ARTICLES

Machiavellian Intelligence

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The hypothesis that intelligence is an adaptation to deal with the complexity of living in semi-permanent groups of conspecifics, a situation that involves the potentially tricky balance of competition and cooperation with the same individuals, has been influential in recent theorizing about human mental evolution. It is important to distinguish among distinct versions of this general idea, for they predict different cognitive consequences and apply to different species of animal. Empirical support is strong in primates for links between (i) social complexity based on evolved tactics that require a good memory for socially relevant information, (ii) neocortical enlargement, and (iii) size of social groupings. However, the evolution of computational thought and the ability to understand other individuals' intentions are not well explained as products of selection for Machiavellian intelligence. Quite different explanations may therefore be required for increases in intelligence that occurred at different times in human ancestry.

Before the surge of field studies in the 1950s and 1960s, researchers had little appreciation for the degree of sociality and the scope of social complexity within the primates. Anecdotal accounts existed of manipulative behavior by pets, especially monkeys and apes, but in general it was assumed that humans were alone in using their mind and intelligence extensively for the business of social competition. The origin of human mentality usually was thought to lie in the challenge of tool making: "When the immediate forerunners of man acquired the ability to walk upright habitually, their hands became free to make and manipulate tools — activities that were in the first place dependent on adequate powers of mental and bodily coordination, but which in turn perhaps increased these powers."[1] Once observational studies in the wild and in naturalistic colonies began, however, it was found that nonhuman primates often rely on the support of other individuals in gaining rank[2,3] and sometimes use decidedly subtle social tactics, such as "protected threat,"[4] reciprocation of help in contests,[5] reconciliation after disputes,[6] and even deception.[7]

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In parallel with this growing realization of primate social complexity came isolated suggestions that primate groups as such might originally have provided a selective pressure for the evolution of cognition as an adaptation to social complexity.[8,9] Most influentially, Humphrey[10] argued that primate and human intelligence is an adaptation to social problem-solving, well suited to forward planning in social interaction but less suited to nonsocial domains. A decade later, the book *Machiavellian Intelligence*[11] brought these strands together and juxtaposed them with some of the most striking evidence of primate social complexity then available, arguing that this was an idea that deserved serious attention. The title of the book was inspired by de Waal's[12] explicit comparison between the chimpanzee social strategies he described and some of the advice offered four centuries earlier by Niccolo Machiavelli. Giving somewhat cynical recommendations to an aspiring prince, Machiavelli was prescient in his realization that an individual's success is often most effectively promoted by seemingly altruistic, honest, and prosocial behavior: "[It] is useful, for example, to appear merciful, trustworthy, humane, blameless, religious — and to be so — yet to be in such measure prepared in mind that if you need to be not so, you can and do change to the contrary."[13] "Machiavellian intelligence" seemed an appropriate metaphor when so many features of primate behavior appear cooperative and helpful, yet evidently result from natural selection, maximizing the inclusive fitness of certain individuals relative to others.[14]

Two separate consequences can be discerned here for anthropologists' understanding of human evolution. Growing realization of the sheer sophistication of social intelligence in primates opened up the possibility that interestingly complex aspects of human cognition might have a long evolutionary history traceable by comparative analysis of the behavior of extant primates, rather than stemming entirely from the adaptations of Plio-pleistocene hominids. This idea has now gained considerable acceptance.[15–18] Second, the specific "Machiavellian intelligence hypothe-

Box 1. Using Brain Size as an Index of Intelligence

The fact that brain size can be estimated accurately even for extinct species has led to its widespread use as an indication of cognitive capacity. Unfortunately, none of the various indices derived from brain size is perfect.[51] Absolute brain size evidently tends to increase with body size (consider the impossibility of a mouse having a brain the size of a horse's), but not linearly (consider how large-brained a horse-sized mouse would appear). In fact, brain size scales allometrically with body size, a power relationship with a slope of approximately 0.75.

