

19 • Evolutionary origins of great ape intelligence: an integrated view

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Among the great apes that once ranged the forests of the Old World, only four species survive. Their evolutionary history reveals a huge range of morphological and behavioral diversity, all of which must be considered successful adaptations in their own time. Some of these attributes (large brains, sclerocarp and hard-object feeding, frugivory, folivory, gigantism, terrestriality, and suspensory positional behavior) survive in modern great apes. Our questions are: what combination of behaviors and attributes characterized the ancestor of living great apes? what was the significance of this suite of features for cognition? and how did it arise in evolution? To that end, we offer our model of a distinct great ape cognition along with its biological underpinnings and environmental challenges, then attempt to trace the evolutionary origins of this ensemble of features.

COGNITION

All living great apes express a distinctive grade of cognition intermediate between other nonhuman primates and humans. Their cognition normally reaches rudimentary symbolic levels, where symbolic means using internal signs like mental images to stand for referents or solving problems mentally. It supports rudimentary cognitive hierarchization or metarepresentation to levels of complexity in the range of human 2 to 3.5 year olds, but not beyond (in this volume, see Blake, Chapter 5, Byrne, Chapter 3, Parker, Chapter 4, Russon, Chapter 6, Yamakoshi, Chapter 9).

Great apes' high-level cognitive achievements are generalized in that they manifest system wide and relatively evenly across cognitive domains (Russon, Chapter 6, this volume). Evolutionary reconstructions, however, have typically fixed on specific high-level abilities, singly or in combination, such as self-concept or intelligent tool use (see Russon, Chapter 1, this volume).

While the challenges these abilities address may have provided the evolutionary impetus to enhancing great ape cognition, evolutionary reconstructions have more to explain than these. No single ability, combination of abilities, or cognitive domain encompasses what sets great ape cognition apart. In the physical domain, great apes do use tools in ways that require their grade of cognition (Yamakoshi, Chapter 9, this volume) but they devise equally complex manual techniques (Byrne, Chapter 3, this volume) and solve equally complex spatial problems (Hunt, Chapter 10, Russon, Chapter 6, this volume). They show exceptionally complex social cognition in social routines, scripts, and fission–fusion flexibility, as well as in imitation, teaching, self-concept, perspective-taking, deception, and pretense (in this volume see Blake, Chapter 5, Parker, Chapter 4, Russon, Chapter 6, van Schaik *et al.*, Chapter 14, Yamagiwa, Chapter 12). Their communication reaches rudimentary symbolic levels, even considering only strictly defined gestures and language (Blake, Chapter 5, this volume), as does their logico-mathematical cognition (e.g., analogical reasoning, classification, quantification) (e.g., Langer 2000; Thompson & Oden 2000). The latter has not figured in evolutionary reconstructions but perhaps it should. Enhanced logico-mathematical capacities offer important advantages; classification and quantification, for example, may aid in managing great apes' broad diets and social exchange (Russon 2002), and analogical reasoning may support limited cognitive interconnections (see below). Others have also emphasized generalized features of great apes' cognitive enhancements (in this volume, Byrne, Chapter 3, Parker, Chapter 4, Russon, Chapter 6, van Schaik *et al.*, Chapter 11, Yamakoshi, Chapter 9). Features our contributors identify include regular, sequential plans of many actions, hierarchical organization, bimanual role differentiation, complex

event representations, scripts and routines, and coordinating more components in solving a task.

Individual great apes can also interconnect abilities from different domains to solve a single problem or use one ability to facilitate another (Russon, Chapter 6, this volume). This is an important source of cognitive power because it enables solving multifaceted problems and boosts problem-specific abilities. It is not commonly recognized in great ape cognition but evidence for its role in exceptionally complex achievements in the wild, for example Tai chimpanzees' cooperative hunting, suggests that it should. It is important in evolutionary perspective because it is a plausible source of the "fluidity of thought" or "multiple intelligences working together" that stands out in humans. Its appearance in great apes ties well with evidence that some of their species-typical problems require coordinating abilities across cognitive domains, for example adjusting foraging strategies as social needs, feeding needs, and their interactions fluctuate (Yamagiwa, Chapter 12, this volume). It also speaks to claims that only humans have this capacity.

Great apes' cognitive achievements appear to be products of generative systems, i.e., systems that construct problem-specific cognitive structures to suit the particular challenges encountered. Their skills in stone nut cracking (Inoue-Nakamura & Matsuzawa 1997), language (Miles 1991; Miles, Mitchell & Harper 1996), and classification (Langer 1996) all show constructive processes. Models characterizing great ape cognition in terms of centralized constructive processes like hierarchization or hierarchical mental construction take this position (Byrne 1995; Gibson 1993). Hierarchization is especially important because hierarchical cognitive systems may be intrinsically generative (Gibson 1990; Rumbaugh, Washburn & Hillix 1996). Generativity helps explain several ostensibly anomalous features of great ape cognition that have incited debate – notably, achievement variability across individuals, tasks, rearing/testing conditions, and communities, and "atypical" abilities that emerge with special rearing. If great apes' cognitive systems are generative, these "anomalies" may simply be normal expressions of generative cognitive systems.

Development is a defining feature of primate cognition. Distinctive in great apes is prolonging cognitive development beyond infancy and emergence of their distinctively complex achievements during juvenility (Parker & McKinney 1999). Prolonged cognitive development probably relates to their more complex social

and ecological challenges compared with other anthropoid primates (Byrne, Chapter 3, Parker, Chapter 4, van Schaik *et al.*, Chapter 11, Yamagiwa, Chapter 12, Yamakoshi, Chapter 9, this volume) coupled with the longer time they need to grow their exceptionally large brains (Ross, Chapter 8, this volume). Great apes' enhanced cultural potential (e.g., more powerful social learning, greater social tolerance) is considered essential to their cognitive development, underlining how difficult these challenges must be. Even with larger brains and more time to learn, immature great apes need more sophisticated and extensive social support than other anthropoid primates.

Many cognitive features believed critical to hominin evolution are then shared by great apes, including symbolism, generativity, and cognitive fluidity as well as specific abilities like complex tool use and manufacture, mental representation of absent items, perspective taking, cooperative hunting, food sharing, and symbolic communication. While great apes share these features only to rudimentary symbolic levels, these achievements are significant comparatively. Rudimentary symbolism in particular has been taken as an exclusively human leap forward in cognitive evolution. If great apes share this capacity, however, it must have evolved with ancestral hominids.

