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THE SOCIAL BRAIN: Mind, Language, and Society in Evolutionary Perspective

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■ **Abstract** The social brain (or Machiavellian Intelligence) hypothesis was proposed to explain primates' unusually large brains: It argues that the cognitive demands of living in complexly bonded social groups selected for increases in executive brain (principally neocortex). The evidence for this and alternative hypotheses is reviewed. Although there remain difficulties of interpretation, the bulk of the evidence comes down in favor of the social brain hypothesis. The extent to which the cognitive demands of bonding large intensely social groups involve aspects of social cognition, such as theory of mind, is explored. These findings are then related to the evolution of social group size, language, and culture within the hominid lineage.

INTRODUCTION

In the century and a half following the discovery of the first Neanderthals, the focus of palaeoanthropology has been on the who's who of hominid evolution. How species are defined has come to occupy the central place in that story, with anatomy perhaps inevitably being the central plank of that endeavor. As appropriate as this has been, it does overlook the fact that what makes us human is not our bodies but our minds. The story of hominid—and hence ultimately human—evolution is thus one that must be told in terms of the evolution of mind. As Lewis-Williams (2002) points out, there have been only two serious attempts to grapple with this problem (Donald 1991, Mithen 1996), and both of these have inevitably been somewhat speculative in nature. I here offer a preliminary attempt to grapple with this problem. My focus is the intersection of brain, mind, and language in hominid evolution.

Ever since Jerison's (1973) seminal study, it has been recognized that primates have unusually large brains for body size. Moreover, within the primates, some species have disproportionately large brains for body size, one of these of course being humans. In general, however, differences in brain size do not reflect proportional increases in all brain components. Rather, the size of the neocortex accounts for most of the deviation from overall trend lines (Finlay & Darlington 1995). Primates have larger brains than other species mainly because they have

larger neocortices. In effect, then, when asking “Why do primates have unusually large brains?”, we are really asking, “Why do primates have unusually large neocortices?”

Traditionally, the assumption has been that changes in brain evolution have been driven by the need to solve ecological problems. Jerison (1973), for example, showed that the brain sizes of ungulates (prey) and carnivores (their predators) covaried across time through the Paleogene and the Neogene, with increases in ungulate brain volume being followed later by a corresponding increase in carnivore brain size. This view has been reflected in the assumption that human intellectual abilities are principally associated with the production and use (in hunting) of tools. However, Byrne & Whiten’s (1988) suggestion that primates differed from nonprimates principally in the complexity of their social skills rather than their foraging or survival skills initiated a new interest in alternative hypotheses for brain evolution in primates.

It is important to appreciate in this context that the contrast between the social and more traditional ecological/technological hypotheses is not a question of whether or not ecology influences behavior, but rather is one of whether ecological/survival problems are solved explicitly by individuals acting on their own or by individuals effecting social (e.g., cooperative) solutions to these problems. In both cases, the driving force of selection derives from ecology, but the solution (the animals’ response to the problem) arises from contrasting sources with very different cognitive demands (individual skills in one case, social-cognitive skills in the other).

I first briefly summarize attempts to test between alternative hypotheses as to why some primates might have larger neocortices than others, and then I consider some of the implications of these findings for cognitive and social evolution within the hominids. In the latter respect, I consider principally the implications for social group size, language evolution, and core aspects of social cognition.

THE SOCIAL BRAIN HYPOTHESIS

Attempts to test the social brain hypothesis have focused on identifying suitable indices of social complexity and appropriate indices of brain volume against which these indices can be correlated, as well as the implications of alternative statistical procedures. I do not comment here on the latter issues: Useful reviews of methodological issues can be found in Barton & Dunbar (1997), Dunbar (1998a), Barton (1999), and Purvis & Webster (1999).

So far, five separate indices of social complexity or skill have been correlated against neocortex volume in primates. These include social group size (Sawaguchi & Kudo 1990; Dunbar 1992a, 1998a; Barton 1996; Barton & Dunbar 1997), grooming clique size (Kudo & Dunbar 2001), the extent to which social skills are used in male mating strategies (Pawlowski et al. 1997), the frequency of tactical deception (Byrne 1995, 1996), and the frequency of social play (Lewis 2001). Each of these