Because it seemed implausible that large animals should in general be more intelligent than small ones, theorists looked to brain enlargement in proportion to body size as an index of cognitive capacity. Various measures of relative brain size have been devised. These include the encephalization quotient (EQ),[105] a species' actual brain size divided by that predicted by allometry for a mammal of its body size, and the comparative brain size (CBS),[106] which focuses on deviations from the allometric scaling line for a particular subgroup of mammals. However, this whole approach leads to odd implications. Two species, each with brains 50% greater than that predicted by allometric scaling, would be treated as cognitively equal (EQ=1.5), even if one had a body weight of 5 gm and the other a body weight of 500 gm. Yet vastly different amounts of neural tissue would be involved.

Deviations from the allometric scaling line also may reflect selection on body size rather than brain size, yet measuring brain size relative to body size treats body size as a given in the equation. For instance, it is reliably found that frugivorous primates have relatively larger brains than do folivorous ones.[106] This can be interpreted in two ways, however. Large brains may be a consequence of selection for cognitive mapping skill, needed more by frugivores for remembering the seasonal location of fruit in a large range. Alternatively, large bodies (and thus relatively small brains) may be a direct consequence of folivory, which requires a large gut and a proportionately large body to support it.[107] Though flawed as a measure of computational power, relative brain size is important. Brain tissue is metabolically costly, and this cost is borne by the energy supply of the whole body. Deviations from the allometric scaling line therefore give some estimate of the metabolic penalty borne by species with large brains and the benefits accruing to species with relatively small brains. Depending on diet adaptations, these costs or benefits may be significant in constraining species' brain evolution.

Clearly, to the extent that the brain is an "on-board computer," body size is irrelevant to its power. However, the brain is to some extent more like a switchboard, dealing with the mundane neural traffic of input and output, which inevitably increases with body size. Unfortunately, the two functions can be separated only in the imagination; in real brains they are intimately related. Various ways of specifically assessing a brain's computational power have been proposed over the years, but none has been entirely satisfactory. Neocortex ratio, the ratio between the size of the neocortex and the size the rest of the brain, is the most recent of these. At the simplest level, this assumes that the "intellectual" part of the brain is localized in the neocortex, which is moot. Among primate species, neocortex volume varies much more than does the volume of other brain areas. It thus appears that for primates these other structures are more "conservative." The use of neocortex ratio can therefore be additionally justified for primates as a measure of recent selection for brain size increases.

It should be noted that neocortex ratio, like absolute brain size, is not independent of body size. In general, larger-bodied mammals have brains that are both larger and more devoted to neocortex. Perhaps, after all, larger animals are simply more intelligent? While this might be so for a limited grouping such as the primates, it is unlikely to apply to all brains. For example, the tiny brains of parrots appear capable of underwriting behavior in many ways similar to that of apes.[108]

sis," that competition with companions is the main biological problem for which increased intelligence is an adaptive solution, took its place alongside other theories concerning the evolution of mind. Compared with many of the challenges posed by the external environment, social complexity has the attractive feature of inherent positive feedback: Because the competitors are conspecifics, any increase in intelligence will automatically spread in the population, thus raising the level of social sophistication needed to excel in the future. Predator-prey interaction, which has a similarly dynamic character, was invoked by Jerison[19] to explain the steady increase of brain size in carnivores and their ungulate prey visible at times in the fossil record.

It must be realized, however, that the notion of Machiavellian intelligence was at that time still vague and ill-formed. Was the hypothesis useful for explaining all evolutionary increases of intelligence in the ancestry of humans and other primates? Specifically, could it account for the rapid increase in cognitive ability during recent hominid evolution? Were large brains in some species of other mammalian groups, such as carnivores and cetaceans, also an evolutionary consequence of social complexity? Did the hypothesis predict that intelligence in general or a specific package of social skills — a "module" of social intelligence — would be promoted? In any case, was the resulting cognitive enhancement based on a dramatic quantitative increase in memory and learning abilities or on something qualitatively different from normal animal abilities and perhaps involving "theory of mind"?[20]