BIOLOGICAL BASES OF GREAT APE COGNITION

The brain

Efforts to establish what in the brain confers high cognitive potential have focused on brain size because it predicts many other brain features (e.g., structures, gyrification, organization). The picture for great apes remains unclear because all available size measures are problematic as indices of cognitive potential and samples of great ape brains have typically been very small (see Begun & Kordos, Chapter 14, MacLeod, Chapter 7, Ross, Chapter 8, this volume). As larger samples are becoming available, within-species variation is appearing to be extensive, so the many published findings based on small samples must now be treated as suggestive. These limitations in mind, modern great ape brains suggest the following cognitive characterization.

Great apes brains appear to follow a distinctively "ape" design (MacLeod, Chapter 7, this volume). All apes, compared with other nonhuman anthropoids,

show more complex cerebral convolutions and an augmented neocerebellum. The neocerebellum connects extensively with the cerebral cortex, and primarily through it the cerebellum contributes to cognitive processes such as planning complex motor patterns, visuospatial problem solving, and procedural learning. These cognitive processes support skills apes need as suspensory frugivores, for example spatial memory, mapping, and complex manipulation. A large sample of primate brains also suggests that apes may have disproportionately larger brains for their body size than other anthropoids; this finding is tentative and runs counter to standard views, but it is consistent with these structural distinctions (see MacLeod, Chapter 7, Ross, Chapter 8, this volume). A distinctive ape brain is also consistent with apes' distinctive life histories: living apes have disproportionately prolonged immaturity with delay concentrated in the juvenile period (Ross, Chapter 8, this volume); fossil hominoids may have shared this pattern (Kelley 1997, Chapter 15, this volume).

Great apes' higher cognitive potential over lesser apes, system wide, may well be a function of absolutely large brain size and its allometric effects on morphology. Large brains provide more "extra" neurons for cognition (Gibson, Rumbaugh & Beran 2001; Rumbaugh 1995). Lesser apes' brains resemble great ape brains morphologically but resemble typical anthropoid brains in absolute size (Begun, Chapter 2, this volume), and do not show these cognitive enhancements. Large brains are also more extensively interconnected; this may enable more complex cortical processing by enabling parallel processing and distributed networks, and so enhance problem solving via simultaneous processing in multiple areas of the cortex and their connecting structures (Gibson 1990). This fits well with great apes' capacity for solving complex problems by interconnecting multiple cognitive structures.

Many specific brain features that distinguish great apes can also be explained by their brains' absolutely large size (e.g., greater lateralization, neocortex expansion, specialized areas). Even if these features owe principally to larger brain size, they can translate into important differences in cognitive potential. Brain structures that increase in size with increases in overall brain size do so at differential rates. Structures implicated in cognition (e.g., neocortex, cerebellum) typically increase at higher rates, so they come to represent a larger percentage of the brain in larger-brained species. For this reason great apes have relatively larger neocerebellar

structures, magnifying the cognitive advantages of an ape cerebellum. This cerebellar advantage may contribute to handling the more severe tasks that great apes face as extremely large-bodied suspensory primates. Large brain size also increases demands on cerebral cortical connectivity that, in humans, may have favored neocortical reorganization towards lateralization and locally specialized functional units (Deacon 1990; Hopkins & Rilling 2000). Great ape brains, all weighing over 250 g, appear to be large enough to experience similar effects: they show two specialized structures implicated in sophisticated communication, a planum temporale and spindle neurons of the anterior cingulate cortex, which are otherwise found only in humans. That the allometric effects of large brain size likely brought specialized structures along with greater interconnectiveness may be related to the co-occurrence of problem-specific and interconnected cognitive structures in great apes and humans.

Life histories

Life history traits are fundamental attributes of a species' biology that govern the pattern of maturation from conception to death (e.g., gestation period, age at weaning, maturation rate—age of female first reproduction, inter-birth interval, longevity). These traits typically occur in packages that fall roughly along a continuum of fast–slow rates of life. They correlate highly with body and brain size, but some taxa depart dramatically from the predicted life history–body size relationship. For their body sizes, primates have greatly protracted life histories with notably delayed maturation compared with most other mammals. Links between the brain and life histories may suggest broader biological factors associated with high cognitive potential. Reasons for specific scaling factors are typically explored by assessing links among ecological, brain, and life–history features.

Anthropoid brain size is linked with delayed maturation, in particular prolonged juvenility. Anthropoids may then make tradeoffs against juvenile growth rates to support their large brains, diverting energy away from body growth to support the brain. Even after removing body size effects, juvenility appears to be further prolonged relative to body size in apes. Great apes may do the same thing to a greater degree. Slower body growth probably affects juveniles, even though most primate brain growth occurs in infancy, because caregivers withdraw support at weaning (Ross, Chapter 8, this volume).

Juveniles' immature foraging skills and the slow rate at which great apes learn, added to withdrawal of caregiver nutritional subsidies, can only prolong the period in which their energy intake does not meet the energetic needs of supporting the brain and body growth. Especially in apes, prolonged juvenility may be best explained as an unavoidable but bearable cost imposed by large brains, rather than as directly adaptive (Ross, Chapter 8, van Schaik *et al.*, Chapter 11, this volume). No clear links occur between the brain and life history in great apes as a distinct group (Ross, Chapter 8, this volume).

Body size

There is no question about great ape body sizes – all are exceptionally large for primates – or about correlations between their large body size and their large brain size (Ward *et al.*, Chapter 18, this volume). Yet the reasons for this relationship are unresolved: direct cause–effect in one direction or the other, parallel adaptations to other selection pressures, or byproducts of selection on related factors.