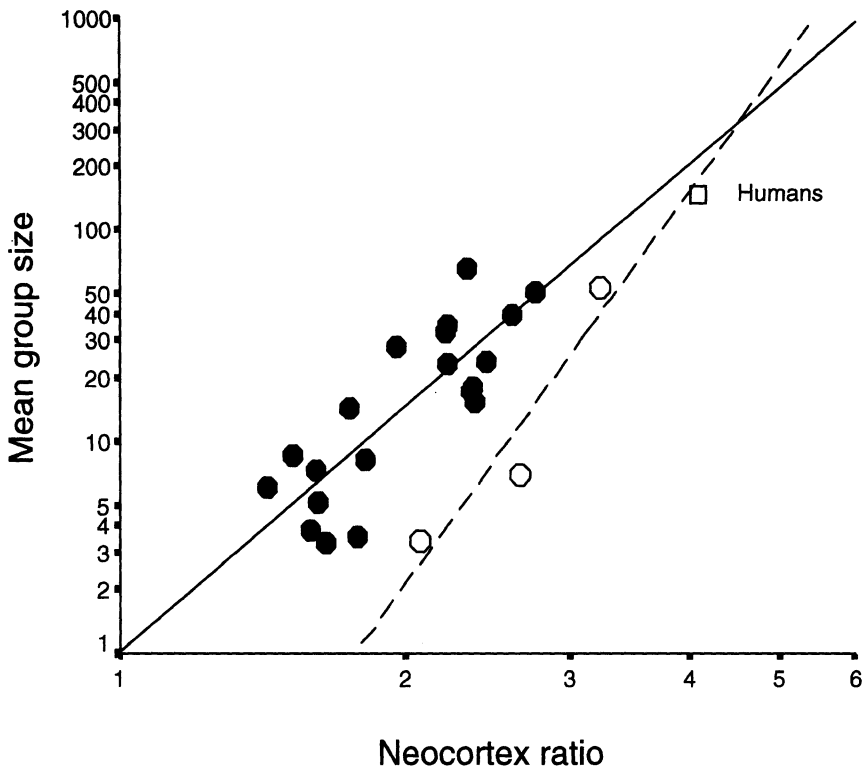


Figure 1 Mean social group size for individual primate taxa (principally, one species per genus) plotted against relative neocortex volume (indexed as neocortex volume divided by the volume of the rest of the brain). Simian (*solid symbols*) and hominoid (*open symbols*) taxa are shown separately. The datapoint for humans is that obtained by Dunbar (1992a). With a logged axis, neocortex ratio is mathematically identical to the more commonly used residuals of logged variables (except that the baseline is taken to be the value of the individual taxon's brain component rather than the scaled average value for the Order or other higher taxonomic grouping). Reproduced with permission from Barrett et al. (2002).

has yielded significant correlations with relative neocortex volume in primates and absolute neocortex volume in the case of group size. Figure 1 plots the relationship for social group size in anthropoid primates. Additional support for the hypothesis comes from two sources: (i) The regression equation for primates predicts group size for species not included in the original dataset from which the relationship was derived (Dunbar 1995); and (ii) similar relationships for social group size have been reported for carnivores and advanced (but not basal) insectivores (Dunbar & Bever 1998) and cetaceans (Morino 1996). In addition, comparable results have been reported from unpublished analyses of bats and ungulates, which suggests that this relationship may in fact be a general mammalian one.

These tests of the social brain hypothesis have, however, been based on correlational analyses and hence do not allow firm conclusions on causality to be drawn. Nonetheless, testing between competing hypotheses adds significantly to the power of any such analyses if it can be shown that only social indices yield significant relationships with brain component volumes. Dunbar (1992a, 1995) compared social group size (as a nominal index of social complexity) against four ecological indices as predictors of relative neocortex volume in primates. These included the proportion of fruit in the diet, home range size, day journey length, and the species' foraging style [in terms of Gibson's (1986) categories of extractive foraging]. Each of these focuses on a different possible ecological skill that might plausibly be implicated in primates' survival skills (e.g., the greater cognitive demands of frugivory and extractive forms of foraging or the need to manage large mental maps). These analyses yielded nonsignificant relationships between all four ecological indices and relative neocortex size (at least when ecological variables are adjusted for relative body size).

These results were subsequently confirmed in a reanalysis of the data by Deaner et al. (2000) using alternative methods for relativizing neocortex volume and alternative statistical procedures. In their analysis, the ecological variable (range size) was favored over group size only when neocortex volume was scaled against body size (an inappropriate procedure, given that body size is phenotypically more variable than brain component volumes and is hence no longer recommended as a basis for scaling in comparative analyses of the brain) and when range size was not scaled for body size (a questionable procedure because body size must have a significant grain effect on how an animal relates to its spatial environment). All other analyses confirmed that social group size is a better predictor of neocortex volume than is range size.

Reader & Laland (2002) analyzed frequencies of behavioral innovation, social learning, and tool use culled from the literature: All three indices yielded significant positive correlations with both the absolute and relative volume of executive brain (neocortex plus striate cortex) in primates, when appropriate controls are made for phylogeny and research effort (indexed as the frequencies with which individual species have been studied). They found that innovation and social learning covary across species and argued that this undermines the claim that there is an evolutionary trade-off between reliance on social experience and on individual experience. In addition, Reader & Lefebvre (2001) showed that there is no correlation between the social learning index and social group size once brain volume has been taken into account. Reader & Laland (2002) conclude that ecological factors may have been as (or more) important than social factors in primate brain evolution.

Because virtually all the instances of behavior in the Reader/Laland database relate to foraging situations, it is not safe to conclude more than that the cognitive processes underpinning "intelligent behavior" are used (or can be used) in the ecological domain (irrespective of whether the origins of brain evolution in primates have been driven by social or purely ecological forces). What these analyses do not test is whether social situations require different or greater cognitive powers

(i.e., executive brain volume) than ecological problem solving. It is important to appreciate that there are two different levels at stake here: One is whether individuals use social transmission of information to solve problems of day-to-day survival and reproduction, and the other is whether individuals are able to exploit and manipulate the mind-states of other individuals in managing the social relationships on which their day-to-day survival and reproduction depend. Social learning competencies are not necessarily an appropriate index of social intelligence in the sense intended by the social brain hypothesis (which principally focuses on the ability to use knowledge about other individuals' behavior—and perhaps mind-states—to predict and manipulate those individuals' behavior). Reader & Laland's findings do, however, allow us to reject unequivocally the first of the two alternatives. In contrast, they do not allow us to dismiss the claim that ecological innovation (including tool use and social learning) is simply a by-product of having large brains (executive or otherwise) for social purposes. Following the lead in developmental psychology, there is a growing view that social intelligence may not be a special module (in the sense that language might be considered a specialized module) but rather is a reflection of the ability to use basic executive functions in a more sophisticated way (for example, by using analogical reasoning, causal analysis, and deeper time depths for predicting future events) as a result of being able to bring greater (or, in terms of the ability to interface different domains, more sophisticated) computing power to bear on the problem at hand (see Mitchell 1997; L. Barrett and R.I.M. Dunbar, submitted).