The 1980s were a phase of tentatively gathering together evidence that

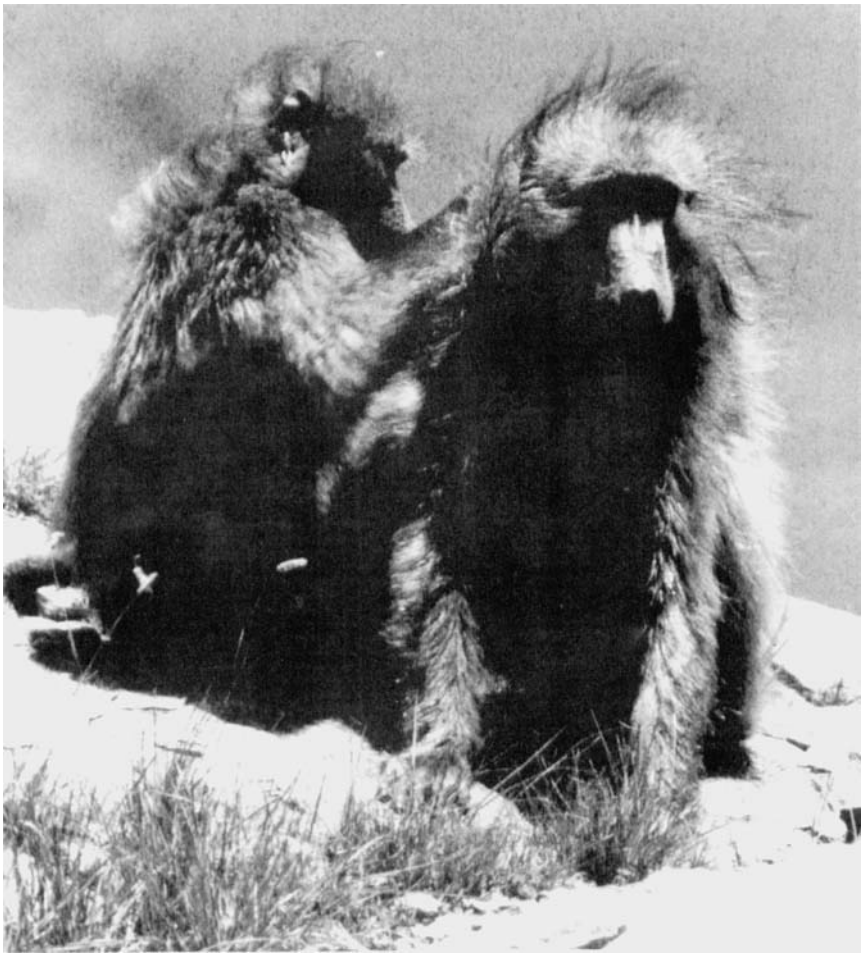

Figure 1. In most Old World monkeys, like these baboons, grooming is used to build up affiliative relationships. In addition to mothers' grooming of infants (most likely to be utilitarian) and monkeys' balanced exchanges of grooming (perhaps reciprocal altruism), individuals devote long periods to grooming potentially useful allies. This may be paid back in other currency: In this example, the female grooming the sole male of a mountain baboon group later received his support in contests with other females. Photo by Richard Byrne.

appeared to support some general version of the hypothesis in order to clarify its possible role. Only in the last few years have specific, testable versions of the Machiavellian intelligence hypothesis been put forward, and certain aspects of the hypothesis have now been evaluated against evidence. As a result, some vexing issues can be resolved, but others are still a matter of debate and current research.

Perhaps the most important idea requiring clarification is the original all-embracing idea of social complexity. Complexity is not an automatic consequence of the number of individuals in a social group (a large but anonymous aggregation may be socially simple), but rather is a function of the range and subtlety of the behavior expressed by its members. Of the complexity observed in simian primate groups, some aspects seem to be species-typical traits that rely only on a good memory for social information, whereas others are more individually varied and suggest more advanced cognition. It is perhaps unlikely that these two sorts of complexity in social life have a common origin, although both may be present in some species.