Because brains scale to body size, ratios between the two have been used to index a species' "encephalization," the extent to which its brain has increased in cognitive potential, by assessing its enlargement beyond the size predicted by its body size. By these measures, great apes appear no more encephalized than other anthropoids: their brains are not relatively larger given their body size, even if they are absolutely larger (but see MacLeod, Chapter 7, this volume). This has prompted some to suggest that body size is the driving evolutionary adaptation and that great apes' large brains are mere side effects of their large bodies (e.g., see MacLeod, Chapter 7, this volume). Analyses that simply seek to "remove body size effects" implicitly take this view. Brain–body mass relationships are much more complex than such corrections suggest (Begun & Kordos, Chapter 14, Ward *et al.*, Chapter 18, this volume) and no acceptable method has yet been developed to apportion relative percentages of brain mass related directly to body mass and to selection for absolutely bigger brains.

ENVIRONMENTAL PRESSURES ON COGNITION

Establishing the function and evolution of complex cognition and its biological underpinnings involves

exploring related behavioral challenges. Behavioral challenges affecting modern great apes are often used to suggest evolutionary selection pressures that may have shaped their cognitive enhancement. Their counterparts in evolutionary history are inferred from indirect indices, for example diet from dental morphology. Ecological challenges that primarily tap physical cognition include diet/foraging (Parker & Gibson 1979), diverse "technical" difficulties (Byrne 1997), and arboreality (Povinelli & Cant 1995). Social challenges, which tap both social and communicative cognition, involve both competition and cooperation (e.g., Byrne & Whiten 1988; Parker 1996; van Schaik *et al.*, Chapter 11, this volume). In light of our characterization of great ape cognition and contributions to this volume, we reconsider these challenges.

Ecological challenges

Food is considered a primary limiting ecological factor of primate populations because of its sparse distribution and anti-predator defenses (Yamagiwa, Chapter 12, this volume). Features considered to challenge cognition include eclectic frugivory, very large dietary repertoires and correspondingly large ranges, and essential "technically difficult" foods. Interest in difficult foods has focused on embedded foods, especially those that elicit tool use, but foods protected by other defenses such as barbs or noxious chemicals and obtained manually present comparable cognitive challenges (e.g., Byrne & Byrne 1991, 1993; Russon 1998; Stokes & Byrne 2001). The distribution of tool use in the wild (chimpanzees and orangutans) probably reflects opportunity and not differential hominid cognitive potential. Bonobos and gorillas can both use tools when opportunities arise.

Fallback foods on which great apes rely during fruit scarcities are often difficult to obtain. This may be especially true of the fallback foods on which orangutans and chimpanzees rely, some of which elicit use of foraging tools in the wild (Yamakoshi 1998; Yamagiwa, Chapter 12, this volume). Seasonal fruit scarcities also probably contribute to great apes' extremely broad dietary repertoires and their flexibility in using individual foods. Cognitively, the latter may require interpreting local indices of change to detect the availability of particular foods, given that great apes inhabit the tropics where seasonal change can be irregular. The last common ancestor (LCA) was also a generalized frugivore that may also

have consumed hard foods needing preparation prior to ingestion and inhabited seasonal forest habitats that probably imposed periodic fruit scarcities. By implication, the same dietary pressures affecting modern great apes also affected the LCA: seasonality, dietary breadth, and the need for fallback foods.

Arboreal locomotion and navigation, two spatial problems, present extreme cognitive challenges to great apes because of their extremely large bodies and forest habitats. Navigating large ranges effectively and efficiently may require mapping skills sophisticated enough to calculate routes and distances mentally. Povinelli and Cant (1995) hypothesized that the great apes' work-it-out-as-you-go, non-stereotypic modes of arboreal locomotion, for example cautious clambering and gap crossing, require minds with the representational capacity to figure in the self. These "cognitive" positional modes are neither shared among nor unique to all living great apes, however (Gebo, Chapter 17, Hunt, Chapter 10, this volume). They are prominent in orangutans and lesser apes but not African great apes. They could have influenced great ape cognitive evolution if the LCA was a large arboreal clamberer but this is uncertain, perhaps even unlikely (Gebo, Chapter 17, this volume). Povinelli and Cant suggested *Oreopithecus* as a model of that ancestor, with the requisite large size and body plan for arboreal clambering. *Oreopithecus* was otherwise very unlike other hominids, however (e.g., folivorous versus frugivorous, unusually small brained), and probably represents an isolated adaptation to a refugium rather than great apes' ancestral condition (see Begun & Kordos, Chapter 14, Gebo, Chapter 17, Potts, Chapter 13, Singleton, Chapter 16, this volume). Even if arboreal locomotion demands complex cognition in orangutans, there is little to indicate that it does, or did, in the great ape lineage.

Social challenges

Primate social life is recognized as having high potential for cognitive complexity. It is puzzling about great apes that they use more complex cognition than other anthropoids to solve social problems, but the problems themselves are not obviously more complex. Their social unit sizes are well within the range of other anthropoids, their demographic composition is no more complex, and few if any more complex social phenomena are known (van Schaik *et al.*, Chapter 11, this volume). To add to

the puzzle, great ape species differ widely in their social systems but are very similar in cognitive potential.

Van Schaik *et al.* propose social challenges in great apes that may help explain their enhanced social cognition: fission–fusion tendencies with individuals out of contact with conspecifics for lengthy periods and foraging females solitary; relatively high subordinate leverage leading to less rigid dominance and enhanced social tolerance; greater intrasexual bonds with non-kin, and extensive flexibility in social organization and affiliation. These are clearly shared by chimpanzees and orangutans, and perhaps by the other species. Most are consequences of large size and exceptionally slow life histories, which reduce vulnerability to predators, increase vulnerability to hostile conspecifics, increase the potential for contest competition (especially for females and in species unable to switch to high-fiber fallback foods), and favor non-kin bonding. They require more complex cognition to handle greater flexibility in social relations and interactions and in the interplay among a more complex array of labile factors (e.g., balance rivalry with interdependence, or social with predation or foraging pressures). Rejoining conspecifics after lengthy absences increases needs for sophisticated navigation, distance communication, and renegotiating relationships. Two examples of complex communication in wild great apes concern rejoining companions: tree drumming (Boesch & Boesch-Achermann 2000) and placing indicators of travel direction (Savage-Rumbaugh *et al.* 1996). Higher subordinate leverage, less rigid dominance, and enhanced social tolerance are likely to improve opportunities for social learning, cultural transmission, and more flexible use of eye contact (Yamagiwa, Chapter 12, this volume). Similar social complexities also occur in some monkeys (capuchins, some macaques), however, so alone they cannot explain the enhanced cognition seen in great apes.

