1 • Evolutionary reconstructions of great ape intelligence

ANNE E. RUSSON
Psychology Department, Glendon College of York University, Toronto

INTRODUCTION

Research increasingly shows great apes surpassing other nonhuman primates in their mentality, achieving abilities traditionally considered uniquely human. Importantly, the cognitive capacities that distinguish them include rudimentary symbolic processes, in the sense of processes that operate on the basis of mental images rather than direct sensory-motor phenomena. Although this view does not represent consensus among experts (e.g., Tomasello & Call 1997), many well-respected researchers now accept this interpretation of the empirical evidence (e.g., Byrne 1995; Langer & Killen 1998; Parker & McKinney 1999; Parker, Mitchell & Boccia 1994; Parker, Mitchell & Miles 1999; Russon, Bard & Parker 1996; Savage-Rumbaugh, Shanker & Taylor 1998; Whiten & Byrne 1991; Wrangham *et al*. 1994).

If great apes are capable of symbolic cognitive processes, views of symbolism as having evolved within the human lineage are incorrect. Implications for understanding cognitive evolution within the primates are complex and important. First, neither the landmark significance of symbolism to cognition nor its importance in understanding the evolution of higher primate cognition is diminished by this revision. What is altered is timing. Symbolic cognition shifts from an achievement of the human lineage to a foundation for it. Second, reconstructions of the conditions leading to the evolution of symbolic processes remain important, but existing reconstructions lose much of their weight because they focus on conditions linked with the divergence of the human lineage. If symbolic processes are the joint province of humans and great apes, ancestral large hominoids are their probable evolutionary source. At this vastly different point in time and probably in space,

a very different set of conditions likely affected them. Finally, what is unique to the human mind must be re-evaluated.

This volume aims to reconstruct the evolutionary origins of great ape intelligence. This is not the first such reconstruction; over half a dozen have been developed over the last 25 years, primarily by scholars of cognition (e.g., Byrne 1997; Byrne & Whiten 1988; Parker & Gibson 1977, 1979; Parker 1996; Povinelli & Cant 1995; Russon 1998). While their expertise on issues of cognition is undisputed, their navigation and rendition of evidence and debate in the other key areas can be less sound. Many extant reconstructions, for instance, rely on outdated or flawed views of modern great ape anatomical or behavioral adaptations, sociality, ecology, or ancestry (for discussion, see Byrne 1997, 2000; Russon 1998). Reconsidering the evolutionary origins of great ape intelligence is well worth undertaking at this time. The accumulation of empirical evidence is generating better models of cognitive processes in living great apes. The body of knowledge on the behavioral, anatomical, social, and ecological traits of living great apes is affording increasingly reliable identification of potentially conservative traits. A recent upsurge of interest in hominoid evolution occasioned by significant fossil finds and increasingly sophisticated molecular taxonomic methods enormously improves the prospects for honing in on the critical pieces of the ancestral hominoid picture that concern cognition.

To orient our attempt, this first chapter revisits existing reconstructions of cognitive evolution that implicate the great apes. Aims are to highlight why and where evolutionary reconstructions of great ape cognition are in need of revision, the factors potentially at play, and our approach to developing a new reconstruction.

RECONSTRUCTING GREAT APE COGNITIVE EVOLUTION

Reconstructing the events responsible for the evolution of great ape cognition entails, in part, a logic that links cognitive capacity with observable physical features (e.g., Byrne 2000; Parker & McKinney 1999). Failure to adhere to this logic undermines many existing reconstructions. Very briefly, great ape cognition requires powerful, sophisticated brains. Whatever the reasons for their evolution, such large brains support increasingly complex behavior. While it is very difficult to establish whether there was direct selection in ancestral great apes for more complex forms of behavior, it is likely that once attained, this capacity was used to ecological and social advantage. So, if common forms of complex behavior can be identified in living great apes that distinguish them from other nonhuman primates, then these behaviors and their putative cognitive, anatomical, ecological, and social correlates may represent conservative traits that owe to common ancestry. Once such a suite of characters is identified, it should be possible to infer related aspects of behavior in ancestral great apes, the ancestral conditions that could have favored them, and the cognitive processes that evolved to govern them.

Reconstructions of cognitive evolution in the primates have further been guided by their own set of premises. First, enhancements to primate cognition are presumed to have been adaptive, i.e., achieving greater behavioral flexibility by enhanced cognition was directly selected for, not an incidental byproduct (e.g., Byrne 1995; Byrne & Whiten 1988; Gibson 1993; Povinelli & Cant 1995; Parker 1996). Brain enhancements that are fortuitous luxuries are unlikely to be maintained or even to occur because brain tissue is especially costly energetically (Aiello & Wheeler 1995; Armstrong 1983). Second, modern cognition (abilities, development, functions), as expressed in natural habitats, is taken as a good proxy for ancestral precursors.