The same distinction neatly categorizes the progress made thus far in understanding the evolution of intelligence. On one hand, we now have a clear understanding of the function and mode of operation of many social skills in primates. Furthermore, the principles of Machiavellian intelligence seem a powerful means of explaining the evolution of these traits. On the other hand, when it comes to the category of more sophisticated social tactics, neither of these claims can be made.

LARGE BRAIN, GOOD MEMORY

Consider first the species-typical traits. These include the acquisition of rank by kin support[21] and the important role of third parties in deciding the outcome of conflicts.[22] Also in this category the use of grooming to cultivate "friendships" with potentially useful individuals[23] (Fig. 1), friendships of long duration that predict the distribution of mutual help,[24–26] as well as the repair of these relationships after conflict by targeted reconciliation.[27] Within species that show one of these tactics, most of the groups that have been studied have manifested the same general patterns, although individuals have differed in how much they used each tactic. It is therefore entirely plausible, even likely, that the traits are strongly channeled genetically, so that each individual does not have to work out the tactic for itself.

Complexity is not an automatic consequence of the number of individuals in a social group (a large but anonymous aggregation may be socially simple), but rather is a function of the range and subtlety of the behavior expressed by its members.

Although all these traits were first identified among Old World monkeys and apes, a steadily increasing number of them have since been recorded in nonprimate species. Zebras show decisive interventions by third parties

in dyadic conflicts.[28] Lions, cheetahs, mongooses, and coatis form long-lasting alliances with each other,[29–32] and in a few cases these alliances certainly involve unrelated individuals. Wolves and hyenas form more transient coalitions;[33, 34] dolphins form both long-term friendships and temporary coalitions.[35] Reciprocal altruism, first identified among baboons,[5, 36] has now been better documented among vampire bats than in any primate.[37] Some "primate specialties" are still thought to exist, including informed choice of potential allies on the basis of individual characteristics[38] and targeted reconciliation after conflict with certain long-term allies.[39] However, future research may challenge even these claims. There appears to be no good reason why such behavioral traits should not evolve in any species that already has or can develop the cognitive capacity to execute them.

What cognitive capacity do all these species-typical traits demand? No such trait could evolve in any species in which individuals could not distinguish conspecific group members as individuals and as kin, remember their relative ranks and past affiliations and, in some cases, remember even the personal histories of help given and received from various others. Successful use of the tactics essentially demands good visual perception and discrimination, attention to social attributes, and a good memory. Therefore social complexity is likely to select for memory efficiency, including rapid learning of socially relevant information. In this selection process, the costs of increased memory efficiency (Box 1) trade off against the benefits of increased social sophistication.

The same conclusion applies to at least one social trait, tactical deception (Fig. 2), that is patchily distributed across individuals and populations and that varies in its precise form from case to case.[40,41] In a corpus of observations contributed by many experienced primatologists, deception of some sort was found in every taxon of monkeys and apes.[42] The great majority of records of deception could be explained solely as a result of learning from natural coincidences, provided individuals first had a rich data base of social knowledge and were able to learn tactics within only a very few trials.[43] This conclusion has been supported by the only study designed to elicit tactical deception under close observation, which found that a mangabey could learn to deceive a conspecific in only three trials.[44]

Effective deception within a semipermanent group of individuals is bound to be frequency-dependent and is likely to be infrequent, accounting for the patchiness of its detection by primatologists. In addition, precisely what tactics an individual learns will depend on its particular experience. Nevertheless, as with species-typical components of social skill, the key cognitive variable for tactical deception is simply an efficient memory for social characteristics. The best evidence of this enhanced memory for social knowledge comes from monkeys[45] and other simian primates, but a range of other animals no doubt have similar, if smaller, capabilities. In captivity, pet dogs and cats readily learn tactics of deception[46] just as their wild relatives form alliances and coalitions.

The precise degree of neocortical enlargement has now been found to correlate with typical group size in both primates and chiropteran bats, analysing over species and across cladistic contrasts.

Considerable brain capacity, particularly neocortical enlargement, seems to be necessary for the efficient memory individuals need to build extensive social knowledge and rapidly learn new tactics. This verdict has come from the use of brain size as a cognitive index.