Great ape sociality should be affected by diet because social groups must adjust to ecological conditions. Effects probably differ more in great apes than in other anthropoids because of great apes' broad, technically difficult, and seasonally varying diet (Yamagiwa, Chapter 12, this volume). Social foraging strategies during fruit scarcities, when dietary and social competition pressures are at their worst, expose these effects. Significant to cognition is that great ape foraging groups change as a function of food availability, although patterns differ between species depending in part on the

preferred type of fallback food. This is consistent with suggestions that fission–fusion in *Pan* functions to allow flexibility in handling challenges that vary over time and space (Boesch & Boesch-Achermann 2000), great ape life allows and requires facultative switches between solitary and gregarious foraging (van Schaik *et al.*, Chapter 11, this volume), and ephemeral activity subgroups show exceptional flexibility relative to ecological conditions (Parker, Chapter 4, this volume). All great apes then share the challenge, as a normal circumstance, of complex problems wherein pressures from two distinct cognitive domains interact.

EVOLUTIONARY RECONSTRUCTIONS

The origin of great ape cognitive capabilities is to be found in the Miocene, when the great apes originated and diversified. Here, we examine the evidence of brain size and morphology, life history, body size, positional behavior, diet, and environment in ancestral hominoids as they relate to the evolution of great ape intelligence. Patterns are summarized in Table 19.1.

Ecology: habitat and diet

The local habitats of early Miocene hominoids were most likely warm, moist forests in tropical and subtropical zones that enjoyed low seasonality and climatic stability (Andrews, Begun & Zylstra 1997; Potts, Chapter 13, this volume). Soft fruit, their dietary mainstay (Singleton, Chapter 16, this volume), would have been available year-round, albeit patchily distributed spatially and temporally.

Hominid emergence in the late middle Miocene, 14–12 Ma, coincides with increasing climatic fluctuation, especially increasing seasonality (Potts, Chapter 13, this volume). This may have restricted soft fruit availability for several months annually, at least in some regions. The earliest Eurasian hominoid, *Griphopithecus*, which is more modern in dental anatomy than *Proconsul*, shows for the first time a fully developed suite of masticatory characters indicative of hard-object feeding (Güleç & Begun 2003; Heizmann & Begun 2001; Singleton, Chapter 16, this volume). The ability of the ancestors of hominids to exploit hard objects may have allowed their expansion into Eurasia at the end of the early Miocene, as a way of avoiding competition with the many frugivores making the same trip northward (Heizmann & Begun

2001). In later hominids, the ability to exploit these resources may have served as an important parachute during times of scarcity in more seasonal environments when soft fruits, generally preferred by hominids, are more difficult to find. Greater seasonality is indicated in both Europe and Asia in the late Miocene, suggesting fruit scarcities with hard objects serving as fallback foods in some taxa. *Sivapithecus* is often reconstructed as having had an essentially soft fruit diet based on microwear (Teaford & Walker 1984), although morphologically it shared many features with hard-object feeders (thick enamel, low, rounded cusps, large molars, thick, massive mandibles), suggesting an ability to exploit hard objects when needed. *Dryopithecus* was not a hard-object feeder and may have lived in less seasonal environments than *Sivapithecus* (Andrews *et al.* 1997; Begun 1994; Singleton, Chapter 16, this volume; Potts, Chapter 13, this volume). However, seasonality was probably greater in environments inhabited by *Dryopithecus* than in most early Miocene hominoid environments, and evidence of the anterior dentition suggests enhanced abilities for pre-ingestive processing of embedded foods (Begun 1992). Either way, late Miocene hominids probably extended their frugivory with fallback foods during fruit scarcities. Their large body size may also represent a response to increased seasonality because it enhances energy-storing capacities for surviving periods of fruit scarcity (Knott 1998; Yamagiwa, Chapter 12, this volume). Living great apes show similar dietary breadth. Species differ in how they adjust to fruit scarcities, but all share the overall pattern of relying on fallback foods. Orangutans and chimpanzees use “hard” fallback foods (e.g., embedded, barks, pith), perhaps analogous to *Sivapithecus*, and gorillas and bonobos lean to folivory (although bonobos appear to enjoy especially rich habitats abundant with THV, which may or may not serve as fallback foods), possibly more similar to the *Dryopithecus* strategy. These environmental pressures and species traits imply considerable cognitive–behavioral adaptation, all in the direction of increased flexibility or adaptability (Potts, Chapter 13, this volume).

The latest Miocene experienced cooling, drying, and more pronounced seasonality, causing a worldwide shift from moist, warm forest to drier, open grassland and a corresponding shift in vegetation (Cerling *et al.* 1997; Potts, Chapter 13, this volume). Effects on hominids’ preferred habitats, moist warm forests, include shrinkage, fragmentation, and retreat. Preferred

Table 19.1. Selection pressures and biological traits in modern great apes and ancestral hominoids

Epoch	Ma	Species	Brain ^{4,5,8}			Body		Environments		Sociality		
			Size (g)	Morphology	Life history	Size (kg-f)	Anatomy ^{3,7}	Diet ²	Local	Regional & global	Sexual dimorph ⁸	Organization
<i>Modern</i>												
		<u>Chimpanzee</u>	325	GA	DM PJ	34-60	Semi-terrestrial knucklewalk & climb	Fruit + hard fallback + omnivory	F-W to O, S+, T	High seasonal Fruit scarcity	Low	(f-f+)
		<u>Bonobo</u>	314	GA	DM PJ	33-45	Mixed knucklewalk & climb	Fruit + THV	F, S-, T		Low	(f-f+)
		<u>Gorilla</u>	426	GA	DM PJ	71-175	Semi-terrestrial knucklewalk & climb	Fruit + folivory fallback, folivory	F, S+, T		High	(f-f+)
		<u>Orangutan</u>	288	GA	DM PJ	36-79	Suspensory clamber & climb	Fruit + hard fallback	F, S+, T		High	(f-f+)
<i>Early Miocene</i>												
20-6		<u>Morotopithecus</u> (E Africa)				30-35?	?Suspensory primitive brachiate & climb	Soft fruit		Less seasonal fluctuation	High	
20-18		<u>Proconsul</u> (E Africa)	146	H [†]	(DM)	10-15	Pronograde arboreal quadruped & climb	Soft fruit	F-W, S-		High	
18-17		<u>Afropithecus</u> (E Africa)			(DM)	25-30	Pronograde arboreal quadruped & climb	Hard object	F-W, S-		High	

Table 19.1. (cont.)