HUMAN COGNITIVE EVOLUTION

Reconstructions of human cognitive evolution regularly borrow the great apes to define the primitive intellect from which human intelligence diverged and upon which it built. I review three recent models to illustrate how scholars of human cognitive evolution have tended to portray great ape cognition and the problems so occasioned.

Donald

Donald (1991, 1993, 2000), a neuropsychologist, modeled the human mind as evolving from the ancestral, prehominin condition in three cognitive transformations, wherein cognitive and cultural evolution are deeply and fundamentally interdependent. These transformations are founded on new memory representations because cognitive systems that are culturally dependent cannot replicate without systems for storing collective knowledge. Donald's starting point is an "episodic" culture in the common great ape–human ancestor, based primarily on modern chimpanzees. From this evolved "mimetic" (*Homo erectus*), "mythic" (*Homo sapiens*), then "theoretic" (modern human) cultures.

Critical to great apes are episodic and mimetic cultures, taken to represent great ape cognition, modern and ancestral, and the step beyond. In positioning great apes as "episodic," Donald characterizes their cognition as governed by procedural memory: able to store perceptions of events but poor at episodic recall, having little voluntary access to episodic memories without environmental cues. This would leave great apes unable, voluntarily, to shape and modify their own actions or to access their stored representations, so unable to invent gestures, mimes, and signs to communicate or to practice their skills systematically. Their experience would be an episodic lifestyle governed by the present. The "mimetic" cultures that followed, enabled by voluntary retrieval of stored memories independent of environmental cues, would surmount this episodic inability. This allows individuals to take voluntary control over their own output, including voluntary rehearsal and refinement, and mimetic skills like pantomime, re-enactive play, self-reminding, imitative learning, and proto-pedagogy; in effect, it allows using their bodies as communication devices to act out events in quasi-symbolic form.

Critics have already shown that "episodic" underestimates great apes. Great apes' capabilities include the episodic recall and the voluntary control over motor output essential to mimesis (Byrne 1997; Byrne & Russon 1998; Matsuzawa 1996; Russon 1998; Schwartz & Evans 2001), bringing them close to the mimetic minds attributed to *Homo erectus* (Byrne pers.

commun.; Mitchell & Miles 1993; Parker & McKinney 1999).

Donald (2000) now accepts that great apes achieve more complex cognition, symbolic skills included, but discounts their importance on the grounds that they represent individual versus collective representational systems (i.e., symbolic cultures). He attributes many of great apes' most impressive achievements (e.g., language, stone tool making) to the transformative powers of human cultural rearing environments which, he believes, can transform them into "superprimates" by exploiting cognitive potential that has remained untapped for millions of years. This position is also disputable. Taï Forest chimpanzees use two gestures with shared collective meanings, leaf-clipping and knuckle-knocking, that verge on collective symbolic representations (Boesch 1996). That human enculturation induces higher than normal cognitive abilities in great apes is not well established and the claim has been contested on several fronts (Parker & McKinney 1999; Russon 1999b; Suddendorf & Whiten 2001).

Cosmides and Tooby

Cosmides and Tooby (1992), evolutionary psychologists, proposed that human cognition evolved through cognitive "modules" biologically designed to address the particular adaptive problems that ancestral humans encountered in their environment of evolutionary adaptedness, taken to be hunter–gatherer lifestyles in Pleistocene environments. Language, theory of mind, spatial relations, and tool use are among the modules proposed. Supposedly, these modules are "content rich," pre-fitted with knowledge relevant to the Pleistocene problems these hunter–gatherers faced, and have changed little since because too little time has passed to allow further evolutionary modification.

Limitations to this model have been pointed out. Mithen (1996) argued that modularity of this sort does not reflect what humans really do, mix and match their thinking. Byrne (2000) identified flaws in the logic and evidence of "adaptation to the Pleistocene." Hominins did change and diverge in the Pleistocene. Human ancestors pursued a lifestyle close to living hunter–gatherers (e.g., large animal hunting, fire, living shelters) only from about 40 000 years ago, too recently to have shaped human cognitive evolution. Finally, human traits offering evidence of evolutionary origins (e.g., infanticide,

homicide, mating systems) long predate hominins in the primates. Traits proposed as significant in human cognitive evolution almost certainly have much longer evolutionary histories than this model allows. Neglecting evidence on modern great apes and other primates leaves this model without a credible point of departure.

Mithen

Mithen (1996), an archeologist, proposed four "acts" in human cognitive evolution. Act 1 opened 6 Ma with ancestral great apes, Act 2 at 4–5 Ma with ancestral hominins, Act 3 at 1.8 Ma with *Homo erectus*, and Act 4 at 100 000 years ago with modern humans. Like others, Mithen uses living great apes, especially chimpanzees, to represent the cognitive capacities existing at the ancestral great ape–human divide.

