

The Social Brain Hypothesis

Robin I.M. Dunbar

Conventional wisdom over the past 160 years in the cognitive and neurosciences has assumed that brains evolved to process factual information about the world. Most attention has therefore been focused on such features as pattern recognition, color vision, and speech perception. By extension, it was assumed that brains evolved to deal with essentially ecological problem-solving tasks.¹

The consensus view has traditionally been that brains evolved to process information of ecological relevance. This view, however, ignores an important consideration: Brains are exceedingly expensive both to evolve and to maintain. The adult human brain weighs about 2% of body weight but consumes about 20% of total energy intake.² In the light of this, it is difficult to justify the claim that primates, and especially humans, need larger brains than other species merely to do the same ecological job. Claims that primate ecological strategies involve more complex problem-solving^{3,4} are plausible when applied to the behaviors of particular species, such as termite-extraction by chimpanzees and nut-cracking by *Cebus* monkeys, but fail to explain why all primates, including those that are conventional folivores, require larger brains than those of all other mammals.

An alternative hypothesis offered during the late 1980s was that primates' large brains reflect the compu-

tational demands of the complex social systems that characterize the order.^{5,6} Prima facie, this suggestion seems plausible: There is ample evidence that primate social systems are more complex than those of other species. These systems can be shown to involve processes such as tactical deception⁵ and coalition-formation,^{7,8} which are rare or occur only in simpler forms in other taxonomic groups. Because of this, the suggestion was rapidly dubbed the Machiavellian intelligence hypothesis, although there is a growing preference to call it the social brain hypothesis.^{9,10}

Plausible as it seems, the social brain hypothesis faced a problem that was recognized at an early date. Specifically, what quantitative empirical evidence there was tended to favor one or the other of the ecological hypotheses,¹ whereas the evidence adduced in favor of the social brain hypothesis was, at best, anecdotal.⁶ In this article, I shall first show how we can test between the competing hypotheses more conclusively and then consider some of the implications of the social brain hypothesis for humans. Finally, I shall briefly consider some of the underlying cognitive mechanisms that might be involved.

TESTING BETWEEN ALTERNATIVE HYPOTHESES

To test between the competing hypotheses, we need to force the hypotheses into conflict in such a way that their predictions are mutually contradictory. This allows the data to dis-

criminate unequivocally between them. In the present case, we can do this by asking which hypothesis best predicts the differences in brain size across the primate order. To do so, we need to identify the specific quantitative predictions made by each hypothesis and to determine an appropriate measure of brain size.

The four classes of hypotheses that have been put forward to explain primate brain evolution are epiphenomenal, developmental, ecological, and social in orientation (Table 1). The epiphenomenal and developmental hypotheses share the assumption that evolution of the brain (or brain part) is not a consequence of external selection pressures but rather simply a consequence of something to do with the way biological growth processes are organized. The epiphenomenal hypotheses thus argue that brain evolution is a mere byproduct of body size evolution, and that brain part size is, in turn, a byproduct of total brain evolution.¹¹

The developmental versions differ only in that they provide a more specific mechanism by presuming that maternal metabolic input is the critical factor influencing brain development. This claim is given credibility by the fact that the bulk of brain growth in mammals occurs prenatally. Indeed, it appears to be the completion of brain development that precipitates birth in mammals, with what little postnatal brain growth occurs being completed by the time an infant is weaned. From this, the conclusion is drawn that brain evolution must be constrained by the spare energy, over and above her basal metabolic requirements, that the mother has to channel into fetal development.¹²⁻¹⁴ Some evidence in support of this claim comes from the fact that frugivorous primates have larger adult brains relative

Robin Dunbar is Professor of Evolutionary Psychology and Behavioural Ecology at the University of Liverpool, England. His research primarily focuses on the behavioral ecology of ungulates and human and nonhuman primates, and on the cognitive mechanisms and brain components that underpin the decisions that animals make. He runs a large research group, with graduate students working on many different species on four continents.