Epoch	Ma	Species	Brain ^{4,5,8}		Body		Environments		Sociality											
			Size (g)	Morphology	Life history	Size (kg-f)	Anatomy ^{3,7}	Diet ²	Local	Regional & global	Sexual dimorph ⁸	Organization								
<i>Middle to Late Miocene</i>																				
16.5–15		<i>Griphopithecus*</i> (W Asia, C Europe, E Africa)				20–25	Prongrade arboreal quadruped & climb													
15.5–14		<i>Kenyanopithecus*</i> (E Africa)				30	Prongrade arboreal quadruped & climb													
12–9		<i>Dryopithecus</i> (Europe)	289	GA?	DM ^{5,8}	20–30	Suspensory brachiata & climb													
12.3–7		<i>Sivapithecus</i> (S Asia)			DM ⁵	20–40	Suspensory arboreal or semi-terrestrial quadruped													
10–9.5		<i>Ouranopithecus</i> (S Europe)				35?	Partly terrestrial?													
8–7		<i>Oreopithecus</i> (S Europe)	112			15	Suspensory brachiata & climb													

Notes:

Epoch: Early Miocene (22–17 Ma), Mid Miocene (17–11.5 Ma), Late Miocene (11.5–5.5 Ma).

Species: underlined, good hominid candidate; *, possible hominid candidate.

Brain: Size (for females, where available): weight in grams; (GA), estimated weight in the modern great ape range; Morphology: H, hominoid; GA, great ape (hominid)?, unknown.

Body size: size (for females, where available): size > 25 kg is interpreted as within the hominid range.

Life history: DM, delayed maturation; PJ, prolonged juvenile period; bracketed values are estimates.

Habitat: Type: F, forest, FP, forest patches; W, woodland; WG, wooded, more grassy; GP, grassy patches; SW, swamp; O, open; OP, open patches; Seasonality: S–, low; S+, higher; Zone: T, tropical; ST, subtropical.

Social: Sexual dimorphism: High (roughly 2:1 M:F); Organization: f–f+ = flexible fission–fusion.

Shading highlights significant traits in living great apes and their appearance in the fossil hominoid record.

Sources: 1, Potts, Chapter 13; 2, Singleton, Chapter 16; 3, Gebo, Chapter 17; 4, Begun & Kordos, Chapter 14; 5, Kelley 1997, Chapter 15; 6, MacLeod, Chapter 7; 7, Hunt, Chapter 10; 8, Begun, Chapter 2; 9, Ward, Flinn & Begun, Chapter 18 this volume.

foods would have been available in smaller patches and more dispersed in distribution, an ecological situation less suitable to large-bodied hominid foragers – especially in groups. Hominid presence is indicated in isolated moist forest and swamp refuges and forest–open woodland mosaics, suggesting they tracked their preferred habitats where possible. Overall, their presence was increasingly restricted southward (Begun 2001, 2002; Harrison & Rook 1997; Potts, Chapter 13, this volume).

Fewer hominids are known in the fossil record of the late Miocene after the last occurrence of *Dryopithecus* and *Sivapithecus* between about 9.5 and 7 Ma. They appear to have become extinct locally while their descendants may have moved south at this time (Begun 2001). In Europe, the most ecologically specialized hominids are known from this time. *Oreopithecus* from Tuscany had an exceptionally small brain, well-developed suspensory positional behavior and highly folivorous diet, while *Ouranopithecus* was among the largest of the Miocene hominids and had a specialized hard-food diet. It is also most likely during this time that the ancestors of the African apes and humans arrived in Africa and that gorillas shortly thereafter diverged from the chimpanzee–human clade. Recent evidence from Thailand suggests that orangutan ancestors may have first appeared in Southeast Asia at this time as well (Chaimanee *et al.* 2003). These patterns overall also suggest habitat tracking, i.e., maintaining established habitat and fruit preferences (Potts, Chapter 13, this volume).

In the Plio-Pleistocene, worldwide climate was marked by strong arid–moist and temperature oscillations, wider climatic fluctuation, instability, profound habitat variability, and arid–monsoon seasonality (Potts, Chapter 13, this volume). Hominids would have experienced increased episodic disturbance, intra-annual variability in food availability, and repeated forest contraction–expansion and fragmentation–coalescence. Predictable effects include impoverished habitat in size and quality, even greater variability in food availability and abundance, changing species communities, changing competitor and predator patterns, and variable population densities (Potts, Chapter 13, this volume). Plio-Pleistocene pressures likely led to further diversification of strategies to augment capacities for handling unpredictable habitat instabilities. Gorillas shifted towards folivory, especially for fallback foods, smaller ranges, and reduced foraging complexity. Chimpanzees shifted

to greater omnivory, including increased meat consumption, and use of savanna habitats. Bonobos maintained forest habitats and increased THV consumption. Orangutans maintained earlier diets and remained in tropical moist forests of southeast Asia, which persisted in large blocks on Borneo and Sumatra until this century. Hominins became increasingly dependent on terrestrial resources and developed a variety of approaches (megadontia, tools) to maximize dietary breadth and ecological flexibility.

The brain

Great apes' distinctive brains seem to be defined by their large absolute size and hominoid morphology. Reconstructing their evolutionary origins comes down to when and why these features evolved. This exercise remains hampered by the dearth of fossil material on ancestral apes, especially crania.