The lack of correlation between social group size and the social learning index used by Reader & Laland suggests that either (a) there may be specialist cognitive demands for purely social tasks that are not required in foraging tasks, or (b) social (but not foraging) tasks involve components not included in the executive brain. Both options receive some support from the literature. Emery & Perrett (2000) have shown that there are correlations between social group size in primates and the volume of the basolateral complex of the amygdala (which has a direct neural input into the frontal lobe of the brain, the principal seat of executive function). The amygdala (part of the ancient subcortical limbic system) is perhaps an obvious candidate for any social function because one of its more important neurological tasks is the recognition and integration of emotional cues. These are likely to be important in any social context and of rather limited relevance for any strictly foraging problem unless these have a direct emotional component (e.g., sighting a predator or conflict with a conspecific over a resource item). It is important to note that it is only the basolateral complex of the amygdala that exhibits a relationship with social group size and not either the amygdala as a whole or other complexes within that structure (Emery & Perrett 2000, Joffe & Dunbar 1997). Similarly, Joffe & Dunbar (1997) were able to show that removing the primary visual cortex (area V1) from the neocortex volume resulted in a significantly tighter correlation between social group size and the remaining non-striate cortex. Although V1 correlates with social group size, it does so only with much greater variance, and the correlation disappears altogether when non-V1 neocortex volume is partialled

out. Indeed, Dunbar (2003) has since shown, using MRI-derived data on brain volume provided by Semendeferi et al. (1997), that frontal lobe volume (widely regarded as the principal site for executive cognitive function) provides an even better fit to social group size (at least for a very small sample of species, principally hominoids).

Reader & Laland's (2002) claim that ecological problem solving might have been the initial impetus that set primate brain evolution in motion does, however, merit serious consideration. They argue that ecological problem solving through behavioral flexibility may have provided the key stimulus to facilitate brain growth within the primates, thus in due course providing the opportunity to exploit the enlarged brains so derived for social purposes. This argument is not implausible. Indeed, a similar argument has been deployed by Barton (1998), who suggested that the dramatic grade shift in relative brain volume found between prosimian and anthropoid primates may owe its origin to the processing demands of color vision associated with a shift in diet from insects to fruits (and the consequent need to be able to detect ripe and unripe fruits against a vegetational background). However, the Reader & Laland (but not the Barton) argument raises questions about why primates should have been singled out in this way. Without knowing exactly where the contrasts between group size and the social learning index lie in relation to the primate phylogenetic tree, it is not possible to decide whether the lack of correlation between these two variables is due to ecological or phylogenetic grade shifts [in their analyses, Reader & Lefebvre (2001) fail to distinguish between prosimians, monkeys, and apes, all of which are now known to exhibit marked grade shifts in brain/behavior relationships; see Dunbar 1993, 1998a; Kudo & Dunbar 2001] or to a genuine discontinuity between ecological and social cognition.

ALTERNATIVE HYPOTHESES

Alternative hypotheses for the evolution of large brains in primates, which view behavioral and cognitive competences as mere by-products of having a large brain, have been proposed. For example, Sacher & Staffeldt (1974) and Martin (1981, 1984) proposed that larger-bodied species incur savings of scale that allow surplus energy to be invested into fetal brain growth in a way that is not possible for smaller-bodied species. The availability of additional brain volume for use in social contexts can thus be seen as a by-product of this brain-to-body-size relationship. However, McNab & Eisenberg (1989) showed that, within mammals, brain size adjusted for body size correlates most strongly with a species' habits and not with its metabolic rate. Similarly, Finlay & Darlington (1995, Finlay et al. 2001) have argued that ontogenetic scaling relationships between brain components are largely responsible for the apparently greater intelligence of larger-brained species.

Although the claim that brain evolution is subject to nothing other than strict scaling laws has been disputed (see Barton & Harvey 2000 and commentaries in Finlay et al. 2000), it remains reasonable to argue that ontogenetic scaling relationships of this kind play an important role in brain evolution when social or

ecological selection factors demand it. Thus, when the ability to maintain large group sizes is at a selective premium, it may be necessary to enlarge the whole brain in order to be able to produce the enlarged neocortex required to support large social groups. Either way, however, neither of these developmental arguments addresses the crucial evolutionary fact that large group sizes incur significant costs, both in ecological (van Schaik 1983, Dunbar 1988, Dunbar 1992b) and reproductive terms (Dunbar 1980), not to mention the energetic costs of large brains (Aiello & Wheeler 1995). Large groups simply cannot be an unintended by-product of having a large brain because the costs of living in large groups would inevitably result in their rapid dispersal if there were no intrinsic advantages to living in large groups to offset these costs. Thus, parsimony drives us toward the view that these explanations are in fact perfectly plausible arguments about developmental constraints, but not about evolutionary processes as such. In other words, they are an essential part of the story, but the explanation for why some primates have evolved larger brains than others (or, indeed, why primates in general have larger brains than other mammals) requires something in addition.