Key Words: brain size, neocortex, social brain hypothesis, social skills, mind reading, primates

TABLE 1. Hypotheses Used to Explain the Evolution of Large Brains in Primates

Hypothesis	Sources
<i>A. Epiphenomenal hypotheses</i>	
1. Large brains (or brain parts) are an unavoidable consequence of having a large body (or brain)	11, 70
<i>B. Ecological hypotheses</i>	
2. Frugivory imposes higher cognitive demands than folivory does	1, 65
3. Brain size constrains the size of the mental map:	1
(a) constraint on size of home range	
(b) constraint on inertial navigation (day journey length)	
4. Extractive foraging hypothesis	3, 4
<i>C. Social hypotheses</i>	
5. Brain size constrains size of social network (group size):	6, 71, 72
(a) constraint on memory for relationships	
(b) constraint on social skills to manage relationships	
<i>D. Developmental hypotheses</i>	
6. Maternal energy constraints determine energy capacity for fetal brain growth	12, 13, 46, 55, 73

to body size than do folivorous primates.¹ This has been interpreted as implying that frugivores have a richer diet than folivores do and thus have more spare energy to divert into fetal growth. Large brains are thus seen as a kind of emergent epigenetic effect of spare capacity in the system.

Both kinds of explanations suffer from the problem that they ignore a fundamental principle of evolutionary theory, which is that evolution is the outcome of the balance between costs and benefits. Because the cost of maintaining a large brain is so great, it is intrinsically unlikely that large brains will evolve merely because they can. Large brains will evolve only when the selection factor in their favor is sufficient to overcome the steep cost gradient. Developmental constraints are undoubtedly important, but rather than being causal their role is that of a constraint that must be overcome if larger brains are to evolve. In addition, Pagel and Harvey¹⁵ have shown that

the energetic arguments do not add up: Precocial mammals do not have higher metabolic rates than do altricial mammals despite the fact that they have neonatal brain sizes that are, on average, twice as large. We therefore do not need to consider either epiphenomenal or developmental hypotheses any further in the context of this article.

This does not necessarily mean that these explanations are wrong. Both kinds of explanation may be true in the sense that they correctly identify developmental constraints on brain growth, but they do not tell us why brains actually evolved as they did. They may tell us that if you want to evolve a large brain, then you must evolve a large body in order to carry the energetic costs of doing so or a diet

Because the cost of maintaining a large brain is so great, it is intrinsically unlikely that large brains will evolve merely because they can. Large brains will evolve only when the selection factor in their favor is sufficient to overcome the steep cost gradient.

that ensures sufficient energy to provide for fetal brain development. No such allometric argument can ever imply that you have to evolve a large brain or a large body. The large brain or brain part is a cost that animals must factor into their calculations when considering whether or not a large body or a large brain is a sensible solution to a particular ecological problem. Shifts to more energy-rich or more easily processed diets may be essential precursors of significant increases in brain or brain part size.² This would explain why frugivores have larger brains than folivores do and why hominids have larger brains than great apes do.

This leaves us with just two classes of hypotheses, the ecological and the social. At least three versions of the former can be identified, which I will term the dietary, mental maps, and extractive foraging hypotheses. In essence, these argue, respectively, that primate species will need larger brains if (i) they are frugivorous because fruits are more ephemeral and patchy in their distribution than leaves are, and hence require more memory to find; (ii) they have larger ranges because of the greater memory requirements of large-scale mental maps; or (iii) their diet requires them to extract resources from a matrix in which they are embedded (e.g., they must remove fruit pulp from a case, stimulate gum flow from a tree, extract termites from a termitarium, or hunt species that are cryptic or behave evasively).

For obvious reasons, I used the percentage of fruit in the diet as an appropriate index for the dietary hypothesis. I used the size of the range area and the length of the day journey as alternative indices for the mental mapping hypothesis, though I present the data only for the first of these here. The first index corresponds to the case in which animals have to be able to manipulate information about the locations of resources relative to themselves in a Euclidean space (an example would be the nut-cracking activities of the Tai chimpanzees¹⁶); the second corresponds to the possibility that the constraint lies in the needs of some aspect of inertial navigation. The extractive foraging hypothesis is less easy to characterize in quantitative terms because there is no objective measure of the degree to which diets vary in their extractiveness. However, Gibson⁴ provided a classification of primate species into four categories of diet that differ in their degree of extractiveness. We can test this hypothesis by asking whether there is a consistent variation in brain size among these four categories, with the species having the more extractive diets having larger brains than those with the less extractive diets.