Proconsulids, early Miocene stem hominoids, were relatively unspecialized pronograde quadrupeds but were distinguished from primitive anthropoids by their large size, taillessness, powerful appendages, and brains with a few hominoid features (Begun & Kordos, Chapter 14, this volume; Kelley 1997, Chapter 15, this volume; Ward *et al.* 1991, Chapter 18, this volume). The early hominids, *Dryopithecus* in Europe and *Sivapithecus* in South Asia, are either known or supposed on indirect but solid grounds to have had brain sizes in the range of modern great apes; where known, their endocasts show greater resemblances to modern hominids than do *Proconsul* endocasts (Begun & Kordos, Chapter 14, this volume). *Sivapithecus* neurocrania are not known. For *Dryopithecus*, partial neurocrania yield brain size estimates at the low end in absolute size but at the high end relative to body mass compared with the ranges for modern great apes. The fact that great apes with brains ranging from 280 to 700 cc, or humans with brains ranging from 1000 to 2000 cc, have not been shown to differ in cognitive capacity could be taken to indicate that there is a loose causal relationship between brain mass and cognitive capacity (Kelley, Chapter 15, this volume). On the other hand, the fact that there is no overlap in brain mass between monkeys and great apes or between great apes and humans suggests that normal brain mass minima in each taxon represent thresholds for cognitive change beyond which cognition is not affected, until the next threshold is attained. If this is the case, and absolutely

large brains are what generate great apes' grade of cognition, then the rubicon represented by *Dryopithecus* and the smallest extant great apes (280–350 cc) evolved in the late middle Miocene with *Dryopithecus* and *Sivapithecus*. The emergence of the hominid-sized brain is associated with increasing seasonality, seasonal fruit scarcities, and frugivorous diet enhanced with hard foods. Though there are indications of hominid-like cerebral reorganization in *Dryopithecus*, its endocast is distinct from that of extant hominids so it is not clear whether their brains provided equivalent cognitive potential. At a minimum however, the cognitive potential of late Miocene hominids spans the considerable gap between great apes and other nonhuman primates, probably coming closer to the former.

The Plio-Pleistocene is likely to have exerted further selection pressures on hominid cognition given its negative effects of great ape habitats. Brain size has not changed, but organizational differences between extant and Miocene hominids probably occurred at this time (Begun & Kordos, Chapter 14, Potts, Chapter 13, this volume). The most telling findings from the fossil record may be that (1) partial de-coupling of size and morphology is a common feature in the evolution of catarrhine brains, and (2) hominoid brain evolution is highly diverse, with reduction in some lineages and increases in others. Some lineages experience brain mass loss in connection with body mass reduction (e.g., *Hylobates*) or independent of body mass change (e.g., *Oreopithecus*). The pattern of brain size diversity in fossil great apes more closely matches broad patterns of diet than of size (Begun & Kordos, Chapter 14, this volume), especially frugivory extended (seasonally) with challenging fallback foods. Brain size has been surprisingly stable in hominid evolution until *Homo*, despite dramatic changes and diversity in body mass, diet, positional behavior, and ecological conditions. It may be that a hominoid brain size at least 250 g represents a rubicon that generates hominid levels of cognitive and behavioral complexity. Conversely, although large bodies do not always imply large brains in hominoids, large brains always co-occur with large bodies.

Body size and life history

Fossil hominids were predominantly large bodied but somewhat smaller than living great apes. The smallest *Dryopithecus* (female *D. laietanus* and *D. brancoi*) was

probably smaller on average than the smallest living great apes, the smallest females possibly weighing about 20 kg (Begun, Chapter 2, Ward *et al.*, Chapter 18, this volume). The smallest *Sivapithecus*, female *S. punjabicus*, probably ranged from close to *Dryopithecus* in body size to as large as the smallest living hominids. Other clearly hominid taxa such as *Ouranopithecus*, other species of *Sivapithecus*, and *Lufengpithecus* are in the size range of large chimpanzees and small gorillas; so is *Morotopithecus*, though it is less clearly a great ape. The LCA was therefore almost certainly large compared with most primates. Hylobatids are small bodied, but this is probably a result of secondary reduction in size compared with the common hominoid ancestor (Begun, Chapter 2, this volume). The range of body sizes in the proconsulids is broad and overlaps with the hominids.

In addition to being the size of an extant great ape, *Sivapithecus* and *Dryopithecus* M1 emergence age estimates suggest life history prolongation roughly equivalent to that of modern great apes (Kelley 1997, Chapter 15, this volume). The stem hominoids *Proconsul* and *Afropithecus* may show the first signs of life history prolongation. *Proconsul* may have been intermediate between hominids and non-hominids in M1 emergence age (Kelley 1997, Chapter 15, this volume), although Begun & Kordos (Chapter 14, this volume) and Kelley (Chapter 15, this volume) both also find *Proconsul* to be equivalent to *Papio* in M1 emergence and brain size. *Afropithecus* may have been within the great ape ranges for M1 emergence and brain size (Kelley & Smith, 2003; Kelley, Chapter 15, this volume). However, in our view the poorly preserved neurocranium of *Afropithecus* tentatively suggests a somewhat smaller brain than in a similarly sized chimpanzee, which would be consistent with the lower end of the range of estimates of M1 emergence and brain size provided by Kelley (Chapter 15, this volume). Either way, the implication is that prolonged immaturity emerged with the hominoids but became more clearly prolonged as brain size increased with the first hominids, because of energetic constraints, social constraints, or both. There is likely a complex inter-relationship among life history, body mass, and body size that has yet to be fully understood in vertebrates in general (Ward *et al.*, Chapter 18, this volume).

Sociality

Characterizing sociality in the LCA is a highly speculative exercise resting exclusively on indirect indices.

Several features of great ape sociality result from large size and exceptionally slow life histories, both of which characterize early hominids (many Chapters in this volume). If, as argued for living great apes, large size and slow life histories give impetus to these social features, then hominids should share them. All great apes but no lesser apes also share fission–fusion tendencies that are affected by fruit scarcities and fallback foods; early hominids likely experienced similar dietary pressures, so they too may have had a fission–fusion form of sociality.

The main influence on female sociality, food availability, depends on fallback foods in great apes (Yamagiwa, Chapter 12, this volume). In chimpanzees and orangutans, which rely on similar hard fallback foods, females restrict their social grouping during fruit scarcities and increase it during periods of abundance. In gorillas and bonobos, which have more folivorous fallback patterns, females grouping patterns remain more stable. The main influence on male sociality, access to females, is primarily shaped by sexual dimorphism in great apes. In highly dimorphic orangutans and gorillas, males tend to be solitary and corral females for mating. In less dimorphic chimpanzees and bonobos, males associate with one another via dominance ranking systems. In early hominids, challenging fallback foods co-occur with high sexual dimorphism (Begun, Chapter 2, Singleton, Chapter 16, Ward *et al.*, Chapter 18, this volume), so their social systems may have resembled the orangutan's, perhaps in less dispersed form. Attributes include polygynous mating systems with solitary males attempting to monopolize multiple females or female ranges, male dominance based on size, and female associations waxing and waning with the seasons.