In summary, parsimony and biological common sense would suggest that it is group size that drives brain size evolution rather than brain size driving group size and that group size itself is a response to an ecological problem [most probably predation risk (van Schaik 1983, Dunbar 1988, Hill & Dunbar 1998)]. Although the hypothesis has been tested by determining how neocortex volume constrains group size and other social indices, the evolutionary logic is that the need to maintain coherent groups of a particular size has driven neocortex volume evolution through its demands on cognitive competences. The most succinct and parsimonious causal sequence with fewest unsupported assumptions is that the window of opportunity provided for more intensely bonded social groups and the social skills that underpin this was the crucial selection pressure for the evolution of large brains, even though simple ecological pressures (e.g., the shift to a more frugivorous diet) may have been instrumental in kicking off the process. In these terms, any associated ecological skills may be seen as the outcome of the opportunity provided by an increase in general purpose intelligence generated off the back of the social requirements. To argue the reverse sequence (that large social groups are a by-product of having evolved large brains to solve simple ecological problems) is, as with the various ontogenetic hypotheses, to leave unanswered the problem of the costs of social living.

SOCIAL VERSUS NONSOCIAL COGNITION

The relationship between indices of social competence and neocortex volume raises questions as to the cognitive mechanisms involved. Social cognition is broadly taken to be synonymous with the phenomenon known as theory of mind (or ToM), the ability to appreciate that another individual has a mind that controls its behavior that cannot be accessed directly but which can be modelled mentally (Tomasello & Call 1998). ToM emerges at an age of about 4–5 years in human

children (Leslie 1987). It represents level 2 in a hierarchically reflexive sequence of reflection on belief states known generically as intentional states ["I *believe* that you *suppose* (that something is the case)" identifies two distinct belief or intentional states]. Normal adult humans have been shown to be capable of working at level 4 (Kinderman et al. 1998), but it is widely believed that monkeys can aspire only to level 1 intentionality (Tomasello & Call 1998, Povinelli 1999). However, evidence for chimpanzees (the only great ape tested so far) is ambivalent, with some studies producing negative results (Call & Tomasello 1999) and others more positive findings (Hare et al. 2000; S. O'Connell and R.I.M. Dunbar, submitted).

It is important to appreciate just what is implied by the social brain hypothesis in this particular context. The most plausible interpretation is that some aspect of neocortex size imposes a limit on the number of relationships that an individual animal can maintain as a coherent set within its mental social world. This probably does not refer to the total social group. Rather, the analyses carried out by Kudo & Dunbar (2001) suggest that it is the inner group social group that an individual primate is most concerned about. This seems to correspond to the number of key social partners an individual animal has (as defined by the number of regular grooming partners). This core social group seems to correspond to the limit on the number of individuals who are willing to act as allies during conflicts. Being able to service an effective set of alliances seems to be crucial in allowing the individual animal to maintain the larger social grouping into which it is embedded (the conventional social group).

The effectiveness of an animal's relationships with its key coalition partners appears to be a function in part of its ability to integrate these individuals into its mental social world (a cognitive problem) and the time it can afford to invest in grooming with these individuals (an ecological problem). The latter, at least, is reflected in the fact that time devoted to social grooming increases more or less linearly with social group size (at least in catarrhine primates) (Dunbar 1991); however, this investment in grooming is not evenly distributed around the group but rather becomes increasingly (and disproportionately) focused on the core partners as group size increases (Dunbar 1984, Kudo & Dunbar 2001). It seems that, as group size increases, monkeys and apes endeavor to invest increasingly heavily in their core social partners. This can be interpreted as reflecting the fact that primates need to ensure that these alliances work effectively in order to buffer themselves against the costs of group living. These costs, which increase proportionately (but not necessarily linearly) as group size increases, reflect both the ecological and reproductive costs of living in close proximity to more individuals. Direct ecological costs reflect the energetic and time costs of the increased day journey lengths needed to accommodate extra individuals' feeding requirements, whereas the indirect costs reflect the disruptions to foraging consequent of contests over access to food. For females, these latter costs may be reflected directly in reduced fertility and lower birth rates (Bowman et al. 1978, Harcourt 1987).

Note that this coalitionary effect may find expression in two alternative forms. One is that allies actually come to the aid of the individual when it is under

attack. But the same functional effect would be produced simply by the presence of grooming partners acting passively to distance individuals whose physical proximity would stress the individual. Although there is unequivocal evidence for active coalitionary support from some species [e.g., gelada (Dunbar 1980, 1989)], there is equally compelling evidence to suggest that interventions of this kind may not necessarily be all that common in other species [e.g., baboons (Henzi & Barrett 1999, Barrett & Henzi 2002, Combes & Altmann 2001, Silk et al. 2003)]. Nonetheless, the functional consequences of managing group cohesion may be effected equally well by either the active or the passive route (or both).

To survive in a large primate group (and so gain the ecological advantages of group size), an animal has to engage in a sophisticated balancing act in which other group members are kept at just sufficient distance to prevent them imposing serious ecological and reproductive costs while at the same time not driving them away altogether. It is coalitions based on grooming partnerships that appear to allow monkeys and apes to do this. And these coalitions are, in turn, possible because of the social cognitive skills that allow primates to weld these miniature networks into effective social units.

Note that these analyses have all involved mean social group size for a species or genus, whereas the social brain hypothesis is couched in terms of the limits to group size. That limit is set by the point where, for any given species, social groups start to become unstable and fission rather easily. We do not at present know exactly where that value is for more than a handful of species. However, it seems intuitively likely that this value will be correlated with other demographic characteristics of that species, and hence with mean group size, thus explaining why we get the observed significant relationship with mean group size.