Finally, we need an index of social complexity. In my original analyses, I used social group size as a simple measure of social complexity. Although at best rather crude, this measure nonetheless captures one aspect of the

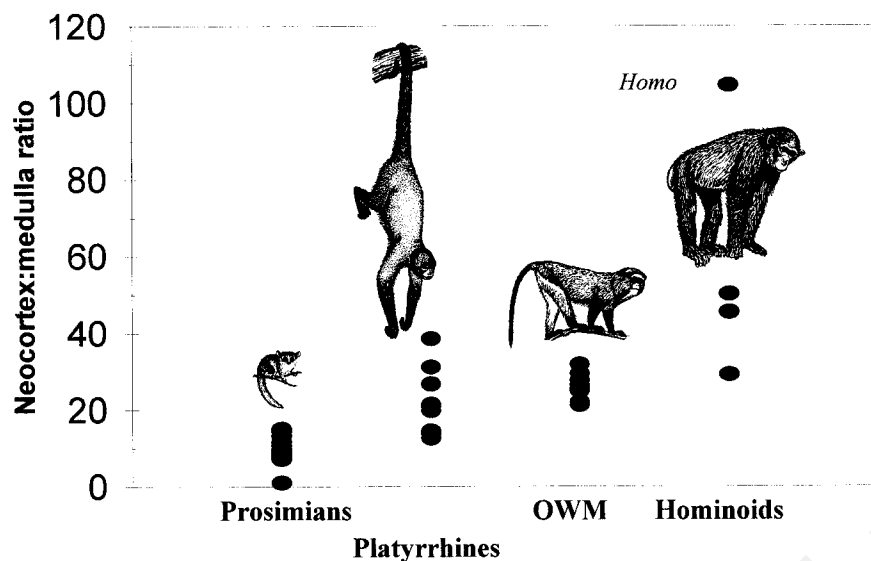


Figure 1. Neocortex volume as a ratio of medulla volume in different groups of primates (after Passingham¹⁹). Source: Stephan et al²⁹

complexity of social groups, the fact that information-processing demands can be expected to increase as the number of relationships involved increases. More importantly, perhaps, this measure has the distinct merit of being easily quantified and widely available. Although it is possible to conceive of a number of better measures of social complexity, the appropriate data are rarely available for more than one or two species.

The second problem concerns the most appropriate measure of brain evolution. Hitherto, most studies have considered the brain as a single functional unit. This view has been reinforced by Finlay and Darlington,¹¹ who argued that the evolution in brain part size closely correlates with the evolution of total brain size and can be explained simply in terms of allometric consequences of increases in total brain size. However, Finlay and Darlington failed to consider the possibility that changes in brain size might actually be driven by changes in its parts rather than in the whole brain. This is especially true of the neocortex, for its volume accounts for 50% to 80% of total brain volume in primates. Thus, changes in the volume of the neocortex inevitably have a large direct effect on apparent change in brain volume that may be quite unrelated to changes in other brain components. This point is given weight by the fact that Finlay and Darlington themselves

showed that neocortex size is an exponential function of brain size, whereas other brain components are not.

Finlay and Darlington¹¹ notwithstanding, there is evidence that brain evolution has not been a history of simple expansion in total volume. Rather, brain evolution has been mosaic in character, with both the rate and the extent of evolution having varied between components of the system. MacLean¹⁷ pointed out many years ago that primate brain evolution can be viewed in terms of three major systems (his concept of the triune brain). These systems correspond to the basic reptilian brain (hind- and midbrain systems), the mammalian brain (palaeocortex, subcortical systems), and the primate brain (broadly, the neocortex). A more important point, perhaps, is that variations can be found within these broad categories in the rates at which different components expanded, which, in at least some cases, have been shown to correlate with ecological factors.¹⁰ Partialling out the effects of body size on the size of brain components suggests that the story may be more complex than Finlay and Darlington¹¹ supposed, with some remodeling of brain growth patterns occurring in the transitions between insectivores, prosimians, and anthropoids.¹⁸

The important point in the present context is that, as Passingham¹⁹ noted, relative to the more primitive parts of

the brain such as the medulla, the neocortex shows dramatic and increasing expansion across the range of primates (Fig. 1). The neocortex is approximately the same size as the medulla in insectivores; however, it is about 10 times larger than the medulla in prosimians and 20–50 times larger in the anthropoids, with the human neocortex being as much as 105 times the size of the medulla.