DISCUSSION

Stem hominoids lived in moist tropical forest habitat with low seasonality, and probably exhibited dedicated frugivory, social complexity commensurate with frugivory, polygynous social structures with relatively high male–male competition, life histories with somewhat prolonged immaturity, brains mostly of anthropoid size and design, and body mass somewhere in the range between monkeys and great apes (10–25 kg). From this starting point and considering the many factors discussed in this book, we suggest the following patterns and processes in the evolution of great ape intelligence (Figure 19.1).

Ecology

Compared with the first hominoids, the first well-known fossil hominids, *Dryopithecus* and *Sivapithecus*, inhabited middle to late Miocene moist tropical forests with greater seasonality, frugivory extended in the direction of challenging foods, polygyny/high male–male competition, life histories with prolonged immaturity and prolonged juvenility, and larger bodies and brains reaching into the modern great ape range. The greater seasonality combined with incorporation of hard or otherwise challenging foods in the diet suggests a dietary shift towards adding fallback foods requiring pre-ingestive preparation as diet supplements during fruit scarcities. Increased absolute brain size indicates increased cognitive potential. Altogether, this suggests that seasonality resulted in a more cognitively challenging diet that favored larger brains. Ecological pressures on hominids intensified under the increasingly seasonal and unpredictable conditions of the latest Miocene and Pliocene–Pleistocene. Their effects on cognitive evolution were perhaps constrained by habitat tracking, with the great apes adopting a more conservative ecological approach and the hominins exploiting more radically different environments.

Brain–Body–Sociality

In the anthropoid/hominoid phylogenetic context, hominid large brain and body size likely co-occurred with slow life histories, prolonged immaturity, lower predation risk, higher vulnerability to hostile conspecifics, stronger relations with non-kin, high subordinate leverage, and relaxed dominance. Which came first is neither interesting intellectually nor a useful question processually. We will never know, and these variables were probably a package as soon as they appeared in early hominids.

Socially, this package is consistent with unusually flexible fission–fusion tendencies and enhanced social tolerance (van Schaik *et al.*, Chapter 11, this volume). The former would have favored larger brains for more complex social problem-solving; the latter may have further boosted cognition by enhancing conditions for socio-cultural learning. Some social intelligence models argue for an “arms race” in cognition, once cognitive solutions to social problems take hold, because competing successfully depends on outwitting increasingly savvy conspecifics (e.g., Ward *et al.*, Chapter 18,

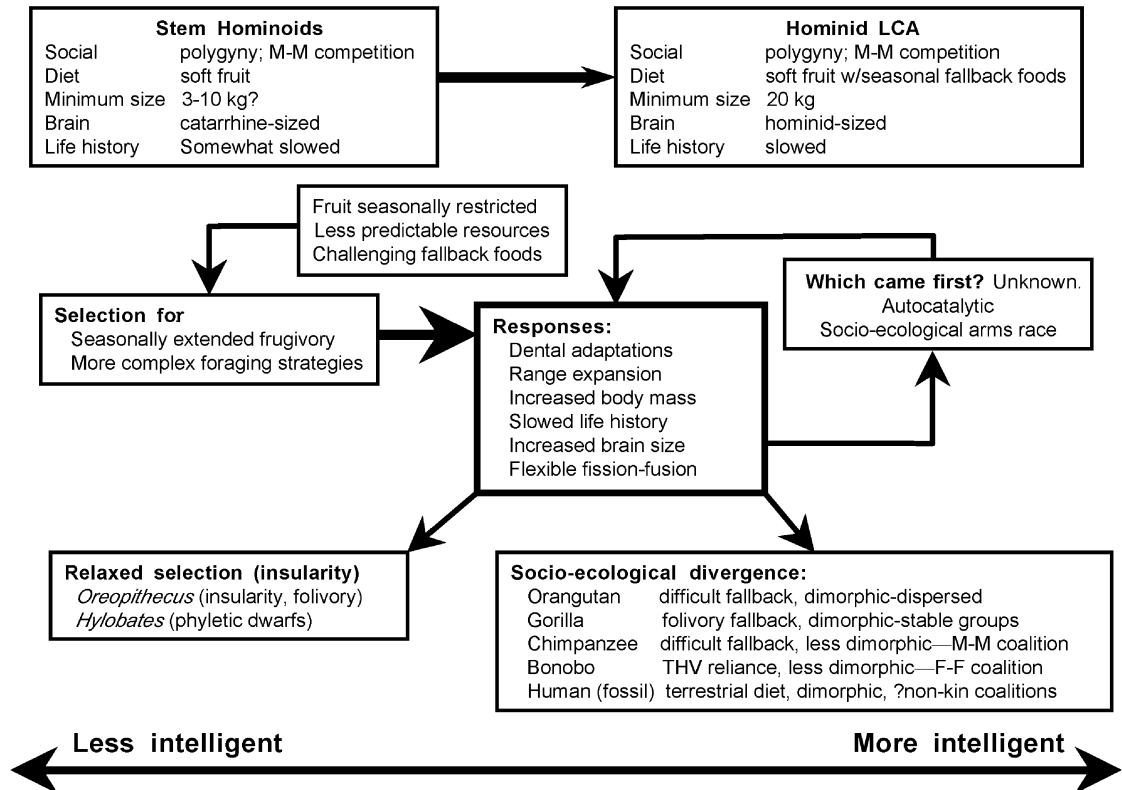


Figure 19.1. Factors implicated in the evolution of great ape intelligence. Early hominids are distinguished from early hominoids mostly by body and brain size and slowed growth. Ecological changes may have been the catalyst for a feedback reaction between larger bodies and slower growth on the one hand and ecological challenges on the other. Which response typical of extant hominids

came first may never be known, and may not even be important. The combination of characters is unique to hominids. While autocatalytic, directionality is not inevitable, as we see in the examples of hominoids that have smaller brains and presumably less intelligence.

this volume). Biological and ecological variables exert similar dynamic effects, and in concert with social pressures they feed back and contribute to further cognitive evolution.