Laboratory tests aimed at directly measuring the "intelligence" of species have been notably unsuccessful.[47, 48] In contrast, brain weight (or, for fossils, cranial capacity) is a straightforward measure and is available for many species. Socially complex mammals like monkeys, wolves, and dolphins have relatively larger brains than do solitary species of similar body size. The precise degree of neocortical enlargement has now been found to correlate with typical group size in both primates and chiropteran bats, analysing over species and across cladistic contrasts.[49,50] No such relationship is found when neocortical enlargement is compared to simple correlates of environmental complexity, such as the size of the home range relative to the size that would be expected for a species of given body weight.

In these analyses, the proportion of the neocortex relative to the rest of the brain is used rather than brain size relative to body size (see Box 1). Group size is only an indirect estimate of the potential social complexity an individual encounters. However, the frequency of deception observed in a primate taxon is well predicted by neocortex size,[51] a fact that supports the interpretation that brain enlargement is required for the efficient memory needed to manage complex social interactions.

In addition, this tight correlation among social skill, group complexity, and brain size gives strong support to the Machiavellian intelligence hypothesis. The brain of a monkey or ape is strikingly larger than that of most mammals of similar size, including the prosimian primates. Several other taxa of highly social mammals also have relatively large brains. Brain tissue is highly costly in metabolic terms. Species with an energy-rich diet, or those able to show dietary flexibility to increase energy supply, are therefore better able to "afford" large brains. This constraint is likely to limit the extent to which a species responds to a selection pressure that favors increased social complexity. It is not coincidental that the large-brained chiropteran bats, carnivores, pinipeds and cetaceans have a high-energy diet, and the large-brained simian primates

A

Figure 2A and B. In multimale groups of mountain gorillas, the dominant or leading male attempts to prevent other males from mating with his adult females. Nevertheless, females sometimes solicit younger males for mating (**A**). These "secret" matings take place out of sight of the leading male, and both parties suppress their normal copulation calls, an example of tactical deception. Such deception is not always successful: On this occasion (**B**), the mating couple have just been interrupted by the leading male. When this happens, the leading male always attacks the female and sometimes attacks the male. These observations provide no evidence that gorillas understand deceit or intend to create false beliefs. However, other evidence suggests that all great apes are capable of some mental-state understanding. Photos by Richard Byrne.

eat much more fruit than (small-brained) prosimian primates. Large brains in mammals are most likely to be a consequence of the intellectual challenges arising from permanent social living,[52] including the consequent opportunities for enhanced learning.[53, 54]

Thus, the first step in the evolution of modern human intelligence goes back to about 40 mya, when the highly social simian primates first arose. To judge from their modern descendants, as well as their pronounced brain enlargement, these early anthropoids showed a massive quantitative increase in memory efficiency and learning speed over their immediate ancestors, and put those attributes to use in subtle social tactics. As the Machiavellian intelligence hypothesis suggests, this was indeed most likely an evolutionary response to a need to deal with the sort of complexity that social circumstances create. The fact that other highly social mammals have large brains supports this conclusion.

MENTAL REPRESENTATION IN APES

When we turn to aspects of primate social complexity that appear to be cognitively more complex, conclusions are less crystallized and generalization becomes murky. The issues here concern only one primate taxon, the great apes. In an eclectic range of studies, great apes have been found to engage in behavior more subtle or complex than that of monkeys, or to perform behavior similar to that of monkeys but to acquire it in more powerful ways. Whereas monkeys routinely take account of third parties, chimpanzees have been described as using "political" maneuvers to play one competitor off against another.[12, 55] Whereas monkeys of all taxa can learn subtle tactics of deception, only the great apes sometimes seem to understand the false beliefs involved.[43,56] Whereas monkeys learn rapidly in social circumstances, various apes have been considered to imitate the learned programs of others, including chimpanzees,[57,58] orangutans,[59,60] and gorillas.[61,62] More striking still, occasional observations have been made that suggest deliberate teaching

by mother chimpanzees.[63,64] Interpopulation differences in chimpanzee behavior are consistent with these signs of special mechanisms of social learning in great apes.[65] Although many species of animal show persisting local traditions in their behavior, chimpanzee tool use goes well beyond this, and has been analyzed as "material culture."[66]

