative interpretation. This is not to say that climatic events, such as glaciations, have not influenced human migration patterns or population expansions and contractions, it appears that they have (Underhill et al., 2001). Rather, patterns of climatic change do not correspond well to evolutionary change in EQ

since the emergence of Homo and thus are not likely to have been the principle force driving the evolution of brain and cognition in humans.

### Ecological

Darwin (1859) argued that relationships and competing interests among species were the driving force of natural selection. Among these are predator-prey relationships, competition among different species for the same food source, and the effects of parasites on physical vigor and health. Parasites, food shortages, and occasional predator attacks do indeed covary with mortality risks for humans in traditional societies today and humans who lived in preindustrial Europe and the United States (e.g., Hed, 1987; Hill & Hurtado, 1996; Morrison, Kirshner, & Molho, 1977). These factors have almost certainly been important components of natural selection during human evolution, but are not in and of themselves sufficient explanations of the increases in hominid brain volume and EQ. If they were, then many species would have evidenced the same increases in brain volume and EQ given that parasites, predators, and food shortages are common selection pressures across species.

Instead, models of the relation between ecological pressures and brain and cognitive evolution in hominids have focused on the ability of hominids to extract biological resources from the ecology and through this improve survival prospects and support accompanying population increases and geographic expansions. The basic idea is supported, in part, by a common pattern across nonhuman species: Species' with complex foraging or predatory demands have a larger brain volume and higher EQ than related species with less complex foraging or predatory demands (e.g., Barton, 1996; Barton & Dean, 1993; T. H. Clutton-Brock & Harvey, 1980; Kaplan & Robson, 2002). For instance, species that rely primarily on leaves and other plentiful foods have smaller brains than their cousins that rely on foods that are spatially dispersed and not always available, such as fruits. The argument is taken one step further with hominids, specifically that hominids evolved into super predators that had (and still have) an extraordinary ability to capture (e.g., hunting) and process (e.g., cooking) other species for use as foods and medicines (Martin, 1967; Wrangham et al., 1999).

Kaplan and his colleagues have clearly demonstrated that humans in traditional societies – at least groups that have not been forced by other humans into resource-poor environments – are highly efficient at extracting life-supporting biological resources from natural ecologies through hunting and foraging (Kaplan et al., 2000; Hill, Boesch, Goodall, Pusey, Williams, & Wrangham, 2001). If the ability to extract and process biological resources was the driving force in the evolution of brain and cognition, then improvements in the ability of hominids to extract these resources should correspond to changes in brain volume and EQ during hominid evolution. To assess this hypothesis, several questions must be answered. Specifically, which social, behavioral, and other adaptations (e.g., manual dexterity associated with tool use; Trinkaus, 1992) allowed hominids to extract and process biological resources? When did these adaptations evolve? Were these adaptations likely to be a sufficient explanation of the changes in brain volume and EQ during hominid evolution?

As an example of how these questions can be approached, consider Teaford's and Ungar's (2002) analysis of tooth size, shape, and wear patterns of australopithecines. Their analysis suggests that A. afarensis and other australopithecines evidenced a shift in diet relative to their predecessors (see also Jolly, 1970). Recent finds by Semaw and colleagues (2003)

suggest that A. garhi constructed a variety of stone tools, including tools used to cut and process meat. These features of tooth morphology and behavioral adaptation suggest that australopithecines were able to eat a wider range of foods (largely seeds and soft fruits, and apparently some meat) than their predecessors and were thus able to occupy a wider range of ecologies. The associated behavioral (e.g., foraging strategy) and cognitive (e.g., determining growth patterns of fruit; Barton, 1996) adaptations may have contributed to the apparent increase in the EQ of australopithecines (see Figure 3.5) relative to their predecessors, but these adaptations occurred millions of years before the rapid rise in EQ associated with the emergence of H. erectus and H. sapiens.

Wrangham et al. (1999) presented evidence consistent with the position that H. erectus used fire for cooking, which enables the use of a wider range of plant and animal species to be used as foods. Foley and others have detailed the relation between advances in the sophistication of tools used for food extraction (e.g., digging sticks) and hunting and the appearance of species since A. afarensis (de Heinzelin et al., 1999; Foley, 1987; Foley & Lahr, 1997). There is evidence that H. habilis used simple stone tools and that increases in the complexity of stone tools and their geographic distribution coincided with the emergence and migration patterns of H. erectus. J. Clark et al. (2003) provided evidence that early modern humans used even more complex stone tools about 150,000 years ago. Nonetheless, the most complex stone tools are found in archeological sites dating less than 50,000 years ago and are found with the fossils of modern humans, H. heidelbergensis, and H. neanderthalensis (Foley & Lahr, 1997). The pattern of tool “evolution” and the likely function of these tools, including hunting and food extraction (e.g., digging up roots), appears to be consistent with Kaplan et al.’s (2000) hypothesis.

Evidence that these changes resulted in the evolution of a super predator comes from patterns of human migration and subsequent mass extinctions of other species. Following the conclusion of Wallace (1911, p. 264) – “the rapidity of the extinction of so many large Mammalia is actually due to man’s agency” – Martin (1967, 1973) presented evidence that mass extinctions of megafauna (prey species weighing 40 Kg or more) were evident in Africa about 50,000 years ago, and later mass extinctions occurred in Australia, Asia, America, and New Zealand after the migration of humans into these regions. Although determining the precise dates of human migration and the extinction of other species poses some technical challenges, Wallace’s and Martin’s conclusion has been supported by a series of recent analyses that employed multiple methods for determining these dates (Alroy, 2001; Ceballos & Ehrlich, 2002; G. H. Miller, et al., 1999; R. G. Roberts et al., 2001).

As an example, evidence presented by R. G. Roberts et al. (2001) indicates a continent-wide mass extinction of Australian megafauna about 46,000 years ago, that is, roughly 5,000 after the arrival of humans. Martin (1973) and Alroy (2001) presented evidence suggesting that the mass extinction of megafauna in North America occurred about 12,000 years ago, that is, roughly 1,000 to several thousand years after the arrival of humans. These mass extinctions have not been correlated with climatic or other ecological changes (e.g., glaciers; e.g., G. H. Miller et al., 1999), although the extinct of some species can, of course, be related to climate and ecological changes and not to human activity (Guthrie, 2003). In any case, analyses of declines in populations of species of large fish and mammals have directly linked these to human hunting and fishing from the time humans were primarily hunter-gathers to modern day (e.g., R. Myers & Worm, 2003; Pandolfi et al., 2003; Walsh et al., 2003).

Further evidence for a co-evolving relation between EQ and hunting and other dietary changes comes from the metabolic requirements of the human brain (Armstrong, 1990). Specifically, there is evidence that the evolutionary increase in brain volume was associated with a corresponding decrease in the mass of the metabolically-expensive gastrointestinal tract (Aiello & Wheeler, 1995), although this evidence is not conclusive (Aiello, Bates, & Joffe, 2001). Evolutionary reduction in the size of the gastrointestinal tract requires change from a low quality (e.g., leaves, plants, grasses) to a high quality (e.g., fruits, meat) diet. The above noted shift in the australopithecine diet is thus consistent with the corresponding change in EQ, as is the rapid increase in EQ associated with the increasingly effective hunting competencies of H. erectus and H. sapiens.