Dunbar (2003) has shown that achieved level of intentionality (assuming level 1 for cercopithecine monkeys, level 2 for chimpanzees, and level 4 for adult humans) correlates linearly (and very tightly) with absolute frontal lobe volume for these species, suggesting an important role for the frontal lobe in social cognition. This finding is supported by the results of brain scan studies of human subjects, which indicate that, when solving social cognition tasks, areas within the frontal lobe (specifically the left medial frontal cortex and the orbitofrontal cortex) are active (Happé et al. 1996, Baron-Cohen et al. 1994).

Two distinct views have been expressed, however, as to what ToM or other forms of social cognition actually involve. One is that social cognition consists of one or more specialized modules, most probably situated in the frontal cortex, that are explicitly dedicated to handling mind-reading. The other is that theory of mind (or ToM) itself is an emergent property of other more fundamental cognitive processes associated with executive function (Mitchell 1997). There are cogent arguments for believing that social cognition of the kind that is so fundamental to human social interaction (for review, see Barrett et al. 2002) may in fact be an emergent property of more fundamental and taxonomically widespread cognitive abilities, and that the difference lies not in specialized elements but in the way the

power of an enlarged neural network allows these to be integrated and brought to bear on specific problems (see L. Barrett and R.I.M. Dunbar, submitted).

THE SOCIAL BRAIN IN HOMINID EVOLUTIONARY HISTORY

We can use the findings discussed above to throw some light on at least three key aspects of hominid evolutionary history. These are the evolution of social group size, the origins of language, and the origins of culture. I deal briefly with each in turn.

Social Group Size

Primate social groups are complex phenomena (often with several levels of organization) whose size is determined by a number of ecological, demographic, and cognitive variables (Dunbar 1996). Consequently, even though there is a typical value for any given taxon, there is considerable variation in group size across the range of habitats occupied by that taxon. The above analyses do suggest, however, that, for any given taxon, social group size is constrained by relative neocortex size, and we can use this to obtain an estimate of likely changes in group size through time within the hominid lineage. When the regression equation for primates was used to predict social group size in modern humans, it yielded a value of about 150 that turned out to be a remarkably common value at one particular level in the hierarchy of social organization in a wide range of societies (Dunbar 1992b, Hill & Dunbar 2003). This level of grouping appears to be intermediate (in terms of organizational structure) between the overnight camps typical of foraging peoples (typically 30–50) and the size of their tribal units (typically 1500–2000), and roughly equivalent to the set of individuals with whom one has a personal as opposed to formal (or impersonal) relationship (Hill & Dunbar 2003). It is equivalent, for example, to the number of people of whom one feels one can ask a favor and expect to have it granted.

Although neocortex volumes are not available for fossil organisms, Aiello & Dunbar (1993) were able to show that these could be estimated from total cranial volume (which is available for a significant number of fossils) using the scaling relationships between brain components of the kind identified by Finlay & Darlington (1995). With neocortex ratios estimated in this way, Aiello & Dunbar (1993) were able to derive a pattern for group size across hominid specimens. These group sizes are bracketed (and thus delimited) by the observed group sizes for living chimpanzees and humans. Figure 2 shows the pattern, based on a new set of analyses, in which populations rather than individuals are used as the unit of analysis and group sizes are predicted from neocortex ratio using the equation specific to hominoids from Dunbar's (1992a) original analyses. Although there are inevitably problems associated with estimating specific values in all such analyses, the important issue here is not so much individual values as the broad pattern across time, which is much less affected by these kinds of problems. This shows

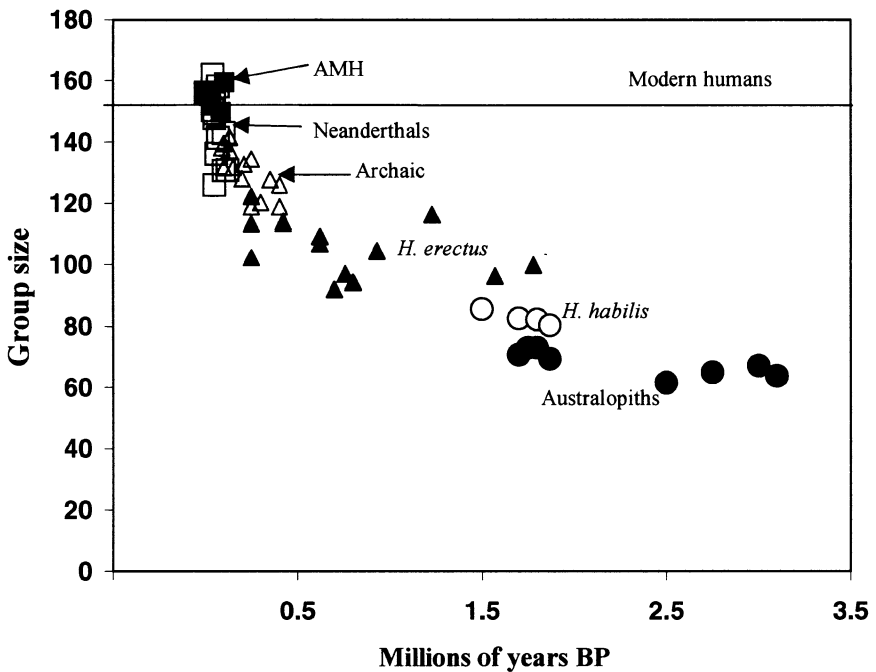


Figure 2 Social group size predicted for individual hominid populations using the regression equation for group size on neocortex ratio for hominoids (including modern humans) shown in Figure 1. The horizontal line represents the value of ~ 150 predicted for (and found in) modern human populations (see Dunbar 1993). Individual populations are defined as all the crania found within 50,000-year time bands at an individual site; a mean cranial volume for that population is then determined from the values for individual crania within that population. Cranial volume is used to estimate neocortex ratio using the regression equations given by Aiello & Dunbar (1993). Data from Aiello & Dunbar (1993).