This suggests that rather than looking at total brain size, as previous studies have done, we should in fact be considering the brain system, namely the neocortex, that has been mainly responsible for the expansion of the primate brain. From the point of view of all the hypotheses of primate brain evolution, this makes sense: The neo-

. . . brain evolution has not been a history of simple expansion in total volume. Rather, brain evolution has been mosaic in character, with both the rate and the extent of evolution having varied between components of the system.

cortex is generally regarded as being the seat of those cognitive processes that we associate with reasoning and consciousness, and therefore may be expected to be under the most intense selection from the need to increase or improve the effectiveness of these processes.

One additional problem needs to be resolved. In his seminal study of brain evolution, Jerison²⁰ argued that brain size can be expected to vary with body size for no other reason than fundamental allometric relationships associated with the need to manage the physiological machinery of the body. What is of interest, he suggested, is not absolute brain size, but the spare brain capacity over and above that needed to manage body mechanisms.

For this reason, Jerison derived his encephalization quotient. All subsequent studies have used body size as the appropriate baseline against which to measure relative deviations in brain size. However, a problem has since emerged: Brain size is determined early in development and, compared to many other body systems, appears to be highly conservative in evolutionary terms. As a result, body size can often change dramatically both ontogenetically across populations in response to local environmental conditions²¹ and phylogenetically^{22,23} without corresponding changes in brain size. This is particularly conspicuous in the case of phyletic dwarfs (e.g., callitrichids and perhaps modern humans and hylobatids²²) and species in which body size may have increased in response to predation pressure following the occupation of more open terrestrial habitats (e.g., papionids²⁴).

The lability of body size therefore makes it a poor baseline, though one that probably is adequate for analyses on the mouse-elephant scale. Consequently, it is necessary to find an internally more consistent baseline for taxonomically fine-grained analyses. Willner²² suggested that either molar tooth size or brain size may be suitable because both are developmentally conservative. Because we are concerned with brain part size, some aspect of brain size seems the most appropriate.

At this point, three options are available. One is to compare the neocortex, the brain part of interest, with the whole brain; the second is to use the rest of the brain other than the part of interest; the third is to use some less variable primitive component of the brain, such as the medulla, as a baseline. Two options are in turn available as mechanisms for controlling for brain size in each of these cases. One is to use residuals from a common regression line against the baseline (e.g., the residual of neocortex volume on total brain volume or medulla volume). The other choice is to use ratios.

We have considered and tested all these options^{10,24} (see Box 1). The results are virtually identical irrespective of which measure is used. One explanation for this may be that all these measures actually index the same

thing, absolute neocortex size, mainly because the neocortex is such a large component of the primate brain. Indeed, the use of absolute neocortex size produces results that are similar to those obtained from relativized indices of neocortex volume.^{24,25} This makes some sense in computational terms: As Byrne²⁶ has pointed out, a 10% increase in the processing capacity of a small computer is worth a great deal less in information-processing terms than is a 10% increase in a large computer. Although residuals from a common regression line would conventionally be considered the safest measure, and have been used in many recent analyses,^{27,28} I shall con-

The neocortex is generally regarded as being the seat of those cognitive processes that we associate with reasoning and consciousness, and therefore may be expected to be under the most intense selection from the need to increase or improve the effectiveness of these processes.

tinue to use my original ratio index because it provides the best predictor (see Box 1).

Finally, it is now widely appreciated that comparative analyses need to control for the effects of phylogenetic inertia. Closely related species can be expected to have similar values for many anatomical and behavioral dimensions merely by virtue of having inherited them from a recent common ancestor. In such cases, plotting raw data would result in pseudoreplication, artificially inflating the sample size by assuming that closely related species are actually independent evolutionary events. The ways of dealing

with this problem include plotting means for higher taxonomic units, performing nested analyses of variance using phylogenetic levels as factors, comparing matched pairs of species, and making independent contrasts that control directly for phylogeny. Each method has its own advantages and disadvantages, but the first and third procedures are particularly associated with loss of information and small sample sizes. I shall use the first and last method, the last because it allows individual species to be compared, but the first because it allows grade shifts within data sets to be identified (a problem that independent-contrasts methods have difficulty dealing with). I shall take the genus as a suitable basis for analysis because genera typically represent different reproductive or ecological radiations and thus are more likely to constitute independent evolutionary events.