Improvements in hunting efficiency and ability to acquire other high-quality foods were presumably supported by corresponding changes in brain and cognition. Indeed, as I describe in chapter 5 (Ecological Modules section), there is evidence for an evolved folk biology in humans. Specifically, brain and cognitive systems that are specialized for the categorization of plants and animals used as food sources, and cognitive specializations for acquiring – for instance by means of hunting – these foods (Atran, 1998). As noted by Aiello and Wheeler (1995), these relations do not, however, provide conclusive evidence that the changes in brain volume and EQ during hominid evolution were solely related to improvements in foraging and hunting competencies, only that they were necessary to support the evolutionary increase in brain volume.

### Social Pressures

#### Ecological Dominance

The patterns described in the above section suggest a gradual improvement during hominid evolution in the ability to extract food from the ecology (Kaplan & Robson, 2002). These competencies became exceptional, in relation to other species, with the emergence of Homo, perhaps beginning with H. erectus. The trend continued with H. erectus and H. Sapiens, as these species became exceptionally skilled at extracting biological resources from a variety of ecologies, and at manipulating and changing these ecologies (e.g., through fire, tool use) in ways that almost certainly had survival and reproductive consequences. As H. erectus and later H. sapiens became increasingly skilled at exploiting and manipulating these ecologies, a situation of ecological dominance was achieved (Alexander, 1989). Once achieved, an evolutionary Rubicon was crossed:

the ecological dominance of evolving humans diminished the effects of ‘extrinsic’ forces of natural selection such that within-species competition became the principle ‘hostile force of nature’ guiding the long-term evolution of behavioral capacities, traits, and tendencies (Alexander, 1989, p. 458).

The pattern of human migration and overkill of megafauna (Martin, 1967) is one example of ecological dominance, and parallels Mac Arthur’s and Wilson’s (1967) analysis of island biogeography. When a species first migrates into an unexploited region, such as an island, that supports the survival and reproductive needs of the species and offers few constraints on population expansion (e.g., few predators), then there are low levels of social competition and a rapid increase in population size. As the population expands, the quantity or quality of the region’s resources necessarily declines, and competition for access to these diminishing

resources necessarily intensifies. The result is an added selection pressure, social competition over survival-related ecological resources..

Ecological dominance results in the same pattern, as it is the ability to very efficiently extract biological resources from the ecology and manipulate the ecology in ways that reduce mortality risks and support subsequent population expansions (Hill et al., 2001; Kaplan et al., 2000). However, as the population expands beyond the carrying capacity of the ecology, the inevitable result is a population crash, as was argued by Malthus in 1798. The combination of ecological dominance, population expansions, and the elevated mortality that defines population crashes result in a fundamental shift in selection pressures. Darwin's and Wallace's (1858, p. 54) conceptualization of natural selection as a "struggle for existence", becomes in addition a struggle with other human beings for control of the resources that support life and allow one to reproduce (Geary, 1998). Social competition is, of course, endemic across species, but becomes an especially potent selection pressure for species that achieve ecological dominance (Alexander, 1989). These species have evolved such that they have adaptations that reduce ecological constraints on population expansions, creating cycles of expansions and contractions, although overall population levels may have remained relatively constant when averaged across these cycles. During contractions, social competition for diminishing resources will necessarily increase in intensity (Malthus, 1798).

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 in order to gain control of resources in the local ecology, and to gain control of the behavior of other people (West-Eberhard, 1983). To the extent that access to these resources covaries with survival and reproductive outcomes – and it does in many contexts (Betzig, 1986; Hed, 1987; Malthus, 1798; United Nations, 1985) – the associated sociocognitive competencies, and supporting brain systems, will necessarily evolve. The point is that Kaplan et al.'s (2000) and others' (e.g., Tiger, 1969) theory of the relation between ecological pressures and hominid brain evolution is consistent with Alexander's (1989) and others' (e.g., Humphrey, 1976) theory of the relation between social pressures and hominid brain evolution. Alexander's proposal implies that ecological pressures were more salient earlier in hominid evolution and social pressures were more salient later in hominid evolution.

### Social Complexity

Sociality and ecological dominance. As noted in the Ecological Pressures section and elaborated in chapter 4 (Comparative Ecology and Brain Evolution section), comparative (i.e., cross-species) evidence supports the view that hunting, foraging, and other food-acquisition behaviors are often related to the evolution and proximate development of brain and cognition, as are other activities such as predator avoidance (e.g., Barton, 1996; Dukas, 1998a; Catania, 2000). These brain, cognitive, and accompanying social and behavioral competencies function to maintain a territory and extract survival-related resources from this territory. These brain and cognitive competencies define the domains of folk biology and folk physics, which I describe for humans in chapter 5 (Ecological Modules section). My point for now is that these brain and cognitive systems are integral to the human ability to achieve ecological dominance, but must also be considered within a wider social context, as represented in Figure 3.7.

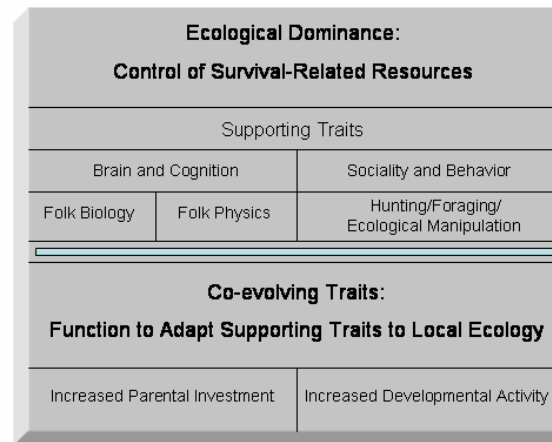


Figure 3.7: Ecological dominance results from the ability to efficiently extract resources from the ecology, and change and manipulate the ecology (e.g., use of fire for slash and burn agriculture) in ways that improve survival and reproductive prospects. The achievement of ecological dominance is dependent on folk knowledge, social cooperation, and the co-evolving traits of parental investment and developmental activity.

As represented in the bottom section of Figure 3.7, there may also be a co-evolving increase in the length of the developmental period (Kaplan et al., 2000; Kaplan & Robson, 2002), and an evolved bias to engage in developmental activities (e.g., play) that result in the proximate adaptation of hunting, foraging, and related behaviors to the demands of the local ecology (Groos, 1898). If an increase in the length of the developmental period and associated activities do in fact result in better adapted competencies, then an additional premium is placed on parenting. At the very least, the length of time during which parents provision and protect offspring must increase, to give offspring the opportunity to practice hunting/foraging and other ecological skills (e.g., tool use). The relations shown in Figure 3.7 are not, however, perfectly coupled. The human developmental period and apparently that of *H. erectus* is actually shorter than would be expected on the basis of brain size alone (Allman & Hasenstaub, 1999; Dean, Leakey, Reid, Schrenk, Schwartz, Stringer, & Walker, 2001). These findings do not invalidate the general relations shown in the figure, but rather suggest that other selection pressures, such as adult mortality risks (Stearns, 1992), operated to reduce the length of the developmental period.