All these claims are controversial, which is unsurprising, since they are used to argue that great apes possess a "uniquely human" ability: to hold information in mind, in the absence of prompting by observable stimuli, about unobservable mental states, such as what other individuals think or know. Rightly, strong evidence is required of any such claim, and some would still dispute that any special explanation is needed for ape behavior.[67,68] Experiments aimed at directly testing for this ability in apes have produced equivocal results.[69,70] Caution is also urged by the fact that tactical deception in monkeys, although often superficially matching the forms of intentional deception in humans, can be convincingly explained as a consequence of rapid learning and a good social memory. Nevertheless, researchers are increasingly concluding that great apes possess intellectual capacities that are qualitatively different from those of monkeys.[52,71,72]

In social circumstances, this ability is described as mental state attribution, or theory of mind.[73] However, the unusual capabilities of great apes do not appear to be limited to social domains. This is clearest in the domain of tool use. Although monkeys, under certain restricted circumstances, can readily learn to use an object as a tool, they seem to have no concept of the essential properties of an effective tool and, when their tool is removed, neither select a replacement on the basis of functional properties nor seem to understand simple physical causality.[74,75] In contrast, tool-using chimpanzees select objects according to an appropriate pattern for the job in hand, and even do so far from the site of need.[76] When a chimpanzee makes a tool by modifying natural materials, this preparation is sometimes done well in advance of using the tool.[77] Chimpanzees also show rudimentary understanding of physical causality.[78] Analysis of a young gorilla's developing ability to use a human as a social tool — that is, as a thing that can voluntarily provide help if properly requested — has shown that gorillas can understand cause and effect, as well as agency, but not necessarily theory of mind.[79]

Even great apes' considerable achievements in social learning are not entirely based on social comprehension. What they need for imitation of novel behavioral routines is an ability to construct programs of motor action by observation of a skilled model, and this may not require mental state attribution.[80,81] However, it certainly does require an ability to comprehend (represent) the structured actions of others in order then to translate them into new motor programs that the individual can employ.[82] Perhaps, then, the difference between monkeys and apes should most accurately be described in terms of mental representation. Great apes apparently can compute with mental representations of information about physical or mental states that are not physically present at the time, not yet in existence, or not observable in principle.[52]

This interpretation points to a second cognitive development in the ancestry of human mentality that occurred approximately 16 mya in the common ancestor of great apes and humans (Fig. 3). Individuals of this species gained an ability to represent properties of the world and to use these representations to compute future behavior. Clearly, this was an essential precursor to the later development of language in the hominid line, as well as other modern human abilities.

The adaptations that enable mental representation and planning — thinking, in everyday terms — have perhaps arisen in no other animal group, although a case can be made for some parallel evolution in toothed whales.[52] The physical underpinning of this change is less clear. All the great apes possess brains that are absolutely larger than the brain of any monkey, so mental representation might be an emergent property of sheer size.[83] The possible cetacean convergence supports this interpretation. Alternatively, an organizational change in information storage in the brain may have occurred — a "software" adaptation — that allowed the flexibility given by mental representation instead of more rudimentary storage of unstructured associations.[51] The lack of any systematic monkey-ape difference in neocortex ratio tends to point in this direction.

What is certain is that the demands of living permanently in a large social group cannot explain such a difference. Great apes simply do not form systematically larger groups than monkeys do: The Machiavellian intelligence hypothesis is no explanation for the evolution of representational understanding in great apes alone. Attention has therefore recently turned to challenges in the physical environment that might have applied with particular severity to ancestral great apes rather than monkeys.

Several theories have been proposed, all centering on the large body size of apes relative to that of monkeys. One possibility is that arboreal clambering by large animals for which a fall would be lethal is best accomplished by advance planning, and presents an engineering problem in which an ability to perceive the self as an object moving in space is advantageous.[84] Thus locomotion could have directly selected for representational ability.