The resulting analyses are relatively straightforward: Figure 2 presents the data for neocortex ratio for the anthropoid primate species in the data base of Stephan, Frahm, and Baron.²⁹ Neocortex size, however measured, does not correlate with any index of the ecological hypotheses, but does correlate with social group size. Similar findings were reported by Sawaguchi and Kudo,³⁰ who found that neocortex size correlated with mating system in primates. Barton and Purvis³¹ have confirmed that using both residuals of neocortex volume on total brain volume and the method of independent contrasts yields the same result. Both Barton¹⁰ and T. Joffe (unpublished) have repeated the analyses using the medulla as the baseline for comparison. More importantly, Barton and Purvis³¹ have shown that while relative neocortex volume correlates with group size but not the size of the ranging area, the reverse is true of relative hippocampus size. A correlation between range area and hippocampus size is to be expected because of hippocampal involvement in spatial memory.^{32,33} This correlation demonstrates that it is not simply total brain size that is important (a potential problem, given the overwhelming size of

Box 1. How to Measure Brains

R. Dunbar and Tracey H. Joffe

The different ways of measuring relative brain size have raised doubts as to the most appropriate technique to use.⁶⁵ Many researchers have preferred to use residuals from the common regression line of best fit for the data set concerned. This provides a measure of the extent to which brain (or brain part) volume deviates from what would be expected for an average member of the relevant taxon of the appropriate size. Although ratios have been used to compare the relative size of brain components,^{29,66} this has been criticized on the grounds that trade-offs within the brain may mean that a given index simply measures total brain size (or the size of a brain part) and thus does not remove the effects of absolute size. Ratios may also be prone to autocorrelation effects, especially when the baseline is taken to be the whole brain and, as in the case of the neocortex, the part in question is a major volumetric component of the brain.

Although there are likely to be some trade-offs of this kind within the brain, the fact that neocortex volume increases progressively across the primate order suggests that such constraints are less likely to have a significant effect on a ratio measure. Of course the residuals procedure is itself a ratio: Encephalization-type indices are calculated as actual volume divided by predicted volume (which, when data are logged, becomes the conventional actual minus predicted values). Thus, ratio measures per se may not be the problem. Rather, the substantive objection is whether or not a ratio partials out the allometric effects of body size. In fact, it seems that neocortex ratios are not correlated with the basal brain (i.e., brain volume excluding the neocortex) within major taxonomic groups (unpublished analyses). Consequently, this criticism has less force than it might appear to have

on first sight. Moreover, any index that uses the whole brain as its base is likely to suffer from autocorrelation effects. Because the neocortex is such a large proportion of the brain in primates, residuals of neocortex from total brain size may simply be a measure of neocortex plotted against itself.

To consider the problem in more detail, we ran a stepwise regression analysis on the 24 species of anthropoid primates, including humans, on the data base of Stephan, Frahm, and Baron,²⁹ with group size as the dependent variable and nine indices of relative brain or brain-part volume as independent variables. In addition to neocortex ratio, these included total brain volume as well as telencephalon and neocortex volume, each taken as absolute volume and as a residual from both body mass and brain volume. All variables were \log_{10} -transformed for analysis. In both cases, neocortex ratio was selected as the variable of first choice. We carried out both regressions on generic plots and independent contrast analyses. For the contrasts analysis, the best fit least-squares regression equation through the origin was:

$$\text{Contrast in } \log_{10}(\text{group size}) = 3.834 \\ * \text{ Contrast in } \log_{10}(\text{neocortex ratio}) \\ (r^2 = 0.395, F_{1,22} = 15.39, \\ P = 0.001).$$

With all other variables held constant, none of the other eight indices made a significant contribution to the variability in group size in either analysis. Table 2 gives the results for the independent contrasts analysis.

Neocortex ratio is thus the single most powerful predictor of group size in these species. While the biological significance of this variable remains open to interpretation, the fact that it provides the best predictor, indepen-

dently of all other confounding measures, suggests that more detailed consideration needs to be given to its significance and meaning. It may be, for example, that body size, rather than being a determinant²⁰ is simply a constraint on neocortex size: A species can evolve a large neocortex only if its body is large enough to provide the spare energy capacity through Kleiber's relationship for basal metabolic rate to allow for a larger than average brain. This interpretation is implied by the Aiello and Wheeler² "expensive tissue hypothesis." It would also be in line with Finlay and Darlington's¹¹ claim that in mammals the evolution of brain-part size is driven, developmentally at least, by the evolution of the whole brain, thus generating very tight correlations between brain-part size and total brain size.