In any case, the take home message is that ecological dominance cannot be achieved without cooperative relationships, including collective hunting and reciprocal sharing of meat, a division of labor, and so forth (Hill, 2002; Kaplan et al., 2000; Kaplan & Hill, 1985). At the same time, these relationships create the potential for larger-scale competition. As noted, an important result of ecological dominance is an expansion of population size. Expansions, in turn, result in diminishing ecological resources and thus create the potential for between-group competition over control of resource-rich ecologies and the forced migration of less competitive groups (Hamilton, 2001). Chagnon (1997) has documented this very dynamic in the Yanomamö, and Horowitz (2001) has documented many instances of similar forms of group-level conflict in human populations throughout the world. It is plausible that the same basic dynamic of between-group competition over resource-rich ecologies contributed to the earlier described migration of

H. erectus and other species of Homo into Asia, Europe, and later Australia and America, although climatic changes likely contributed to migration patterns as well (deMenocal, 2001).

Social dynamics. Social dynamics required to achieve ecological dominance and to support group-level conflict over preferred ecologies should favor the evolution of the suite of co-evolving traits shown in Figure 3.8, and elaborated in Table 3.1 (see Carroll, 2003, for related discussion). The basic human social structure is presumed to consist of kinship groups that cooperate in order to compete with other kinship groups over control of resource-rich ecologies, and to manipulate reproductive dynamics (Geary & Flinn, 2001). Within-group relationships will entail a balance of cooperation to meet shared goals and conflict due to divergent goals. In theory and typically in practice, the relative bias toward cooperation or conflict varies directly with degree of genetic relatedness between the individuals (e.g., Chagnon, 1997; Hamilton, 1964, 1975; Segal & Hershberger, 1999; Trivers, 1974; West-Eberhard, 1975). When combined with the potential for group-level conflict, these within-group dynamics create pressures for the evolutionary elaboration of a folk psychological system, as emphasized by many contemporary scientists (e.g., Barton, 1996, 1999; Brothers & Ring, 1992; Cosmides, 1989; Dunbar, 1993; 1998; Geary & Flinn, 2001; Humphrey, 1976; Pinker & Bloom, 1990; Premack & Woodruff, 1978; Sawaguchi, 1997), and suggested by Darwin (1871) more than 130 years ago.

The competencies that support human social dynamics are similar in many respects to those common in other species (see Table 3.1). Across species of primate, the complexity of social dynamics is positively correlated with brain size, and both social complexity and brain size are correlated with length of the developmental period and maximum life span (Allman & Hasenstaub, 1999; Allman, McLaughlin, & Hakeem, 1993; Dunbar, 1993; 1998; Joffe, 1997). Maximum life span, in turn, is associated with levels of parental investment (Allman, Rosin, Kumar, & Hasenstaub, 1998). In short, larger brains and higher EQs are generally associated with complex social systems, a long development period and long adult lifespan, and high levels of parental investment, as well as complex foraging/hunting demands (Kaplan & Robson, 2002).

For humans, extended parental investment typically occurs in the context of a wider kinship network that facilitates the feeding and protection of children, and supports the extended developmental period. The latter allows individuals to engage in the activities, such as peer relationships and rough-and-tumble play (Bjorklund & Pellegrini, 2002; Groos, 1898; P. Smith, 1982). Although the issue is debated, one proposed function of these activities is to enable children to adapt social and sociocognitive competencies to the social conditions of the local group (Geary, 1998). Children learn, based on their personality and social and other skills (e.g., athletic), how to influence the behavior of other people and how to obtain culturally-valued resources (e.g., meat obtained through hunting or money), competencies and knowledge that are predicted to enhance survival and reproductive prospects in adulthood.

The gist is that in traditional societies today (e.g., Chagnon, 1997), and presumably during recent hominid evolution, kinship groups and reciprocal relationships – called friends by psychologists (Hartup & Stevens, 1997) – create social coalitions. The individuals that compose these coalitions cooperate in order to compete with other coalitions over ecological control, and

Table 3.1

Co-evolving traits associated with human social competitionI. Large brain and complex social competencies

1. The overall size of the human neocortex is larger than expected for a primate of the same body and brain size (Rilling & Insel, 1999), but this difference appears to be due to expansions in size or changes in complexity of only a few areas of neocortex (Rilling & Insel, 1999; Semendeferi, Lu, Schenker, & Damasio, 2002).
2. Although results are preliminary, the neocortex appears to be larger than expected in those areas that support social competencies (Rilling & Insel, 1999), such as language (discussed more fully in chapter 7).

II. High levels of paternal investment

1. Paternal investment is only evident in 3 to 5% of mammalian species (T. Clutton-Brock, 1989).
2. Even for these species, humans are unique in that paternal investment occurs in a social context of large multimale-multifemale communities, and where most adult members of these communities reproduce (Alexander, 1990).
3. In non-industrial societies, paternal investment reduces child mortality rates, and in many societies contributes to children's ability to acquire social-competitive competencies (Geary, 2000).

III. Long developmental period and adult lifespan

1. Relative to other mammals and primates, children have a very long developmental period that is characterized by slow development during middle childhood and high dependency on adult caregiving (Bogin, 1999).
2. During this period of slow growth, children engage in many activities, such as peer play, that likely facilitate social and social-cognitive competencies (e.g., Pellegrini & Bartini, 2001).
3. Relative to other great apes, humans have a very long adult lifespan, and low juvenile and adult mortality rates (Allman et al., 1993; Hill et al., 2001).
4. The extended adult lifespan, including menopause in women, allows parents to invest in children during the long developmental period (Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998; Williams, 1957).

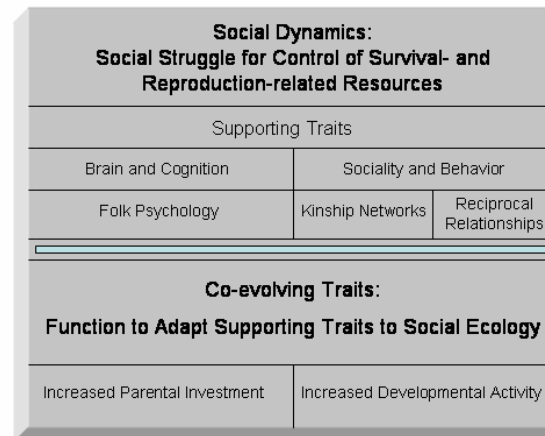


Figure 3.8: Social competition is a significant selection pressure for humans, and centers on attempts to achieve access to and control of resources that covary with survival and reproductive outcomes in the local ecology. These control-related activities are dependent on folk knowledge, social cooperation, and the co-evolving traits of parental investment and developmental activity.



to manipulate reproductive dynamics. Within kinship groups, high levels of parental investment afford children the opportunity to engage in activities (e.g., peer relationships; Harris, 1995) that allow the competencies needed to achieve ecological dominance (e.g., play hunting; Kaplan et al., 2000; Kaplan & Robson, 2002), compete for mates, manipulate and control social relationships, and parent, among other activities, to be practiced and adapted to local conditions (Bjorklund & Bering, 2003; Geary, 2002a, 2002b).