that group size probably remained within the broad range for living great apes until well into the *Homo erectus* period and only began to rise significantly above this level from about 1 MY. From that point on, however, group size appears to increase at an exponential rate.

Origins of Language

These results suggest that the pressures exerted by social group size are unlikely to have started to bite until quite late in hominid evolution. Whatever mechanisms are used to bind ape social groups would have sufficed for their hominid counterparts until well into the *erectus* period. These mechanisms were, of course, principally social grooming. The upper limit on time spent grooming by any freeranging primate population is 20%. If modern humans (with their groups of about 150)

bonded their social groups using grooming in the conventional primate manner, then the regression equation relating grooming time to group size in Old World monkeys and apes would predict that about 43% of day time would have to be devoted to social grooming. The mean amount of time actually spent in social interaction (principally conversation) by a set of seven modern human populations (with samples from both traditional and postindustrial cultures) is exactly 20% (Dunbar 1998b). Dunbar (1993) argued that language evolved to bridge this gap in bonding time requirement because it allows time to be used more efficiently.

This increased efficiency arises from at least three key features of language. One is that several individuals can be “groomed” at once, in contrast to conventional grooming where only one individual can be groomed at any one time (a problem we still encounter when we resort to the human equivalent of grooming, namely cuddling and petting). The second is that it is possible to timeshare with speech in a way that is not possible with grooming: We can talk and walk or feed, whereas grooming is an exclusive activity (even in modern humans). Third, language allows us to exchange information about events within our social network that happened during our absence: For nonhuman primates, what they do not themselves see they never know about. As a result, humans are able to maintain a better knowledge database on a larger social network than any nonhuman primate.

We can use the regression equation relating social grooming time to group size to estimate grooming time requirements for fossil hominids and, in this way, gain some insight into when language might have evolved. Figure 3 plots the percentage of day time that would have to be devoted to social grooming obtained by interpolating the predicted group sizes for each hominid population shown in Figure 2 into the grooming time equation for Old World monkeys and apes. Because these are simply transformations of brain volume, the pattern across time necessarily reflects the changing size of hominid cranial capacity and is subject to all the usual caveats about compounding error variances. Our concern, however, is less with the exact values than with how this pattern relates to the benchmarks for pongid and modern human grooming time requirements, on the one hand, and the likely limits on how much time could be dedicated to social interaction of this kind.

Recognizing that living catarrhine primates (at least) have an observed upper limit on grooming time at 20% of their time budget, we can make some allowance beyond this for time budgets to be squeezed under strong selection pressure for larger groups. This might allow an additional 5% of time to be allocated to social grooming. If vocal exchanges allow primates to extend the interaction process into foraging and travel by a form of vocal grooming at a distance (as certainly happens in gelada baboons and, perhaps, bonobos and callitrichids), then we can probably add the equivalent of another 5% grooming time. That is to say, the use of vocal exchanges to reinforce grooming relationships may allow group size to increase by an amount equivalent to about 5% of grooming time (but probably not more) without adding significantly to the time budget. This would give us a rubicon at around 30% of grooming time requirement beyond which group size could not increase unless language came into play. Mapping this value onto Figure 3