TABLE 2. Stepwise Regression Analysis of Indices of Brain Component Volume as Predictors of Group Size in Anthropoid Primates, Based on Independent Contrasts Analysis*

Independent Variable	<i>t</i>	<i>P</i>
Absolute brain volume	-1.69	0.107
Residual of brain volume on body mass	-0.91	0.371
Absolute telencephalon volume	-1.72	0.101
Residual of telencephalon volume on body mass	0.61	0.546
Residual of telencephalon volume on brain volume	1.69	0.107
Absolute neocortex volume	-1.70	0.104
Residual of neocortex volume on body mass	0.56	0.583
Residual of neocortex volume on brain volume	1.60	0.136
Neocortex ratio (against rest of brain)	3.79	0.001

*Sample: 24 species of anthropoid primates from Stephan, Frahm, and Baron.²⁹

the primate neocortex). Moreover, it points to the specific involvement of the neocortex.

The validity of this relationship could be tested directly by using it to predict group sizes in a sample of

species for which brain volumetric data were not available in the original sample of Stephan, Frahm, and

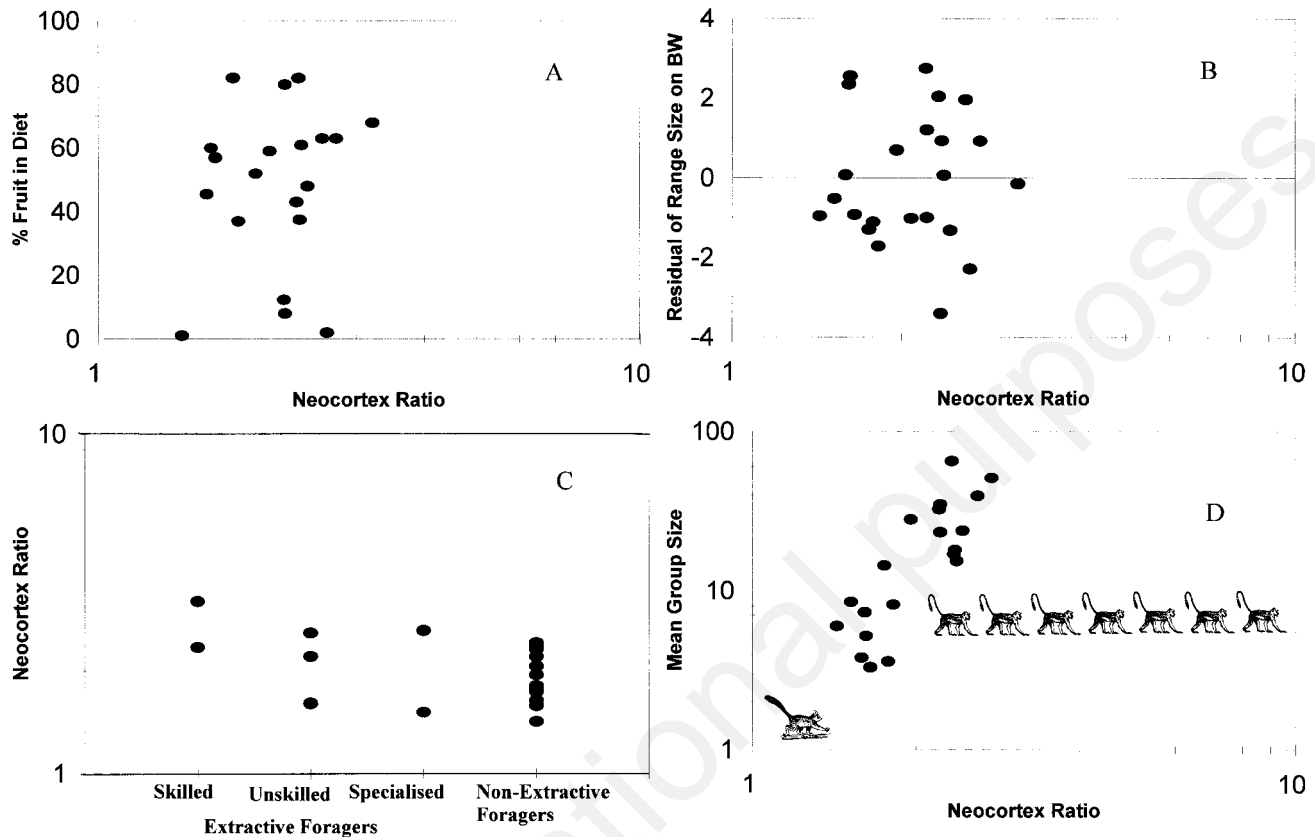


Figure 2. Relative neocortex size in anthropoid primates plotted against (a) percentage of fruit in the diet, (b) mean home-range size scaled as the residual of range size regressed on body weight (after Dunbar²⁴), (c) types of extractive foraging (after Gibson⁴), and (d) mean group size. (a), (b), and (d) are redrawn from Dunbar²⁴, Figures 6, 2 and 1, respectively; (c) is from Dunbar,³⁵ Figure 2.

Baron.²⁹ I did this by exploiting the fact that neocortex ratios can be predicted from total brain volume,³⁴ a result that, in fact, follows directly from the Finlay and Darlington¹¹ findings. The result was a significant fit between predicted neocortex ratio and observed mean group size for a sample of 15 New and Old World monkey species.³⁵

Barton²⁷ noted that the original analyses of Dunbar²⁴ seemed to imply that variation in neocortex size was much greater than variation in group size in the prosimians. Using Dunbar's²⁴ data on group size, Barton suggested that the relationship between neocortex and group size did not apply in the case of prosimians. However, the data on prosimian group sizes in this sample suffered from a paucity of data, particularly for the nocturnal species. Because many of these are described as semi-solitary, it was conservatively assumed in the Dunbar²⁴ database that their group size was one. More recent field studies have produced markedly improved es-