### Forms of Social Relationship

A complete description and analysis of the many forms of human social dynamic is beyond the scope of this treatment (for a few examples see Caporael, 1997; Bugental, 2000; Buss, 1994; Geary, 1998; Horowitz, 2001). My goal is more modest; specifically, to provide a framework for organizing and conceptualizing the most fundamental of these dynamics and to do so within a broader comparative background. At its root, and as elaborated in the Motivation to Control section, the social behavior of individuals is ultimately focused on attempts to organize the social and material world so as to direct resources to themselves and their kin. Social cooperation results when resource control requires collective effort, and conflict results as different individuals and kinship groups compete to maintain control of or gain access to the same resources.

However it is packaged, social dynamics are centered on survival and reproductive activities, and parental investment and associated components of sexual selection are the core of these activities, as I describe in the first section. In the second and third respective sections, I provide examples of how male-male competition and female-female competition result in social dynamics that, in theory, should place a premium on sophisticated sociocognitive competencies. My point in this section is that humans are a highly social species and the accompanying relationships are the most demanding and complex endeavors that people must cope with day after day, and to be successful in life. Most other primates are highly social as well, but the most important result of runaway social competition – following the achievement of ecological dominance – is an evolutionary elaboration of social competencies and a ramping up of social complexity: This, in turn, results in another evolutionary elaboration of social competencies and so the cycle continues.

Parenting and sexual selection. Parenting and the reproductive dynamics that define sexual selection provide a way to organize the most fundamental human social dynamics, and those of many other species (Andersson, 1994; T. Clutton-Brock, 1991; Darwin, 1871; Geary, 1998). Human fatherhood provides a particularly interesting segue into this framework. This is because fatherhood occurs against a background in which there is little or no such investment in 95% to 97% of other mammalian species (T. Clutton-Brock, 1989; for an exception see Dunbar, 1995), and because it greatly complicates human reproductive dynamics. As described in chapter 2 (Sexual Selection and Social Dynamics section), when one sex invests in parenting, the other sex competes over access to this investment (Trivers, 1972). When both sexes parent and all parents are not equal, then both males and females compete for the parental investment of the opposite sex. Fatherhood then results in female-female competition over this investment and male choice of spousal partners, along side male-male competition and female choice. To further complicate matters, paternal investment results in the formation of families and extended spousal relationships, and the long developmental period results in more extensive and extended parent-child relationships than in nearly all other species. As outlined in Table 3.2, these

dynamics can be boiled down to three categories, intrasexual competition, intersexual choice, and family relationships (Geary, 2002b). The combination results in a degree of social complexity that is extreme, even among primates.

Table 3.2

Forms of social conflict and competition

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Intrasexual competition

Male-male competition

1. In traditional societies, men form kin-based coalitions that compete for control of mating dynamics (e.g., exchange of brides) and control of the resources that covary with survival and reproductive outcomes in the local ecology (Chagnon, 1988; Geary, 1998). Men also form dominance hierarchies within the in-group coalitions, and compete for position (and influence) in the hierarchy. Competition is often physical and deadly (Keeley, 1996).

Female-female competition

1. Women form social networks that are commonly nested within the kin-based coalition of men. In these and other contexts, women compete for access to resources, including access to resource-holding or socially-influential men. Relative to men, this competition is less physical (Campbell, 1999) and involves subtle manipulation of social relationships, with the goal of organizing these relationships so as to maximize the woman's access to resources that covary with survival and reproductive outcomes in the local ecology (Geary, 2002).

**Intersexual choice**

Male choice

1. Paternal investment leads to the prediction that men will be selective in their mate choices (Trivers, 1972), and this is the case. Men's mate choices are influenced by fertility cues (e.g., age), as well as by indicators of women's social and maternal competence (Geary, 1998).

Female choice

1. Women's mate choices are influenced by men's social and parental competence. More so than men, women also focus on men's social status, including material resources, social influence, and cues to their ability to acquire and maintain these resources (Buss, 1989, 1994). Women are also sensitive to indicators of their ability to influence potential mates, and thus gain access to their resources.

**Family Relationships**

**Spousal**

1. Spouses, of course, cooperate in raising children, but extended maternal and paternal investment also results in strong potential for conflicts of interest (Kaplan et al., 2000; Svensson & Sheldon, 1998). The nature of these relationship can vary from one culture to the next (Draper, 1989; Draper & Harpending, 1988), but the same central conflicts are predicted; 1) extent of maternal versus paternal investment; 2) resource control (e.g., spending on children or status-oriented objects); and, 3) marital fidelity.

**Parent-offspring and sibling**

1. Parents, of course, invest time and resources to promote the well-being of offspring, but offspring typically press for additional resources (Trivers, 1974), sometimes with accompanying morbidity and mortality costs to parents (Westendorp & Kirkwood, 1998). The long developmental period of humans results in an extended parent-child relationship and thus the potential for extended conflicts over parental allocation of resources
2. Siblings will also compete for parental resources.

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Adapted from "Sexual selection and human life history," by D. C. Geary, 2002, *Advances in Child Development and Behavior*, 30, p. 66. Copyright 2002 by Academic Press. Reprinted with permission.

Male-male competition. Male-male competition occurs within men's social groups, and between their social groups. The former is associated with attempts to achieve social status and dominance and thus the ability to influence the behavior of other members of the group, and the latter is typically focused on achieving control of resource-rich ecologies and facilitating competition for mates, as in raiding to capture wives or social politics in negotiating marital partners (Chagnon, 1997). The resulting competition is often lethal (Chagnon, 1988, 1997; Daly & Wilson, 1988), especially when it involves between-group competition (Horowitz, 2001). This form of competition requires the development and maintenance of male coalitions, as I

described in chapter 2 (Coalitional Competition section in chapter 2; de Waal, 1993). The dynamics involved in creating and maintaining coalitions is universal and colloquially known as politics (D. Brown, 1991). The formation of a within-coalition dominance hierarchy not only determines men's relative social status and how resources acquired by the coalition are distributed, it is necessary for effective coalitional competition.

My point is that social dynamics for men require striking a balance between maintaining a cooperative relationship with a large number of other men and at the same time competing with these same men for in-group social dominance. Political activities and coalitional competition thus require considerable social competency, although these skills differ from those that support women's relationships (Geary & Flinn, 2002).

Female-female competition. Women, of course, form cooperative social groups (Taylor et al., 2000), but typically within territory defined by men's coalitions (D. Brown, 1991; Pasternak, Ember, & Ember, 1997). Participation in these social networks provides women with social and emotional support and stability for themselves and their children. Stability of the social network, including the marital relationship, improves physical (Flinn & England, 1995) and psychological (Leadbeater, Blatt, & Quinlan, 1995) health, and through this survival prospects of children in some contexts (United Nations, 1985). Unlike men, female-female competition is not coalitional, but is still related to attempts to achieve access to desired resources, including mates. Rather than physical competition or direct status-related activities, female-on-female aggression is more commonly relational. It involves learning about the emotional states, secrets, intentions, and so on of other women and if necessary using this information to manipulate the web of social relationships within which the women are embedded (Björkqvist, Lagerspetz, & Kaukiainen, 1992; Björkqvist, Osterman, & Lagerspetz, 1994; Crick, Casas, & Mosher, 1997; Feshbach, 1969).