Mithen assumes a fundamentally modular cognitive architecture (after Cosmides & Tooby 1992), and a recapitulationist position, that the sequence of developmental stages can be read as re-iterating the phylogenetic sequence of ancestral adult forms. Within this framework, he proposes three phases of cognitive evolution based on children's cognitive development (after Karmiloff-Smith 1992): generalized intelligence, specialized intelligences, and cognitive fluidity. Generalized intelligence comprises a suite of general-purpose, associative-level learning and decision-making mechanisms used in all domains to modify behavior in light of experience (e.g., trial and error learning, stimulus enhancement). Specialized intelligences are biologically designed modules for specific problem domains, operating in virtual isolation of one another. Three are proposed: social (for social interaction and mind-reading), natural history (for understanding the natural world, especially biology), and technical (for manufacturing, manipulating, and throwing stone and wooden artifacts). Cognitive fluidity is achieved by interconnecting specialized intelligences, allowing them to work together by enabling the flexible flow of knowledge and ideas among them.

Mithen portrays ancestral great ape cognition, Act 1, at the interface between phases 1 and 2: equipped with generalized intelligence, a social intelligence, and an incipient natural history intelligence (for resource distribution) that generated capacities comparable to those of other haplorhines but *somewhat* more powerful. Act 2 added further modularization, Act 3 added a language

module that connected with the social but not technical or natural history modules (which remained isolated from each other), and Act 4 broke down barriers between modules to allow cognitive fluidity.

Many experts portray great ape cognition very differently. To illustrate, Mithen attributed chimpanzees' tool and foraging expertise to general intelligence, i.e., associative learning, whereas substantial evidence exists of their using rudimentary symbolism and hierarchization (e.g., Byrne 1995; Matsuzawa 2001; Parker & McKinney 1999; Russon 1998, 1999a; Suddendorf & Whiten 2001). He also claimed great apes show domain isolation because they miss opportunities at the social–foraging interface, like failing to learn foraging skills socially or use material culture to serve social strategies, whereas considerable evidence shows they use social learning in acquiring foraging skills (Byrne & Byrne 1993; Parker 1996; Russon 1999b; van Schaik & Knott 2001; van Schaik, Deaner & Merrill 1999; van Schaik *et al.* 2003; Whiten *et al.* 1999) and use tools socially (Boesch & Boesch-Achermann 2000; Goodall 1986; Ingmanson 1996; Peters 2001).

Summary

While most reconstructions of human cognitive evolution recognize the hominids as defining the cognitive platform from which hominins diverged and their evolutionary context, all suffer from underestimating that cognitive platform and therefore, from misidentifying the evolutionary conditions involved.

RECONSTRUCTIONS OF PRIMATE COGNITIVE EVOLUTION

Reconstructions of cognitive evolution within the primate order tend to fall into two categories, social and ecological, according to the type of selection pressure promoted as most influential, and to presume that influences operate in similar fashion across the order as a whole or at least across the haplorhines.

Social intelligence

The suggestion that primates' complex social lives shaped the evolution of their intellect can be traced to Jolly (1966), Kummer (1967), and Humphrey (1976). Tripartite relations, maneuvers to influence powerful individuals and potential allies, and tactical deception are among the facets of primate sociality singled out as cognitively complex. If communicative signals were selected for the signaler's competitive advantage more than for honest exchange (Krebs & Dawkins 1984), spiraling evolutionary arms races could have occurred, first to improve schemes for outwitting competitors (favoring abilities for agonistic cooperation and perhaps for generating misleading signals), then for dupes to enhance their abilities to detect honest information behind misleading signals. Such reasoning spawned the influential Machiavellian Intelligence hypothesis on the nature and evolution of primate cognition (Byrne & Whiten 1988). Cooperative advantages gained via social reciprocity, tallying favors exchanged, recognizing and categorizing conspecifics by family membership, etc. are also potential selection pressures in primate cognitive evolution (Cheney & Seyfarth 1990; de Waal 1996).

The social intelligence hypothesis argues that the social pressures on primates are more complex than the ecological pressures typically proposed as prime movers of cognitive evolution, range size and frugivory. Social problems present highly changeable information from changing animate partners, sensory input from diverse modalities, and multiple individual and social attributes. Social cognition must operate on this multifaceted information in parallel; ecological cognition, supposedly, faces a much lighter parallel mental load (Barton & Dunbar 1997). Accordingly, social pressures were the primary forces shaping primate cognitive evolution.

Dunbar and his colleagues have been major proponents of this hypothesis. They consistently find that their index of intelligence (neocortical ratio, the size of the neocortex relative to basic brain structures) correlates with indices of social complexity (group size) but not ecological complexity (range size or day journey length, adjusted for body size) in species where individuals live in intensely social groups rather than simple aggregations. Correlations hold within primates (within haplorhines, between strepsirhines and haplorhines, perhaps between haplorhines and hominins: Barton 1996; Dunbar 1992, 1995, 1998), within carnivores, and within cetaceans (Kudo & Dunbar 2001). They conclude that in such taxa, cognitive capacities constrain the number of individuals that can co-exist in one social group (Barton & Dunbar 1997; Dunbar 1992, 1998). This work is problematic with respect to primate cognitive evolution for at least two reasons. First, social complexity

depends on factors beyond group size, such as group structure, group organization, and the range and subtlety of members' behavior (Byrne 1999, and see Parker, Chapter 4, van Schaik, Preuschofr & Watts, Chapter 11, this volume). Second, these studies and accounts concern cognition as a constraint on sociality, not sociality as a selection pressure for cognitive enhancement, so they say little about cognitive evolution (Parker & McKinney 1999).