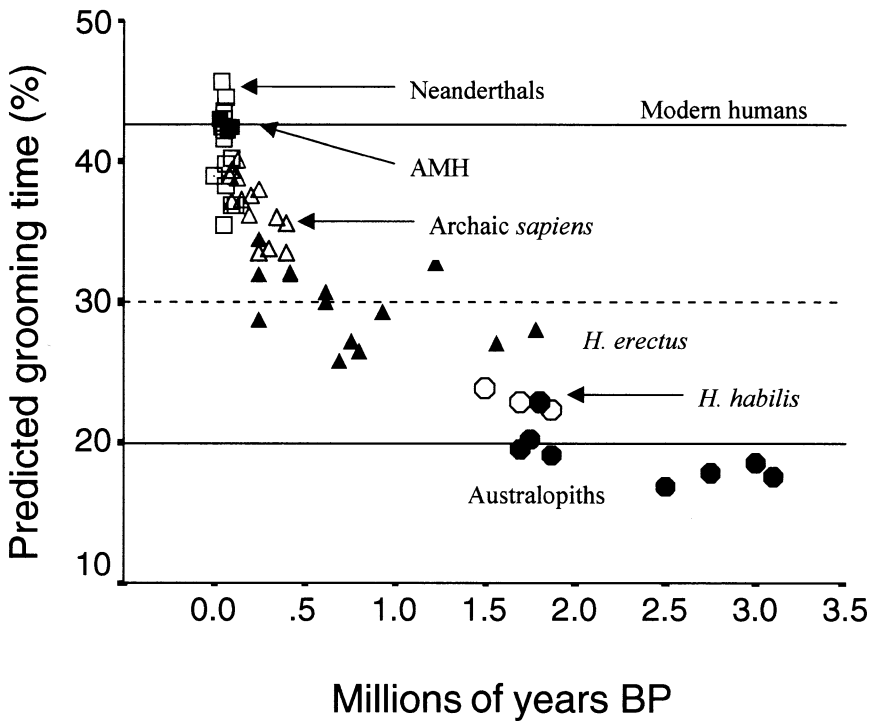


Figure 3 Hominid grooming time requirements plotted against time. Grooming time is determined by interpolating the values for group size shown in Figure 2 into the regression equation for grooming time versus group size obtained from Old World monkeys and apes. The solid horizontal lines represent the maximum grooming time observed in any wild primate group ($\sim 20\%$) and the time investment that would be required to service relationships in modern human groups of ~ 150 if this was done by social grooming alone ($\sim 43\%$); the dashed line represents the putative threshold at $\sim 30\%$ of time, beyond which group size could not have increased without a method of social bonding that used time more efficiently (i.e., language). Reproduced with permission from Barrett et al. (2002).

suggests that language, at least in some form, would have had to have evolved by around 0.5 MY. The distribution of datapoints on the graph suggests that *Homo erectus* populations, taken as a whole, simply sit astride this rubicon, but *H. sapiens* populations all exceed it. I take this as evidence to support the claim that language (in some form) must have evolved with the appearance of *H. sapiens* and that *H. erectus* almost certainly lacked a language capacity.

This conclusion fits well with two other sources of evidence that point more or less at the same time slot for the evolution of language, namely the size of the hypoglossal canal at the base of the skull and the size of the thoracic vertebral canal. The hypoglossal nerve enervates the tongue, and, because the canal is significantly

larger in modern humans than in other primates (when controlling for differences in body size), Kay et al. (1998) proposed that a comparison of its size in fossil hominid crania should tell us when speech evolved. Similarly, MacLarnon & Hewitt (1999) pointed out that the modern human vertebral canal has a distinctive enlargement in its thoracic region that is not present in other living primates, which seems likely to reflect increased enervation for the control of breathing. Because speech requires very fine control over breathing (speech requires a prolonged steady outflow of breath), the relative size of the thoracic canal may give us another benchmark for the appearance of speech. Both indices are of modern proportions in archaic *H. sapiens* but of pongid proportions in all earlier specimens (although there is a considerable time gap separating the latest specimen with the pongid pattern from the first that shows a modern human pattern in both cases).

Although there has been some dispute as to the real significance of these last two anatomical findings, the consistency of these three very different sets of data is surely significant. All three agree that there is evidence for the presence of speech for archaic *H. sapiens* but not for *H. erectus*. This is also in broad general agreement with recent genetic evidence suggesting that two key point mutations, which seem to be associated with grammatical competence (*FoxP2* genes on chromosome 7), are likely to have appeared within the last 200 KY (Enard et al. 2002; see also Lai et al. 2001).

In reviewing the pattern of grooming time in Figure 3, Aiello & Dunbar (1993) argued that we should probably not expect language to have arisen as a single phenotypic or genotypic event but rather as a series of stages. They characterized these as involving (i) a conventional primate grooming-based process for the australopiths as a group; (ii) increasing use of vocal chorusing to bond groups in the way that gelada and other living primates already do (characteristic of *H. erectus*); (iii) the appearance of socially focused language designed to expand the range and quality of interactions needed to support larger groupings (associated with the appearance of archaic *H. sapiens*); and finally (iv) language as we now have it (involving extensive use of metaphor and technical knowledge). Aiello & Dunbar (1993) equated the latter with the Upper Palaeolithic Revolution (reflecting the use of language to reflect on, discuss, and teach about other worlds) and argued that this largely involved a software rather than a hardware (i.e., neurological) change.

A plausible interpretation of the suggestion that language evolved out of a phase of increasingly extended vocal exchanges is that such vocal exchanges are likely to have involved chorusing (in the sense of communal singing). This interpretation would imply (a) that language evolved out of wordless singing [a view in keeping with the suggestion that language has vocal and not gestural origins (for an overview, see Barrett et al. 2002, pp. 328–34)] and (b) that music had an early (and perhaps separate) development as part of the bonding mechanism that welds human groups together.

Two alternative pathways can be envisaged here that have yet to be explored in any detail. One is that music has a very ancient history, dating back to at least the early *H. erectus* period when the demand for grooming time first significantly exceeded the limiting values seen in nonhuman primates (~20%). In this

scenario, formal (i.e., grammatical) language evolved with the appearance of archaic humans approximately 0.5 MY, and Neanderthals presumably were capable of speech (though perhaps only in the social sense). The alternative hypothesis is that the sea change in grooming time requirements at ~0.5 MY suggested by Figure 3 marks the point at which musical chorusing evolved into a particularly intense form, with the kinds of vocal exchanges seen before that during the *H. erectus* period being more similar to the counter-calling seen among contemporary primates. Grammatical speech may then be a later development [perhaps associated with anatomically modern humans (AMH) around 200 KY]. This scenario would explain why the anatomical evidence suggests that breathing control and articulation (both as essential for singing as for speech) apparently evolved around 0.5 MY but the genes for grammar did not appear until much later. On this reading, Neanderthals may have been very socially intense, but their groups would have been much smaller than those of AMH because they lacked grammatical language (without which it would be impossible to maintain large dispersed social groups).