The successful use of this form of aggression per force requires considerable sociocognitive competencies (Geary, 2002a). As an example of the complexity of this competition, consider again Figure 2.3 and display 2.1. Recall, as group size increases, the number of dyadic relationships each individual must potentially monitor increases exponentially. Not only does relational aggression required gathering information about all of the other individual girls and women in the social group, information on the nature of dyadic relationships between these other girls and women must be gathered as well. If this were not complex enough, the successful use of relational aggression requires that girls and women manipulate their relationship with other girls and women, and manipulate the nature of the relationship between dyads of other girls and women.

Summary. The complexity of intrasexual competition and other forms of relationship arises from the behavior and social activities of each individual as she or he attempts to organize the social and material world in terms of their own best interests. Conflicts are inevitable because the best interests of any two individuals, except perhaps monozygotic twins (Segal, 1993; Segal & Hershberger, 1999), do not completely overlap. Social competencies evolved to facilitate cooperation when interests do overlap (Trivers, 1971), and to facilitate the ability to outmaneuver individuals with competing interests (Humphrey, 1976). In this view, the earlier noted runaway selection occurred as a result of these dynamics; specifically, because access to and control of significant resources requires some level of influence over the behavior of other

people, people whose self interests differ and are thus attempting to organize the social world in different ways.

As a brief aside, it might be argued that cultural activities, such as art, music, and literature, do not at first glance seem to fit this bare bones view of human nature. However, the theme of many of these works is the human condition, that is, affective (e.g., emotions) and social dynamics that covary with survival and reproductive outcomes in traditional societies (e.g., love, suffering; Whissell, 1996), and the production of these works often has an element of social competition among artists in the genre (G. F. Miller, 2000).

### Sexual Selection and Population Genetics

Genetic studies of human populations and related species not only allow inferences to be drawn about the timing and pattern of human evolution as described earlier (Origins section), they also allow inferences to be drawn about human social dynamics, including migration patterns (Seielstad, Minch, & Cavalli-Sforza, 1998) and patterns of social competition (Wyckoff, Wang, & Wu, 2000; Underhill et al., 2001). The basic method involves comparing the geographic distribution and variability of mutations in mitochondrial DNA (mtDNA) genes and genes on the Y chromosome. mtDNA genes are inherited from mother, and males inherit the Y chromosome from their father. Because of this, differences in the geographic distribution and variability of mtDNA- and Y-chromosome genes can be used to make inferences about ancestral maternal and paternal migration patterns and reproductive dynamics. Although there are other potential reasons, restricted variance in Y-chromosome genes could result from male-male competition and female choice of mating partners. These common features of mammalian reproductive dynamics result in fewer males than females reproducing in any given generation (Andersson, 1994; T. Clutton-Brock, Harvey, & Rudder, 1977), and thus less variability in paternal than maternal ancestry. If male-male competition and female choice, that is, sexual selection, influenced human evolution, then there should be less variance in Y-chromosome than in mtDNA-genes in most human populations, and this is the case (Anagnostopoulos, Green, Rowley, Lewis, & Giannelli, 1999; Dorit, Akashi, & Gilbert, 1995; Hammer et al., 2001; Wells et al., 2001; J. Wilson, Weiss, Richards, Thomas, Bradman, & Goldstein, 2001; Underhill, Jin, Zemans, Oefner, & Cavalli-Sforza, 1996; Underhill et al., 2000).

Further evidence for sexual selection comes from mtDNA- and Y-chromosome patterns that indicate ancestral males were often from geographically distant populations (Bortolini et al., 1999; Carvajal-Carmona et al., 2000; Merriwether et al., 1997; Mesa et al., 2000; J. Wilson et al., 2001). One of the more extreme results was reported by Carvajal-Carmona and colleagues. Here, mtDNA- and Y-chromosome patterns were assessed for a Columbian (South America) population that was established in the 16<sup>th</sup>-17<sup>th</sup> centuries. The results revealed that the maternal ancestry of this population was largely (> 90%) Amerindian (i.e., native South American), whereas the paternal ancestry was largely (94%) European. When combined with historical records, these genetic patterns paint a picture of male-male competition in which European men displaced Amerindian men to the reproductive benefit of the former and at a large cost to the latter. Related studies have found similar though less extreme patterns in other South and North American populations (Bortolini et al., 1999; Merriwether et al., 1997). Underhill et al.'s (2001) analysis of Y-chromosome genes from 1,062 men from various parts of the world suggest a repeating pattern of one population of men replacing another population of men in Africa,

Europe, and Asia (see also J. Wilson et al., 2001), although the extent of replacement can vary from one region to the next (e.g., Capelli, et al., 2003).

Most of these genetic studies also reveal that men in most local communities are more closely related to one another than are women, but women have more kin ties to other communities in the region (e.g., Seielstad et al., 1998; Wells et al., 2001; J. Wilson et al., 2001). These genetic footprints, so to speak, support the proposed social structure for male-male competition noted in Table 3.2, and often documented in ethnographic studies (D. Brown, 1991; Chagnon, 1988); specifically, that men tend to form kin-based coalitions. The pattern is also consistent with ethnographic studies of marriage patterns, whereby men typically stay in their birth group – a necessary feature of kin-based male coalitions – and women immigrate to the group of their husband (Murdock, 1981). At the same time, genetic and historical records suggest that more distant migrations are initiated by men who are migrating in search of material resources, social status, and reproductive opportunity (Hammer et al., 2001; Semino et al., 2000).

When these genetic patterns are combined with historical, anthropological, and archeological information (e.g., Chagnon, 1988; Keeley, 1996), a picture of recent human evolutionary history comes into focus. A central, but certainly by no means the only, feature of this history has been the formation of male kin-based social coalitions. These coalitions engaged, and still engage, in group-level male-male competition, that is, warfare, over control of life supporting ecologies and control of reproductive dynamics. One result of coalitional warfare and supporting within-group dominance hierarchies was – and still is in many societies – polygyny, which, in turn, results in fewer men reproducing than women. As I just noted, women often migrate to the group of their husband, and once they have migrated they should, in theory, attempt to organize social relationships in ways that enhance their well-being and that of their children (Geary, 2002a). Attempts to organize these relationships contribute to female-female competition (sometimes with co-wives) and spousal conflict.

Sexual selection might also be the mechanism by which both interbreeding and replacement models of human evolution can be reconciled (see Origins section). Replacement would occur among males through coalitional male-male competition. Interbreeding would occur among males of successful coalitions and the females that resided with the males of unsuccessful coalitions. Of course, social dynamics are not always hostile and are often cooperative, in terms of economic trade and exchange of marital partners from one group to another. The point is that these genetic studies are consistent with the view that social competition and reproductive dynamics contributed to human evolution. To the extent that these dynamics were dependent on social and sociocognitive competencies, they contributed to the evolution of brain and cognition, as I describe in later chapters.