Concerning great ape cognitive evolution, five issues deserve mention. (1) Most social activities promoted as cognitively complex (e.g., tripartite relations, tallying social exchange) occur in many haplorhines so they require only the cognitive capacities of monkeys, not the advanced capacities distinctive of great apes. Possible exceptions include high-level tactical deception (Byrne & Whiten 1997), consolation (de Waal & Aureli 1996) and symbolic communication (Boesch 1996; Savage-Rumbaugh *et al*. 1996). (2) Studies of group size–neocortex size correlations have included *Pan* and *Gorilla* but not the orangutan, who is large-brained and semi-solitary (Dunbar 1992, 1998). (3) Social intelligence proponents probably underestimate the ecological complexities facing great apes. Great apes' "technical" skills for obtaining difficult foods bear witness to the complexity of these ecological pressures (Byrne & Byrne 1991; Byrne, Corp & Byrne 2001; Russon 1998, 2003; Stokes 1999; Yamakoshi & Sugiyama 1995), and these pressures are multifaceted in arboreal or competitive conditions. These technical capacities are also relegated to evolutionary side effects under the social intelligence hypothesis, which fits poorly with the sense that they are central to great ape adaptation (Byrne 1997). (4) These social complexity measures do not reflect impressions that sociality is more complex in great apes than other haplorhines (e.g., Byrne 1995, 1997; Parker & McKinney 1999). (5) Close analysis of group–brain size correlations suggests cognitive differences between great apes and other haplorhines (Dunbar 1993; Kudo & Dunbar 2001), with great apes seeming to use more "computing power" than monkeys to manage the same number of relationships (Dunbar 1998). In other words, group size does not completely account for differences in cognitive power between haplorhines and great apes. While this hypothesis has been valuable in identifying the complex social pressures facing primates, it has offered little to reconstructing the evolution of a distinctive great ape cognition.

Ecological hypotheses

Diet

Diet, frugivory in particular, is the ecological pressure most often linked to the evolutionary enhancement of primate cognition. Foods distributed unpredictably in time and space or over large supplying areas, dietary diversity, and diets that rely on foods that are difficult to obtain have all been promoted as setting a selective premium on high intelligence (Clutton-Brock & Harvey 1980; Galdikas 1978; Gibson 1986; Menzel 1978; Menzel & Juno 1985; Milton 1981, 1988; Parker 1978; Parker & Gibson 1977; Wrangham 1977).

Fruit is especially patchy in spatial and temporal distribution compared with foliage, so frugivory could promote abilities like memory, spatial reasoning, or cognitive maps (Milton 1981, 1988). Two sympatric New World monkeys, frugivorous spiders and folivorous howlers, support this prediction: spiders have greater relative brain size, larger home ranges, and a more protracted dependency/learning period (Milton 1988). Frugivory also correlates positively with brain size in haplorhines although the effect is much smaller than group size (Barton 1996; Byrne 1997), as well as in bats, rodents, insectivores, and lagomorphs (Milton 1988). Diversifying the diet to include protein- and fat-rich foods may be responsible for large day ranges in frugivorous primates, chimpanzees included, rather than searching for ripe fruit (Hladik 1975).

The main problem with this broad view of dietary niche for reconstructing great ape cognitive evolution is that it does not distinguish great apes from other haplorhines. Although all great apes retain basically frugivorous diets and monkeys evolved greater capacities for folivory, some monkeys and the lesser apes have diets similar to those of great apes. Dietary pressures distinctive to great apes are more likely to be found in specific dietary features. Foods that are difficult to obtain, for instance, have often been proposed as selection pressures favoring the enhancement of great ape cognition, to enable the complex techniques needed to obtain them. Pressures stem from food defenses that pose "technical difficulties," like embeddedness, toxicity, or antipredator behavior in animal prey (e.g., Byrne 1997; Boesch & Boesch-Achermann 2000; Hladik 1977; Parker & Gibson 1977). Such defenses are common in foods that supplement fruits in great apes, especially fallback foods needed in periods of fruit scarcity. Both

embeddedness and technical difficulty have inspired hypotheses on the evolution of a distinctively "great ape" cognition (Byrne 1997; Parker & Gibson 1977).