timates of the sizes of social groups and, in the case of the semi-solitary species, daytime nest groups.³⁶ Re-analysis of the data for prosimians using these improved estimates of social group size suggests that these species do in fact adhere to the same relationship between neocortex and group size as that which pertains for other primates.²⁵ More importantly, the regression line for this taxon is parallel to, but shifted to the left of, that for other anthropoid primates (Fig. 3).

This relationship has now been shown to hold for at least four other mammalian orders: bats,¹⁰ carnivores and insectivores,^{37,38} and odontocete cetaceans.^{39,40} In the case of the insectivores, the data points are shifted far to the left of those for the primates, as might be expected of a taxonomic group that is considered to be broadly representative of the ancestral mammals.³⁷ However, the relationship is weak in this case, probably because estimates of group size are particularly uncertain for insectivores.

Surprisingly, the data for the carnivores map directly onto those for the simian primates, that is, the regression lines for the two data sets do not differ significantly. However, the carnivores do not exhibit as wide a range of neocortex ratios or group sizes as do anthropoid primates. The fact that the prosimians lie to the left of both these taxonomic groups implies that the carnivores represent an independent evolutionary development along the same principles as the anthropoid primates, the difference being that they just have not taken it as far as primates have. One reason for this may be that the carnivore social world is olfaction-dominated rather than vision-dominated, as in the case of the primates. Barton^{10,27,41} has pointed out that the shift to a diurnal lifestyle based on color vision, perhaps initially diet-driven, but leading to a shift into vision-based communication, may be the key feature that has spurred on the dramatic development of the primate neocortex.