Additional pressures between the brain and sociality may have arisen through prolonging juvenility, which has been linked with their large brains' higher energy demands (Kelley, Chapter 15, Ross, Chapter 8, this volume). Prolongation increases vulnerability for juveniles, who are handicapped by poor foraging skills and small size. Learning foraging skills is exceptionally slow and difficult because of great apes' difficult diets; complex skills for obtaining their most difficult foods, some of them fallback foods, may not be mastered until near adulthood. Juveniles' poor foraging skills and slow learning essentially extend their dependency, aggravating

pressures on caregivers, especially mothers. These pressures have been linked with enhancing apprenticeship (e.g., imitation, teaching) as a means of speeding their skill acquisition (e.g., Parker 1996).

Body–diet–brain

Brain size correlates with diet more closely than with body size (Begun & Kordos, Chapter 14, this volume). Large bodies are none the less linked with diet. The hominid combination of body size, diet, and brain size probably aggravated cognitive challenges.

Hominids, exceptionally large bodied, would have required more and/or better food than smaller-bodied hominoids, although not proportional to their greater size because of their lower metabolic rates. Fruit

specialists' diets are typically diversified because fruits are energy rich but poor in important nutrients like proteins and fat; hominids in particular are too large to be dedicated frugivores, and at some point they diversified their diets to include foods richer in protein and fat (Waterman 1984; Yamagiwa, Chapter 12, this volume). Whenever large body size appeared between stem hominoids and early hominids, broadening the diet was one probable avenue of obtaining more food. Compared with stem hominoids, early hominid dentition indicates expanding beyond soft fruits to eclectic frugivory or additional hard foods. If modern great apes are any index, their broader diets increased cognitive challenges by increasing foraging complexity, which increases memory load and the range and complexity of skills needed to locate and obtain food.

Large brains, with their high energetic costs, favor better-quality diets (e.g., meat in hominins). Non-fruit foods are generally differently distributed and more highly defended against predators than fruits. Effects on behavior include broadening and/or shifting foraging ranges and foraging skill repertoires; this increases the variety and especially the complexity of foraging skills, which translates into greater cognitive challenges. In hominids, then, improving diets to support large brains likely generated new pressures to enlarge the brain even more. In other words, hominid diets and large brains may have generated their own dietary cognitive arms race.

Diet–Sociality

Hominid diets and sociality mutually affect one another, as shown by great apes' foraging strategies during seasonal fruit scarcities. Foraging strategies are affected by both fruit scarcities (through females) and social pressures (through male competition). For cognition, this is the sort of intertwined tangle of complex social and ecological demands that requires interconnected cognition, that is, handling diverse demands in one integrated solution; it is a recurrent feature of normal great ape life. Potts, Chapter 13, and Ward *et al.*, Chapter 18, this volume also recognize this situation.

This myriad of interdependent biological, social, and ecological factors affecting intelligence in hominids is complicated beyond our ability to discern first causes or prime movers. We do know, however, that these attributes co-occur only in hominids. Some of them occur in other mammals, but never all together and never

to the degree expressed in hominids. First causes may then be less important to present day outcomes than changes induced by multiple interdependencies among these factors.

It is also probable that in the evolution of hominid brains, this attribute package entailed "arms races" involving both ecological (dietary) and social pressures. Arms races are always constrained by initial conditions. As Ward *et al.*, Chapter 18, this volume note, within a taxon individuals compete mainly with conspecifics. Pressures on a hominid come from other hominids in their ecological and social context. Given their different evolutionary trajectories, arms races in different social, biological, and evolutionary contexts should produce different outcomes. This is the reason we do not see monkeys, even capuchins and baboons, as intelligent as great apes and humans. Monkeys experience different ecological conditions and do not need to be as intelligent as great apes to compete with other monkeys. For the hominids, diet and moist tropical forests are good candidates for constraints. The great apes never really got out of the fruit market and that may have limited their capacity to take in enough energy to enlarge their brains beyond some ceiling. Their persistent tracking of moist tropical forests would impose other constraints on their adaptation, especially given ever-dwindling forest size and productivity. The possibility that some sort of systemic equilibrium sets in is suggested by the distinct "grades" of intelligence and brain–body size scaling patterns that are evident within the primates, as opposed to continuous gradation.

CONCLUSIONS

Our interpretation of available evidence is that the evolution of a great ape grade of intelligence involved a web of factors, causally interrelated and mutually adjusted. Constituent pressures and traits may have affected one another in spiraling or arms race fashion before reaching the particular combination seen in the hominids. Great ape adaptation constitutes an integrated package of cognitive–behavioral–social–morphological traits dovetailed to a particular constellation of ecological and social pressures and possibilities, rather than an assemblage of individual traits adapted independently to specific pressures. Their cognitive system, one component of this package, was shaped by all these traits and shaped all these traits in turn.

Many cognitive enhancements taken as key hominin adaptations are now recognized in great apes, and were probably present in the common ancestor of all hominids. While these cognitive enhancements do not reach human levels in any great ape, they none the less point to the ancestral condition of hominid cognition. These include enhancements to individual cognitive abilities (e.g., distance communication, mental representation of distant entities, spatio-temporal mapping, adaptability to novel and variable situations, attributing others' perspectives, tool manufacture and use, food sharing, cooperative hunting) as well as to centralized processes (e.g., rudimentary symbolism, generativity, multiple intelligences working together). Evidence offered here indicates that these cognitive enhancements are part and parcel of a biological package that evolved with the great apes, including larger brains, larger bodies, and extended life histories, in concert with the package of socio-ecological pressures they faced and created. This is consistent with other recent findings, for example that cultures in orangutans and chimpanzees show complexities previously thought possible only in humans (van Schaik *et al.* 2003; Whiten *et al.* 1999).

The cognitive achievements of humans originated as cognitive responses in fossil great apes to increasingly difficult life in the evolving sub-tropical forests of Eurasia. The unique cognitive adaptations of hominins evolved in response to the more severe challenges (for an ape) of more open forested or grassland ecological settings, and are mere elaborations of the cognitive adaptations of their great ape ancestors. In other words, the origin of the human cognitive capacity makes sense only in the light of great ape cognitive evolution.

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