Ranging

Two ranging patterns might underpin evolutionary enhancements to primate cognition, range size and terrestriality. Increased range size could favor enhanced memory and cognitive maps (e.g., Clutton-Brock & Harvey 1980). Terrestrial life could have exerted selection pressures because it increases predation risks. Primates' preferred evolutionary response to predation appears to have been increased social group size, which could then have been the direct pressure for enhanced intelligence (e.g., Dunbar 1992; van Schaik 1983). Range size is a function of diet, body size, and group size, however. Gorillas that eat more fruit have longer daily travel distances than those that eat less (Yamagiwa 1999); frugivorous spider monkeys have larger home ranges than folivorous howlers (Milton 1988); and larger groups are likely to have to travel farther than smaller ones to fulfill their food needs. Accordingly, links between range size and cognition may owe to these underlying parameters. Further, neither range size nor terrestriality distinguishes great apes from other haplorhines, so neither can account for the evolution of great ape cognition.

Summary

Primate-focused reconstructions are unsatisfying as reconstructions of great ape cognition because they do not distinguish great apes from other haplorhines. They are valuable in offering broader views of evolutionary pressures affecting great apes as primates, the range of ecological and social pressures worth exploring in greater depth, and the haplorhine pattern from which they differ. Limits to these hypotheses do, however, illustrate the need to determine what promoted the great apes' evolutionary divergence from other halorhines in their cognition.

RECONSTRUCTIONS OF GREAT APE COGNITION

Some reconstructions address the evolution of a distinctive great ape cognition, considering that cognitive evolution within the primate order probably involved three major grade shifts, not the two shifts typically portrayed (strepsirhine to haplorhine, haplorhine to hominin) (Byrne 1997; Byrne & Whiten 1997). The third shift, intervening temporally between them, is from most haplorhines to hominids (great apes and humans), with all hominids showing greater cognitive sophistication.

Most of these hypotheses were stimulated by Parker and Gibson's (1977) extractive foraging model, which singled out great apes and cebus for their "intelligent" tool using abilities. Several constitute revisions of earlier reconstructions, provoked by inconsistent findings. Most are synthetic, in that they propose a suite of selection pressures acting in concert, or sequentially, to produce the distinctive mentality characteristic of all living great apes.

Extractive foraging

Parker and Gibson (1977, 1979; Gibson 1986) hypothesized that seasonal reliance on embedded foods and prolonged ontogeny shaped hominid cognitive evolution. Ancestral great apes faced selection pressures imposed by omnivorous diets with seasonal reliance on embedded foods like hard-shelled fruits and nest-building insects. Embedded foods demand extractive foraging techniques; when needed seasonally, they favored the evolution of flexible techniques assisted by "intelligent" tool use (i.e., tool users understand the causal dynamics involved; Parker & Potí 1990), which require enhanced cognitive abilities. Reliance on tool-assisted extractive foraging favored prolonging ontogeny because foraging independence requires complex skills. These complex skills require advanced cognitive abilities, so prolonging ontogeny helped immatures by extending parental support and cognitive development. Extending dependency increased pressures on caregivers, especially mothers, by interfering with further reproduction, and favored the ability for imitation to speed offsprings' acquisition of foraging skills. They hypothesized that intelligent tool use evolved independently in *Cebus* for similar reasons.

Valuable features of this model include the effort to identify specific dietary features that distinguish the hominids and the incorporation of prolonged ontogeny, a life history parameter that distinguishes hominids from other haplorhines. Prolonged ontogeny extends cognitive development and parental support into the juvenile period in great apes (Parker & McKinney 1999).

Imitative abilities in particular emerge near the onset of juvenility, when the most complex facets of foraging skills are likely being acquired.

This hypothesis remains prominent although several limitations are recognized. (1) Great apes surpass *Cebus* cognitively so if extractive foraging explains their common intelligent tool use, additional factors are needed to explain great apes' greater cognitive power. (2) Whether seasonal extractive foraging affects great apes differently than other haplorhines is unclear; baboons, for instance, are omnivorous seasonal extractive foragers but do not show comparable cognition (e.g., Byrne 1997). (3) Singling out embeddedness neglects other food defenses requiring equally complex techniques, such as spines, toxins, distasteful exudates, and digestive inhibitors (e.g., Byrne 1997; Russon 1998). (4) Intelligent tool use may not qualify as synapomorphic in great apes relative to other haplorhines. It is absent from the vast majority of wild great ape populations (van Schaik *et al*. 1996) and in the two species where it can be habitual, orangutans and chimpanzees, it is rare in most (orangutan) or some (chimpanzee) populations (Chapman & Wrangham 1993; van Schaik & Knott 2001; Wrangham *et al*. 1993). (5) These complications impose two additional assumptions on this hypothesis, both open to question: living chimpanzees best represent the common great ape ancestor in diet and foraging strategy, and intelligent tool use characterized the common ancestor but was subsequently lost or reduced in most descendants. (6) Intelligent tool use is not itself a cognitive process, but an expression of means–ends cognition. Means–end cognition also generates manipulative foraging techniques and cognitively, great apes' manipulative techniques are very similar to their tool-assisted ones (Byrne & Byrne 1991; Byrne *et al*. 2001; Stokes & Byrne 2001; Matsuzawa 2001; Russon 1998; Yamakoshi & Sugiyama 1995; and see Byrne, Chapter 3, Yamakoshi, Chapter 9, this volume). Great apes' intelligent tool use could reflect means–ends cognitive processes that evolved for other purposes and were subsequently recruited for tool use. (7) If tool-assisted extractive foraging qualifies as a cognitive adaptation in great apes then so should cooperative hunting. It too is an important contributor to foraging success, primarily in chimpanzees (Boesch & Boesch-Achermann 2000). (8) This hypothesis has difficulty explaining the wealth of cognitive enhancements that great apes show beyond foraging, especially in the social domain.