### Motivation to Control

There is general consensus among clinical and research psychologists that humans have a basic motivation to achieve some level of control over relationships, events, and resources that of significance in their life (Fiske, 1993; Heckhausen & Schulz, 1995; Shapiro, Schwartz, & Astin, 1996; Taylor & Brown, 1988; S. Thompson, Armstrong, & Thomas, 1998), although there is no consensus as to whether this motivation to control has evolved. My proposal is that the mechanisms of natural and sexual selection will operate such that a motivation to control will necessarily evolve if the associated behavioral biases contribute to the ability to achieve access to

and control of resources that tend to covary with survival and reproductive outcomes, and if individual differences in this motivational tendency are heritable. The thesis here and elsewhere (Geary, 1998) is that the human motivation to control is indeed an evolved disposition and is implicitly focused on attempts to control social relationships and the behavior of other people, and to control the biological and physical resources that covary with survival and reproductive prospects in the local ecology. My proposal here is that the combination of mechanisms represented in Figure 3.9 guides and supports attempts to achieve access to and control of these resources. In the first section, I present evidence for a relation between achieving control and survival and reproductive outcomes, and in the second I flesh out the mechanisms that enable the achievement of this end.

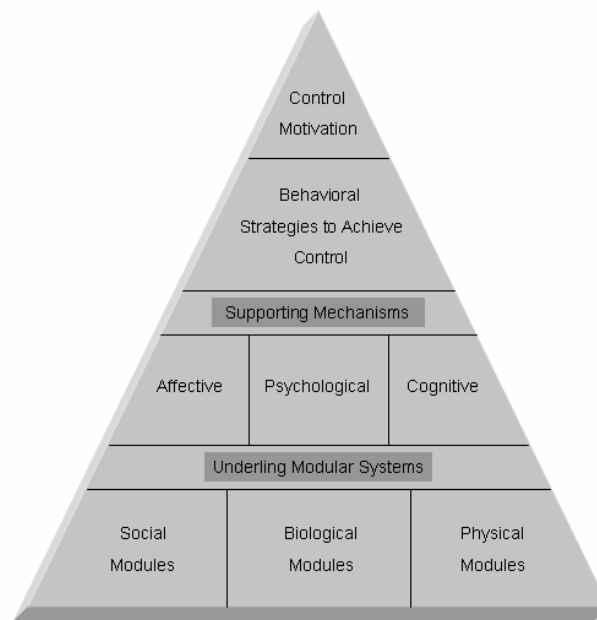


Figure 3.9: The apex and following section represent the proposal that human behavior is basically driven by a motivation to control the social, biological, and physical resources that have tended to covary survival and reproductive outcomes during human evolution. The midsection shows the supporting affective, conscious-psychological (e.g., attributional biases), and cognitive (e.g., working memory) mechanisms that support the motivation to control and operate on the modular systems shown at the base.

### Benefits of Control

The same relation between resource control and survival and reproductive outcomes described for other species in chapter 2 (e.g., Social Selection Pressures section) is evident in most human societies (Ellis, 1993, 1994), although this relation is not always apparent in resource-rich Western culture. For humans and other species, the resources that covary with these evolutionary outcomes fall into three categories, social, biological, and physical (for related discussion see Henriques, 2003). Biological resources include food and medicine, and physical resources include the territories that contain biological resources and that support homes, agriculture, pastures, and so on. Coalitional control of biological and physical resources results in ecological dominance, as I described earlier. Although humans have psychological mechanisms that obscure the fact that they often use social relationships and other people for their own ends (Alexander, 1989), use them they do. Other people are resources if they have

reproductive potential (e.g., young females; Buss, 1994; Singh, 1993), social power, or access (e.g., through monetary wealth) to the biological and physical resources that covary with well-being and status in the culture (Irons, 1979). The goal of developing a relationship with an individual who has social power and wealth is fundamentally an attempt to influence the behavior of this individual and through this to achieve access to power and wealth (Geary & Flinn, 2001; Fiske, 1993).

In most contexts and for most people, the motivation to control is constrained by formal laws, informal social mores (enforced, for example, through gossip; Barkow, 1992), and by psychological mechanisms (e.g., guilt) that promote social compromise and reciprocal social relationships (Baron, 1997; Trivers, 1971). For most people, adherence to these laws and mores provides benefits that are sufficient to avoid the risks associated with attempts to achieve, for instance, absolute despotic control (Simon, 1990b). Still, consideration of history's despots allows a peeling away of these constraints and a more direct glimpse at the motivation to control. By definition, despots are individuals who have considerable social power and whose behavior is not typically constrained by psychological or social consequences. With the absence of reciprocal cultural mores (i.e., democracy) and a professional police force and military that will suppress despotic behavior, these individuals and their coalitions gained control of the first six human civilizations – ancient Mesopotamia, Egypt, the Aztec and Inca empires, and imperial India and China (Betzig, 1986, 1993). Across these and many other civilizations, the activities of despots were (and still are) centered on diverting the material and social resources of the culture to themselves and to their kin, typically to the detriment of many other people. On the basis of the historical record, they lived in opulence and the men almost always had exclusive sexual access to scores – sometimes thousands – of women (Betzig, 1986, 1992).

Regardless of how one might morally evaluate these activities, despots and their kin were better fed, in better health, and had more children than their subjects (e.g., Betzig, 1992). In addition to the historical record, a recent genetic study provides direct evidence for the reproductive benefits of despotism. In this study, Zerjal et al. (2003) analyzed the Y-chromosome genes of 2,123 men from regions throughout Asia. They found that 8% of the men in this part of the world have a single common ancestor who emerged from Mongolia and lived about 1,000 years ago. The geographic distribution of these genes fit well with the historic boundaries of the empire of Genghis Khan (c. 1162-1227), who was known to have had hundreds of wives and many, many children. They estimated that Genghis Khan and his close male relatives are the direct ancestors of 16 million men in Asia, ranging from northeast China to Uzbekistan, and the ancestors of about 0.5% of the world's total population.

Genghis Khan is, of course, an extreme example. As with other traits, it is almost certain that there are individual differences in the intensity of the motivation to control and individual differences in the manner in which it is expressed (e.g., Pratto, 1996). Heritable personality differences, for instance, might reflect the evolution of different strategies for obtaining access to social and material resources (Buss, 1991; MacDonald, 1995; McCrae & Costa, 1997; D. Rowe, 1994), with the desire for despotic control being only one of these alternative strategies (D. Wilson, Near, & Miller, 1996). However it is achieved, gaining some level of control over the activities of daily life, important social relationships, and material resources affords many of the same benefits, albeit on a much smaller scale, as those enjoyed by despots. Even in resource-rich Western culture, socioeconomic status (SES), that is, the ability to influence other people and control material resources, is associated with a longer life span and better physical health

(e.g., Adler, et al., 1994; R. Bradley & Corwyn, 2002; Reid, 1998; Rodin, 1986), although it is not correlated with happiness or the subjective evaluation of well-being (Diener & Diener, 1996; D. Myers & Diener, 1995; Lykken & Tellegen, 1996).