Implications for Culture

Culture, and particularly those aspects of high culture that seem to be so crucial to the human condition, depends on advanced social cognition. This is especially clear in the context of religion and its use both in terms of facilitating a more benign world (pleading with or placating supernatural forces to ensure that the natural world behaves in a beneficial way) and in terms of using the supernatural to enforce the social norms of society. It quickly becomes apparent that the cognitive demands of such phenomena are very considerable and rapidly far exceed those required for the much simpler tasks of everyday social interaction. For a supernatural-based religion to have any force in making us toe the social line, I have to *believe* that you *suppose* that there are supernatural beings who can be made to *understand* that you and I *desire* that things should happen in a particular way. This involves four levels of intentionality (marked by the italicized words). Making religion a social as opposed to individual phenomenon thus adds significantly to the cognitive load needed to underpin it. Without working at this level, we will be unable to ensure that our actions are coordinated (as in the performance of rituals) or that we can agree that infringements of the social mores are to be discouraged (i.e., to accept adherence to social norms without the need for punishment). In contrast, conventional interpersonal attempts to insist that you adhere to a social norm require only three levels of intentionality (I *intend* that you *believe* that you must behave in the way that the rest of us *want*). It is the reference to an external supernatural world that cannot be immediately apprehended that adds the key extra layer of intentionality that pushes the cognitive demand to the limits of normal human capacity at level 4. For the individual that conceives all this as a good idea, there is an additional level that he/she needs to aspire to: I *believe* that I can *persuade* you to *believe* that there are some supernatural beings who will *understand* what it is that we all *want*. Kinderman et al. (1998) found that, although level 4 intentionality was the typical level achieved by normal adult humans, a small

proportion of individuals can achieve higher levels as a matter of course. It is these individuals that presumably act as the cultural leaders of the societies they live in.

Because Dunbar (2003) found a more or less linear relationship between achievable level of intentionality and frontal lobe volume in the catarrhines, we can interpolate hominid frontal lobe volumes into this equation to see how level of intentionality might have increased through hominid history. We can obtain reasonable estimates of frontal lobe volume by interpolating cranial volumes (corrected to give brain volume) into the regression equation relating frontal lobe volume to total brain size for anthropoid primates following the same logic as that used by Aiello & Dunbar (1993) and exploiting the relationships between brain components noted by Finlay & Darlington (1995). Once again, there will inevitably be some level of error variance in these estimates, but as a first pass it provides us with at least a hypothesis to work from.

The results (Figure 4) suggest that the level-4 intentionality threshold was unlikely to have been breached prior to the appearance of anatomically modern

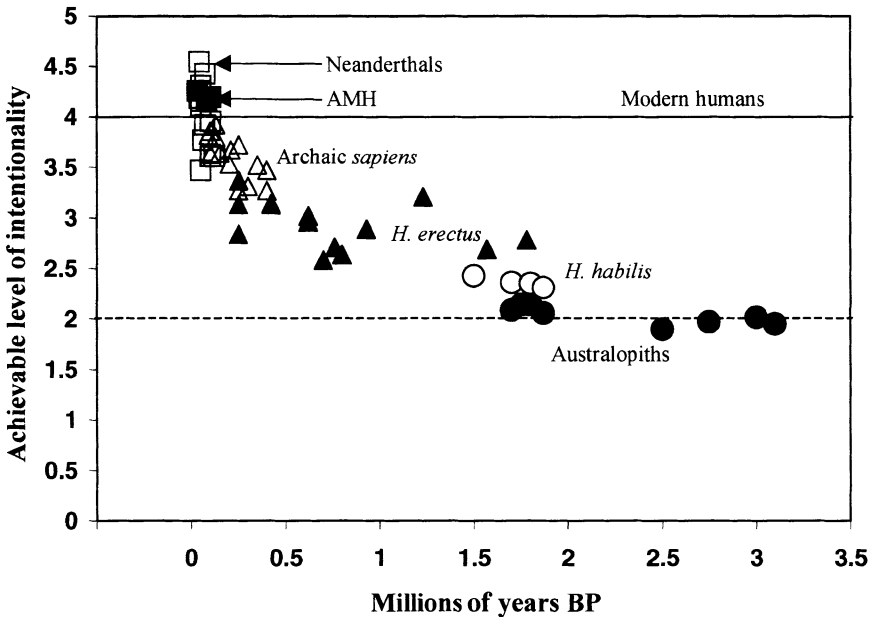


Figure 4 Achievable level of intentionality (or advanced theory of mind) for individual hominid populations, plotted against time. The horizontal lines demarcate level 2 (minimal theory of mind, representing the absolute upper limit for nonhuman primates) and level 4 (the level characteristic of normal human adults and the minimum level required for religion). Frontal lobe volume for fossil hominids is estimated from cranial volume using the regression equation for modern anthropoid primates; these are then interpolated into the regression equation relating achievable level of intentionality versus frontal lobe size in living catarrhines given by Dunbar (2003).

humans (AMH). All archaic *H. sapiens* populations lie just below the critical threshold. Note, however, that Neanderthal populations straddle the line, although there is in fact evidence of increasing cranial volume over time among Neanderthal specimens. In contrast, *H. erectus* populations seem to be more or less evenly distributed around level 3, which would imply a level of cognitive skill much below that required to support advanced human culture. This suggests that religion (at least) and presumably higher culture in general was lacking in *H. erectus* and probably came into being only with the appearance of the earliest populations of archaic *H. sapiens*. This conclusion is broadly in accord with the archaeological record for the Upper Palaeolithic Revolution.

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