Apprenticeship

Parker (1996) extended the extractive foraging model to propose that what evolved in great apes was an apprenticeship system wherein cognitive capabilities depend on rich social input during development. Apprenticeship, here, means guided participation in shared activities of a routine nature (Rogoff 1992). Parker proposed the co-evolution of a suite of interrelated cognitive abilities in hominids – imitation, intelligent tool use, self-awareness, demonstration teaching – that enabled immatures to acquire the tool-assisted extractive foraging skills essential and unique to their clade and that relieved maternal pressures by boosting offsprings' capacities to acquire this expertise.

The particularly valuable feature of this model is that it integrates social and ecological hypotheses: it situates sophisticated cognitive abilities for social transmission at the heart of the evolutionary enhancements that characterize great ape cognition, portrays social and ecological abilities working together rather than in isolation, and envisions cognitive enhancements as achieved through changes to ontogeny. This set of social and physical abilities occurs as an interrelated cluster in living great apes (Mitchell 1994), supporting the suggestion that they evolved as an interrelated suite to support tool-assisted extractive foraging. That social input is essential to great apes' cognitive development and acquisition of ecological skills is amply supported, although not restricted to tool skills (e.g., Parker & McKinney 1999; Tomasello & Call 1997).

As a derivative of the extractive foraging hypothesis, however, this model faces the same limits associated with exclusive concentration on tools and extractive foraging. Further, even the extended suite of cognitive abilities hypothesized to have evolved in response to these selection pressures neither covers nor generates the full range of cognitive advantages that great apes show over other haplorhines.

Arboreal clambering

Povinelli and Cant (1995) proposed large body size combined with arboreal travel as the selection pressures that favored evolutionary enhancements to intelligence in the common ancestor of great apes. They argued that arboreal travel pressures acting on extremely large-bodied primates favored the cognitive capacity for a

self-concept, in particular the self as a causal agent, to allow individuals to figure the effects of their own body weight into their arboreal travel. Modern orangutans model the last common ancestor, their arboreal travel problems model ancestral selection pressures, and their clambering mode of arboreal locomotion expresses their cognition (clambering is primarily suspensory, orthograde locomotion that employs all four limbs in irregular fashion to grasp and hold multiple supports). This meshes with impressions that orangutans' cognitive prowess is most evident in arboreal locomotion (e.g., Bard 1993; Chevalier-Skolnikoff, Galdikas & Skolnikoff 1982; MacKinnon 1974). Povinelli and Cant identified *Oreopithecus* as a highly suspensory fossil hominid exemplifying this lifestyle.

This hypothesis is valuable in bringing attention to the intellectual challenges of arboreal travel for large-bodied primates and in incorporating the fossil record, but several limitations are recognized. (1) It applies to orangutans but not clearly to other great apes or their common ancestor. Not all great apes rely on arboreal travel. Neither was the ancestral hominid condition clearly arboreal: orangutans' postcranial adaptations for arboreal locomotion are recently derived, they differ substantially from those of the other living great apes, and the ancestral condition *vis-à-vis* arboreality is ambiguous (e.g., Begun 1992; Martin & Andrews 1993; Moyà-Solà & Köhler 1993; Pilbeam 1996, Tuttle & Cortright 1988). (2) It argues for the evolution of a single cognitive ability, self-concept, so it does not explain the broad range of abilities seen in great apes and their generally high level, i.e., their cognitive systems. (3) It considers only selection pressures for a self-concept, but construes self-concept as dependent upon a generalized cognitive capability, mental representation, i.e., recalling to mind or "re-presenting" mental codes for entities and simple object relations in the absence of their normal sensory and motor cues. Enabling a self-concept, then, either required evolving the generalized capacity for mental representation or tapped a pre-existing representational capacity; either scenario requires further explanation. (4) It is not certain that ancestral hominids had brains large enough for such cognitive abilities. The large hominid that Povinelli and Cant suggest may have faced such arboreal pressures, *Oreopithecus bambolii*, had an unusually small brain (Harrison & Rook 1997), not the large brain associated with sophisticated abilities like self-concept and mental representa-

tion. (5) How to test this hypothesis empirically remains a puzzle.