Large size also indirectly puts a premium on efficient feeding, especially in direct competition with Old World monkeys, species that can digest a wider range of plant foods than can great apes. Perhaps, then, the ability to process plant foods that are nutritious but difficult to separate from a matrix or other physical defenses was selected in ancestral great apes.[85] During their development, extant mountain gorillas that confront this sort of problem rapidly acquire novel programs of manual actions for handling hard-to-eat foods; these programs are complex in structure and hierarchical in organization.[86,87] A representational understanding of action would pay here, both for remembering organized programs of manual actions and for understanding the actions of others and so learning from them.

More narrowly, perhaps tool use

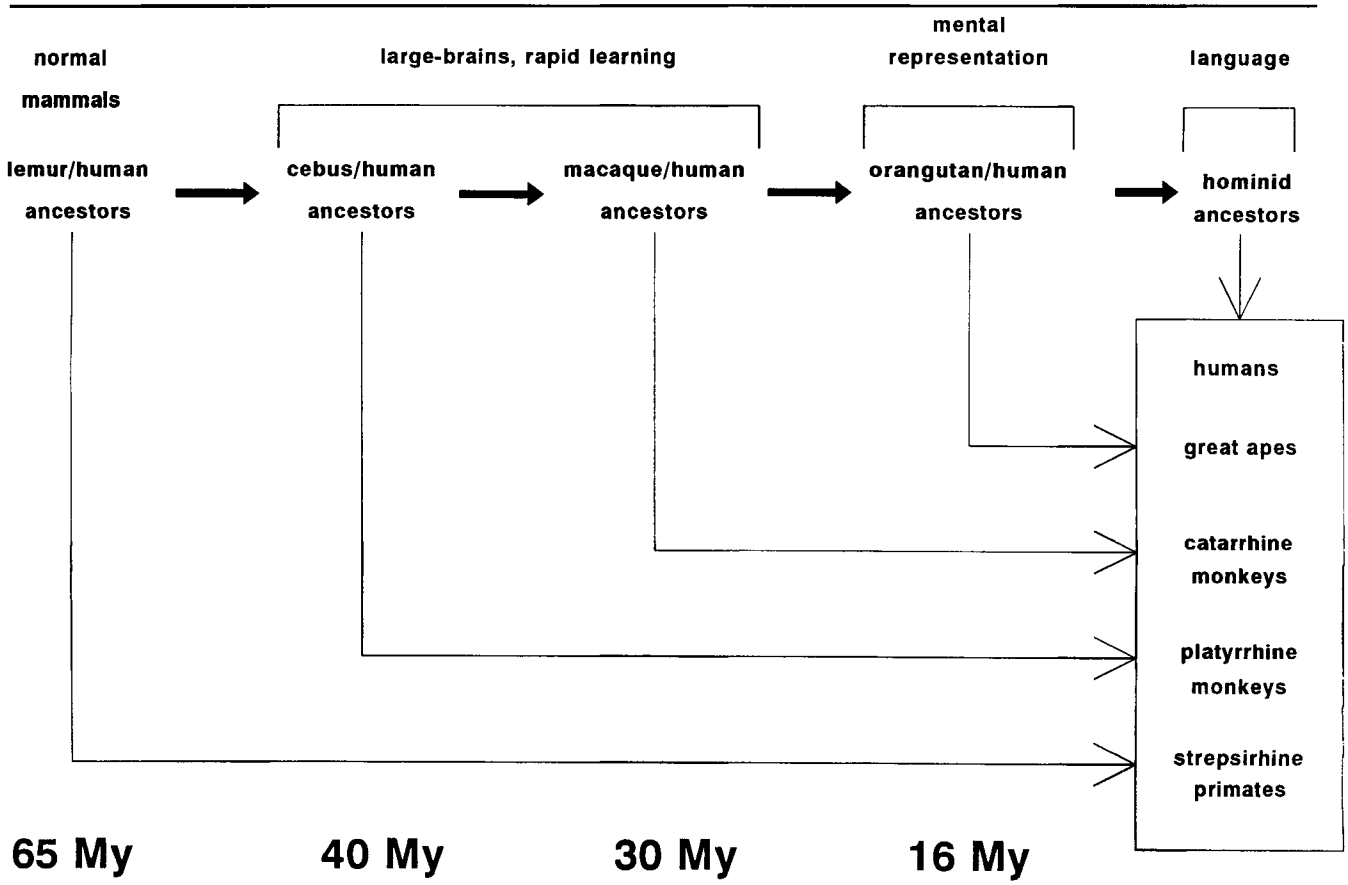

Figure 3. Hypothetical series of ancestor species (horizontal), whose cognitive adaptations led ultimately to the human mind, in relation to their modern descendants.

was advantageous to the ancestral ape population for efficient extraction of certain embedded foods.[88,89] Only common chimpanzees and one orangutan population use tools now, but in captivity all great apes demonstrate the potential to do so.[90] It is possible that recent changes in the diets of pygmy chimpanzees, gorillas, and most orangutans may secondarily have caused loss of the trait.

Finally, perhaps efficient food monopolization was enabled by a change to sleeping near food, which involved the construction of arboreal platforms to give safety from predators.[85,91] The "nests" or "beds" that great apes construct for sleeping and resting are often elaborate structures. These nests show skillful constructional behavior and are made by all great apes, and perhaps their possible significance has been overlooked. At present, all these theories are speculative, and can be evaluated only by their relative plausibility, self-consistency, and partial match to the behavior of modern great apes. It would be premature to attempt to decide among them, but it may well be that physical, not social challenges, resulted in the evolution of mental representation capability among the great apes and ourselves.

THE HOMINID TRANSITION

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According to the interpretation developed here, the cognitive "distance" between the abilities of modern humans and those of the last common ancestor shared with a living ape is considerably reduced compared with more traditional views.[92,93] On the basis of the robust scaling relationship between group size and cranium size among living primates, it also has been argued that Machiavellian intelligence explains some of the final cognitive steps in human evolution.