In preindustrial and industrializing Western societies, and in traditional societies today (Hill & Hurtado, 1996; United Nations, 1985), SES was considerably more important than it currently is in Western culture (Hed, 1987; Herlihy, 1965; Klindworth & Volland, 1995; Morrison, Kirshner, & Molho, 1977; H. Schultz, 1991; Vallin, 1991; Volland, 1988). In fact, parental SES often influenced which infants and young children would live and which would die. As just one example, during the 1437-1438 and 1449-1450 epidemics in Florence, Italy, child mortality rates increased 5- to 10-fold and varied inversely with parental SES even at the high end of the continuum (Morrison et al., 1977). As another example, in an extensive analysis of birth, death, and demographic records from 18<sup>th</sup> century Berlin, H. Schultz (1991) found a strong correlation ( $r = .74$ ) between parental SES and infant and child mortality rates. Infant (birth to 1 year) mortality rates were about 10% for aristocrats but more than 40% for laborers and unskilled technicians.

A senior official of the welfare authorities (Armenbehörde) observed in 1769 that among the poor weavers of Friedrichstadt 75 out of every 100 children borne died before they reached 'adulthood' (presumably twelve years of age). ... He rightly regarded the poverty or affluence of the parents as the decisive factor in determining whether the children thrived or died... (H. Schultz, 1991, p. 243).

Given these relations, it is not surprising that individual and group-level conflicts of interest are invariably over access to and control of social relationships, other people, and the biological and physical resources that covary with survival or reproductive prospects in the local ecology and culture (Alexander, 1979; Chagnon, 1988; Horowitz, 2001; Irons, 1979; Keeley, 1996). Although these relations are often masked by the wealth and low mortality rates enjoyed in Western societies today, the implication is clear: In most human societies and presumably throughout hominid evolution, gaining social influence and control of biological and physical resources, that is, food, medicine, shelter, land, and so forth, covaried with reproductive opportunity (i.e., choice of mating partner), reproductive success (i.e., offspring survival to adulthood), and survival prospects. In other words, heritable individual differences in human, and presumably earlier hominid, social competencies and behavioral strategies that enable achievement of social influence and resource control will result in the evolution of these traits, and the evolution of supporting affective, psychological, and cognitive mechanisms. A fundamental motivation to control has evolved in humans, and probably all species at an abstract level, because success at achieving control of social relationships and biological and physical resources very often meant the difference between living and dying.

### Modules and Mechanisms

Let us now turn our attention to the bottom sections of Figure 3.9, the affective, psychological, and cognitive mechanisms and underlying modular systems that support control-related behavioral strategies. I describe the modular systems at the base of the figure in chapter 5. The brain and cognitive systems that compose these modules are predicted to have evolved to



process information (e.g., facial features) in the above noted domains of resource control, that is, social (conspecifics), biological (e.g., other species that serve as food or medicine), and physical (e.g., demarcating the group's territory). As I noted earlier and will elaborate in chapter 5, biologically-oriented anthropologists and psychologists refer to these modular systems as components of folk psychology, folk biology, and folk physics, respectively (e.g., Atran, 1998; Baron-Cohen, 1995; Brothers & Ring, 1992; Carey & Spelke, 1994; Coley, 2000; R. Gelman, 1990; Humphrey, 1976; Povinelli & Preuss, 1995; Premack & Woodruff, 1978; Pinker, 1997). The point for now is that these systems draw attention to and process information patterns that have covaried with survival and reproductive outcomes during hominid evolution and are thus integral features of the behavioral strategies needed to achieve these outcomes.

### Mechanisms

Psychological. As I describe in greater detail in chapter 7 (Mental Models and the Motivation to Control and Social Cognition and Folk Psychology sections), psychological mechanisms are conscious, explicit mental representations of situations that are centered on the self and one's relationship with other people and one's access to biological and physical resources that are of significance in the culture and ecology in which the person is situated. The representations are of past, present, or potential future states and might be cast as visual images, in language, or as memories of personal experiences (i.e., episodic memories). In chapter 7, I emphasize the ability to create a mental representation of a desired or fantasized state, such as a relationship with another individual, and to compare this to a mental representation of one's current state, such as the nature of the current relationship with this other individual. These are psychological representations of present and potential future states that are of personal significance and are the content on which more general reasoning and problem-solving processes are applied. These psychological representations might also result in the generation of feelings associated with the current psychological state or potential changes in this state (Damasio, 2003).

Explicit attributions about the self or other people provide further examples of psychological representations. It is common for people, as an illustration, to make attributions about the cause of failures to achieve social influence or other desired outcomes. An attribution of this type might involve an explicit evaluation about the reason for one's failure to achieve a desired outcome – determining that the failure was due to bad luck – and would function to direct and maintain control-related behavioral strategies in the face of any such failure (Heckhausen & Schultz, 1995). Another example involves attributions about favored in-group members and disfavored members of an out-group. These attributional biases have been extensively studied under laboratory conditions and are particularly salient during times of intergroup competition and hostilities (e.g., Stephan, 1985). Horowitz's (2001) seminal analysis of ethnic conflict in the real world is consistent with these laboratory studies and with the position that conflict is invariably over resource control. Hostile and otherwise unfavorable attributions about the character and intentions of the out-group often include rumors of an intended out-group attack or conspiracy to, for instance, poison the in-group's food supply, attack the women, and so forth. These attributional biases justify, facilitate (e.g., gaining support of other members of the in-group), and precede violence. The resulting conflict is often deadly and just as often results in the self-serving elimination of economic or social competitors. The attributional biases not only justify this self-serving violence, they simultaneously protect individuals from the affective consequences, such as guilt and remorse, which could result if the violence were directed against a member of the in-group.

Cognitive. I also describe in chapter 7 the cognitive mechanisms that operate on psychological content (Brain and Cognitive Systems section), including working memory, attentional control, and the ability to inhibit automatic processing of external information (e.g., Baddeley, 2000a; Bjorklund & Harnishfeger, 1995; Cowan, 1988). I describe associated reasoning and problem-solving competencies in chapter 6 (Newell & Simon, 1972). These cognitive and problem-solving processes are the mechanisms that allow individuals to mentally represent and manipulate information processed by sensory and perceptual systems (e.g., sounds, and words; Baddeley & Hitch, 1974), and the more complex forms of information processed by the social, biological, and physical modules. Working memory, for instance, enables the short-term retention of spoken utterances, which may facilitate vocabulary learning and other specific competencies.

However, the most important function from the perspective of this book concerns the relation between these cognitive and problem-solving mechanisms and the generation of and manipulation of psychological representations. In other words, working memory and attentional and inhibitory control are the content-free mechanisms that, for instance, enable the integration of a current psychological state with memory representations of related past experiences, and the generation of mental models or simulations of potential future states (Alexander, 1989; Baddeley, 1994; Johnson-Laird, 1983). Perhaps this fine a distinction between cognitive and psychological processes is unnecessary, but I have done so to emphasize that the content of mental representations (the psychological component) is important from an evolutionary perspective. In much of the research in experimental psychology, the focus is on cognitive mechanisms, such as working memory, and not so much on the content on which these mechanisms operate (Miyake & Shah, 1999).