Technical intelligence

Byrne (1997, 1999, 2000; Stokes & Byrne 2001) argued that what sets great apes apart from other haplorhines are numerous "technical" problems exacerbated by their exceptionally large body size. Significant among them for their cognitive challenge are foraging, ranging, arboreal locomotion, and nest building. Large size aggravates foraging problems for great apes, so they need greater foraging efficiency and rely more heavily on high-quality, physically defended foods (e.g., embedded). Large size probably also increases the difficulty of ranging, arboreal travel (per Povinelli & Cant 1995), and finding secure sleeping sites. Ancestral hominids would have faced similar selection pressures for improved foraging, aggravated by large body size, slow and inefficient locomotion ("brachiation"), and dietary constraints (unspecialized guts, no cheek pouches). These pressures favored solutions of greater complexity and efficiency. The unique evolutionary solution of the hominids was to organize voluntary behavior hierarchically. Cognitively, hierarchization involves reorganizing and refining cognitive structures into multi-leveled programs. It brings abilities like mental representation, planning and insight to cognition and increased speed and efficiency to behavior. It affects cognition generally, so it could have evolved in response to any of these problems. Payoffs are most evident in foraging-related activities but because hierarchization is generalized, it brings matching payoffs to social cognition such as understanding social partners as active agents with intentions.

This hypothesis accounts for the complex "technical" skills unique to the great apes and for the cognitive difficulties that even gorillas, the most folivorous great apes, face in foraging. In proposing cognitive advances that were generalized, it provides an explanation for cognitive enhancements across domains, as products of this overall increase in cognitive power. Others also single out cognitive hierarchization (e.g., Gibson 1990, 1993; Matsuzawa 2001; Russon 1998), which has been shown in food processing techniques in chimpanzees, gorillas, and orangutans (Byrne & Byrne 1991; Byrne *et al.* 2001; Russon 1998; Stokes & Byrne 2001) but not vervets (Harrison 1996). This hypothesis may, however, invite the same criticism launched at the social intelligence

hypothesis: enhancements to social cognition are thereby relegated to automatic side effects, which sits poorly with the obvious advantages they provide and ignores the possibility of adaptive advances to social cognition. Also not incorporated are several factors known to affect great ape cognition (e.g., prolonged ontogeny) and the interplay among critical factors (e.g., effects of large body size on sociality, interactions between technical and social pressures).

Arboreal foraging

Russon (1998) reconsidered the suite of selection pressures proposed to have shaped great ape cognitive evolution – large size, difficult diet, prolonged ontogeny, arboreal travel – then revisited existing reconstructions. The main revision concerned arboreality. Arboreal travel has been advocated as a cognitive selection pressure, but arboreal foraging may be more important. Arboreality clearly complicates the cognitive challenges of obtaining difficult foods, at least in orangutans and chimpanzees (Russon 1999b; Stokes & Byrne 2001). Arboreal foraging, as a hypothesis, blends and extends technical intelligence and apprenticeship models: "technical" difficulties associated with a difficult dietary niche, large body size, and prolonged ontogeny all imposed cognitive selection pressures on ancestral great apes; and arboreality exacerbated foraging pressures. It argues for centralized hierarchization as a key underpinning for great ape cognition and for development is a critical factor in moderating ecological pressures and cognitive capabilities. What is valuable here is the attempt to generate a reconstruction that integrates the suite of plausible selection pressures, all proposed cognitive advances, and current evidence. Like the technical intelligence hypothesis, however, arboreal foraging suffers from relegating advances in social cognition to side-effects.

DISCUSSION

This overview emphasizes the need to revise reconstructions of great ape cognitive evolution. With evidence and opinion increasingly recognizing a distinct "great ape" cognition, reconstructing cognitive evolution in the primates, from the whole of the order to modern humans, first and foremost requires the incorporation of more accurate representations of great ape cognition. In particular, many existing reconstructions have not differentiated the great apes from other haplorhine primates so they have underestimated great ape capacities, especially for symbolic processes. Recognizing primitive symbolism as the province of the hominids obligates substantial revisions of reconstructions of human cognitive evolution. Reconstructions of great ape cognitive evolution suffer similar problems, typically owing to considering sets of problem-specific cognitive abilities that fall short of representing the full cognitive breadth and complexity that great apes express. The few models that could account for great apes' full range of cognitive advances do so by proposing the emergence of generalized processes, such as mental representation or hierarchization, that enhanced cognitive capacities across the board.

Concerning selection pressures, many of those currently proposed to have favored evolutionary enhancements to primate cognition are not unique to hominids. Other primates have societies as complex, diets as diverse, seasonal, patchy, or embedded, and ranges as large, terrestrial, or arboreal as great apes, and great apes themselves vary on most of these. Explaining a unique great ape cognition requires at least one selection pressure on cognition, or an interaction among several pressures, that uniquely affected their common ancestor. In that context, ecological pressures currently appear to be the most likely to have shaped great ape cognitive evolution although social pressures may yet be shown to have had an important influence. Most of the plausible pressures are in any case interrelated, making it likely that a set of pressures, interacting or acting in sequence, shaped their cognitive enhancements.