[94] Extrapolating this to extinct hominids predicts groups so large that social grooming, a means of building a network of allies within the competitive environment of a group, would require too much of the daily time budget to be feasible. Dunbar[95] therefore argues that speech evolved as an efficient replacement for grooming: Speech does not require use of the hands, which can thus collect food concurrently. This speculation is difficult to test because there seems no objective means of discovering the "natural" group size of modern humans, let alone that of extinct hominids, which would be necessary to avoid the somewhat circular use of brain size.

At present, other, more familiar theories for the rapid increase in brain size in early hominid evolution also lack any clear empirical support. Thus, there seems to be no evidence of a tight relationship between the sophistication of stone tools and hominid brain size.[96] Evidence of organized big-game hunting, which would have required greater coordination than that of modern chimpanzees, is very weak for any hominids before anatomically modern humans.[97] It is unclear how the hypotheses that the rapid increase in hominid brain size was caused either by aimed throwing[98] or by the release of a venous-system constraint[99] can be tested at all.

In this climate of uncertainty, the possibility that social complexity might have spurred the rapid development of brain size in early *Homo* remains viable and has interesting implications regarding the mind of modern humans. In many ways, we seem better able to deal with problems couched in social terms than to deal logically with the same tasks in nonsocial guises.[100–102] We also show a surprising propensity to treat physical systems as if they were awkward social companions.[10,103,104] Perhaps these effects are indeed a legacy of selection, acting during hominid evolutions for adaptations to permit Machiavellian social skill.

Because, on the interpretation urged here, early hominids already possessed some representational understanding of the physical and social worlds, selection for social skill would be expected to have produced very different results than did the selection for social skill that occurred much earlier in the ancestor humans share with monkeys, an animal quick to learn, attuned to social variables, but unable to imagine hidden or future states of the world. We may never obtain cast-iron evidence for what led finally to the evolution of human speech and linguistic ability, but the close coupling of linguistic with social skill in humans makes Machiavellian intelligence an attractive possibility for theorists.

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