### Evolutionary Function

My proposal in chapter 7 (Problem Solving and Human Evolution section) is that the evolved function of these cognitive mechanisms and the above noted psychological mechanisms is to generate a mental representation of the social, biological, and physical world. I assume that humans are biased to generate a fantasy representation of how the world “should” operate, that is, a representation of the world that would be most favorable to the individual’s reproductive (e.g., fantasy of the “perfect” mate; Whissell, 1996) and survival interests. This mental representation serves as a goal to be achieved and is compared against a mental representation of current circumstances. Working memory mechanisms then serve as a platform for simulating social and other behavioral strategies that will reduce the difference between the ideal and actual states. These problem solving (Newell & Simon, 1972) activities are ultimately directed toward the goal of attempting to achieve access to and control of social and other resources, as noted.

Following Damasio’s (2003) distinction, affective mechanisms are separated into emotions, which are observable behaviors (e.g., facial expressions or social withdrawal), and feelings, which are nonobservable conscious representations of an emotional state or other conditions that can potentially influence the individuals’ well being (see Mental Models and the Motivation to Control section of chapter 7). Affective mechanisms guide behavioral strategies. The associated emotions provide feedback to other individuals (e.g., a frown may automatically signal disapproval) and feelings provide feedback to the individual (Campos, Campos, & Barrett, 1989). The latter provides an indicator of the effectiveness of control-related behavioral

strategies. Positive feelings provide reinforcement when strategies are resulting in the achievement of significant goals, or at least a reduction in the difference between the current and desired state, and punishment (negative feelings) and disengagement when behaviors are not resulting in this end (J. A. Gray, 1987; Henriques, 2000).

The associated brain systems should function, in part, to amplify attention to evolutionarily significant forms of information, such as facial expressions, and produce emotions, feelings, and corresponding behavioral tendencies that are likely to reproduce outcomes that have covaried with survival or reproduction during hominid evolution (Damasio, 2003; Lazarus, 1991; Öhman, 2002). For instance, positive affect should function, in part, to maintain the forms of social relationship that are commonly associated with the achievement of survival and reproductive ends, and this appears to be the case. Happiness is strongly related to the strength of reciprocal and romantic relationships (Diener & Seligman, 2002), the former being sources of social support and allies during times of social conflict and the latter obviously related to reproductive goals.

As argued by Darwin (1872/1998) and confirmed by contemporary scientists (e.g., Ekman, 1992), emotions are effective social signals that influence the emotions, feelings, and behavior of other people. Hagen (1999, 2003) has cogently argued that affective states, such as depression, can result in a host of social and behavioral changes that may be a form of social manipulation, that is, a strategy to organize the social world in ways that enhance the individual's self interest. As an example, postpartum depression involves social withdrawal and a shutting down of behavioral systems associated with care of the newborn and the self. This form of depression is expressed through behaviors and emotional signaling and often occurs when the new mother does not have adequate social or economic support (Hagan, 1999). The behavioral depression is a reaction to this lack of support and is simultaneously analogous to a labor strike, whereby the woman signals she will not invest in the well-being of the newborn. The newborn's father and other kin are, of course, invested in the well-being of the newborn and often respond to the mother's depression by providing additional social or economic support to the mother and the newborn. In this view, postpartum depression can be an emotional/behavioral strategy that elicits investment in the newborn and the mother that they otherwise would not receive. Moreover, because the mother is "suffering" the risk of social retribution for not providing the expected level of maternal care is reduced.

### Summary and Conclusion

Much is now known about human origins and our hominid ancestors, despite the sometimes rancorous debates about the associated evidence and its implications for understanding human nature (e.g., Wolpoff et al., 2000; Templeton, 2002). To be sure, the fossil record is incomplete and subject to legitimate scientific disagreement, but if one peers through the dust generated by these disagreements an interpretable pattern can be seen. Whether our ancestral line stretches back to A. garhi or to A. africanus matters little to the issues addressed here. Individuals of these and other australopithecine species had larger brains than extant chimpanzees, but brain volumes that were about 1/3 that of modern humans, and an EQ that was less than 1/2 that of modern humans. Given that one of these, or some yet to be discovered sister species, was the ancestral species of modern humans, a high level of confidence can be placed on the conclusion that substantial changes in brain volume, EQ, and brain organization have occurred since the emergence of the genus Homo. Whether H. habilis was a member of this

genus or an australopithecine is less important than the clear and substantial increases in brain volume and EQ that were associated with the emergence of *H. erectus* – there is general agreement that this was indeed an ancestor of modern humans (B. Wood & Collard, 1999) – and further increases with the emergence of humans.

The primary concern here is the selection pressures that drove these changes, and this is where the issues become more clouded. In fact, as I noted earlier and will discuss more fully in chapter 4 (Allometry and Size of the Neocortex section), there is debate as to whether the increases in brain volume and EQ during hominid evolution were the result of evolutionary selection at all or simply a by product of the evolution of other traits. The gist of Vrba's (1974, 1995b) climate-driven turnover pulse hypothesis is that much of the change in brain volume and EQ during hominid evolution was an incidental effect of increases in body size. There are many reasons, as I described earlier, for questioning this conclusion, not the least of which being that the calculation of EQ controls for changes in body size. Nonetheless, the speciation events predicted by the model might explain the adaptive radiation and emergence of several species of hominid 3.0 to 2.0 MYA, one of these species being the ancestor of modern humans.

My conclusion and that of most other scientists is that some combination of ecological and social pressures drove the evolution of brain and cognition during human evolution. The basic issues concern whether the primary selective pressures were largely ecological or social in nature. There is a tendency for anthropologists to emphasize ecologically-based adaptations, such as those involved in acquiring (e.g., through hunting) and processing (e.g., cooking) food (e.g., Kaplan et al., 2000; Wrangham et al., 1999), and a tendency of primatologists and psychologists to emphasize social adaptations, such as those required to maintain reciprocal relationships or to socially manipulate conspecifics (e.g., Dunbar, 1993; Humphrey, 1976). Alexander's (1989; see also Flinn, Geary, & Ward, 2003) model of ecological dominance combines the two classes of selection pressure, with adaptations to ecological pressures being primary earlier in human evolution and adaptations to social pressures being primary later in human evolution.

My motivation-to-control framework builds on Alexander's (1989) proposal and attempts to bundle these different forms of selection pressure together and link them to the affective, psychological (e.g., attributional biases; Stephan, 1985), and cognitive (e.g., working memory; Baddeley, 2000a) processes that are traditionally studied by psychologists. The gist is that affective, psychological, and cognitive processes support behavioral attempts to gain access to and control of the types of social (e.g., mates), biological (e.g., food), and physical (e.g., territory) resources that have tended to covary with survival and reproductive outcomes during human evolution (Geary, 1998). The framework also provides a means of linking these psychological and cognitive mechanisms to general intelligence and thus provides a means to link ecological and social selection pressures to the evolution of general intelligence. The basic argument is that many of the same mechanisms that support the motivation to control, such as efficiency of working memory and problem solving mechanisms, appear to contribute to individual differences in general intelligence. The motivation to control thus provides the link between models of brain and cognitive evolution and empirical research on general intelligence, as I describe in chapter 8 and chapter 9. Before these links can be fully integrated into an evolutionary perspective, discussion of research and theoretical issues associated with the evolution and development of the brain and cognitive modularity must be addressed and are thus the subject of the next two respective chapters.