If no existing reconstruction meets current standards, all help show the way forward. More accurate and complete portrayals of great apes are needed in virtually every facet of this exercise: modern great ape cognition, modern great ape adaptation, and great ape evolutionary history. We need accurate characterizations of the capacities and processes that distinguish great ape cognition from that of other nonhuman primates, of modern humans and, to the degree possible, of ancestral hominins. We need better understanding of modern great ape adaptation, especially the biological substrate that supports their cognition (e.g., the brain, life histories) and the social and ecological challenges to their cognition (e.g., diet, locomotion, habitat), as bases for establishing what roles their advanced cognitive capabilities play. In some cases, evidence on modern great

ape adaptation is the only available basis for inferring shared ancestral traits and conditions. Finally, we need better representations of great apes' evolutionary history, both the traits of ancestral hominids and the conditions in which they lived – representations that are especially difficult to construct, given the incomplete evidence available.

Even with the incomplete material that has been woven into evolutionary scenarios, the difficulty of incorporating all the factors likely to be relevant and of representing the balance among them is increasingly evident. Accurate reconstruction may well require unraveling the effects of multiple pressures, including identifying which were fundamental and which represent compensations, determining which operated as constraints and which opened adaptive opportunities, and establishing the sequence of pressures and cascading effects. It remains to be seen whether the evolutionary record will eventually yield answers to these questions.

THE CURRENT VOLUME

This volume works toward developing the most comprehensive reconstruction of great ape cognitive evolution possible today, by assembling and integrating opinion from experts in each of the disciplines with evidence to offer on this issue – specialists in great ape cognition, behavior, ecology, sociality, and anatomy as well as paleontologists expert in the study of corresponding ancestral hominid traits. Contributors were asked to discuss their area of expertise with attention to implications for great ape cognition and its evolution.

We used existing reconstructions of primate cognitive evolution to guide our choice of topics. These suggest a variety of abilities that may represent cognitive adaptations along with modern and phylogenetic features that may underpin variation in cognitive capacities within the primate order (e.g., diet, range size, social complexity, terrestriality–arboreality). Several of these features, singly or in concert, assume distinct qualities in the hominids and so could underlie distinct forms of cognition in that clade. Whether any of these abilities constitute cognitive adaptations and whether any of these features qualifies as a direct pressure favoring evolutionary enhancements to cognition, all are useful in suggesting the major dimensions along which the hominids are distinct from other haplorhine primates that may somehow be tied to their cognitive capacities.

Correspondingly, we organized this volume into three parts, which address (1) what distinguishes great ape cognition, (2) what features of behavior, anatomy, sociality, and ecology characterize living great apes as a clade and show strong links to their cognition and (3) the corresponding conditions in the common ancestral hominid. The first part offers an overview of the cognitive capacities that characterize modern great apes and distinguish them from other nonhuman primates, to establish what intellectual phenomena may require evolutionary explanations different from those that apply to all haplorhine primates. The second and third parts assemble and assess evidence on ecological, social, behavioral, and anatomical factors linked with these distinctive cognitive phenomena in living and ancestral large hominoids. Our aims are first, to assess whether the factors proposed could be linked with enhanced cognition in the ways portrayed by existing reconstructions, and second, to explore other factors and/or interactions among them that may have contributed to that cognition. Our final chapter attempts to integrate this material into a coherent, overall picture of the evolutionary origins of great ape cognition.

REFERENCES

Aiello, L. & Wheeler, P. (1995). The expensive tissue hypothesis. *Current Anthropology*, **36**, 199–221.

Armstrong, E. (1983). Metabolism and relative brain size. *Science*, **220**, 1302–4.

Bard, K. A. (1993). Cognitive competence underlying tool use in free-ranging orang-utans. In *The Use of Tools by Human and Non-Human Primates*, ed. A. Berthelet & J. Chavaillon, pp. 103–13. Oxford: Clarendon Press.

Barton, R. A. (1996). Neocortex size and behavioral ecology in primates. *Proceedings of the Royal Society of London, Series B*, **263**, 173–7.

Barton, R. A. & Dunbar, R. I. M. (1997). Evolution of the social brain. In *Machiavellian Intelligence II: Extensions and Evaluations*, ed. A. Whiten & R. W. Byrne, pp. 240–63. Cambridge, UK: Cambridge University Press.

Begun, D. R. (1992). Miocene fossil hominoids and the chimp–human clade. *Science*, **257**(2058), 1929–33.

Boesch, C. (1996). Three approaches for assessing chimpanzee culture. In *Reaching into Thought: The Minds of the Great Apes*, ed. A. E. Russon, K. A. Bard &