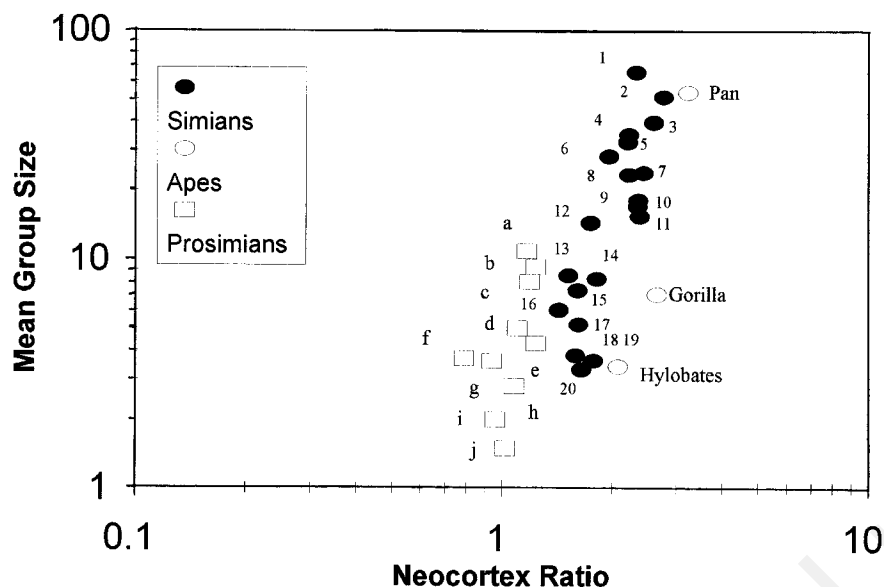


Figure 3. Mean group size plotted against neocortex ratio for individual genera, shown separately for prosimian, simian, and hominoid primates. Prosimian group size data, from Dunbar and Joffe,²⁵ include species for which neocortex ratio is estimated from total brain volume. Anthropoid data are from Dunbar.²⁴ Simians: 1, *Miopithecus*; 2, *Papio*; 3, *Macaca*; 4, *Procolobus*; 5, *Saimiri*; 6, *Erythrocebus*; 7, *Cercopithecus*; 8, *Lagothrix*; 9, *Cebus*; 10, *Ateles*; 11, *Cercocebus*; 12, *Nasalis*; 13, *Callicebus*; 14, *Alouatta*; 15, *Callimico*; 16, *Cebuella*; 17, *Saguinus*; 18, *Aotus*; 19, *Pithecia*; 20, *Callicebus*. Prosimians: a, *Lemur*; b, *Varecia*; c, *Eulemur*; d, *Propithecus*; e, *Indri*; f, *Microcebus*; g, *Galago*; h, *Hapalemur*; i, *Avahi*; j, *Perodictus*.

REFINING THE RELATIONSHIP

The social brain hypothesis implies that constraints on group size arise from the information-processing capacity of the primate brain, and that the neocortex plays a major role in this. However, even this proposal is open to several interpretations as to how the relationship is mediated. At least five possibilities can be usefully considered. The constraint on group size could be a result of the ability to recognize and interpret visual signals for identifying either individuals or their behavior; limitations on memory for faces; the ability to remember who has a relationship with whom (e.g., all dyadic relationships within the group as a whole); the ability to manipulate information about a set of relationships; and the capacity to process emotional information, particularly with respect to recognizing and acting on cues to other animals' emotional states. These are not all necessarily mutually exclusive, but they do identify different points in the cognitive mechanism that might be the crucial information-processing bottleneck.

Although visual mechanisms are likely to be important for social interaction, and may well have been the

initial kick for the evolution of large brains in primates,¹⁰ it seems intrinsically unlikely that the ultimate constraint lies in the mechanisms of the visual system itself.²⁸ Although there is a correlation between the relative size of the visual cortex and group size in anthropoid primates, the fit is much poorer, and the slope significantly shallower than that between the nonvisual neocortex and group size ($r^2 = 0.31$ vs $r^2 = 0.61$, respectively) (Fig. 4). Partial correlation analysis indicates that only the correlation for the nonvisual relationship remains significant when the other component is held constant²⁸ (though this is not true for prosimians²⁵). A more important point is that the volume of the lateral geniculate nucleus, a major subcortical way station in visual processing, does not correlate with group size at all, indicating that pattern recognition per se is unlikely to be the issue.²⁸ It may be of some significance that the absolute size of the visual cortex seems to reach an asymptotic value in the great ape clade, whereas the nonvisual neocortex continues to increase in size. One interpretation of this is that visual processing does not necessarily continue to improve indefinitely as the

size of the cortical processing machinery increases, at least relative to the opportunity cost of taking cortical neurons away from other cognitive processes.

It seems equally unlikely that the problem lies with a pure memory constraint, though memory capacity obviously must impose some kind of upper limit on the number of relationships that an animal can have. There are three reasons for this claim. First, in humans at least, memory for faces is an order of magnitude larger than the predicted cognitive group size: Humans are said to be able to attach names to around 2,000 faces but have a cognitive group size of only about

The social brain hypothesis implies that constraints on group size arise from the information-processing capacity of the primate brain, and that the neocortex plays a major role in this. However, even this proposal is open to several interpretations as to how the relationship is mediated.

150. Second, there is no intrinsic reason to suppose that memory per se is the issue. The social brain hypothesis is about the ability to manipulate information, not simply to remember it. Third, and perhaps most significantly, memories appear to be stored mainly in the temporal lobes,⁴² whereas recent PET scan studies implicate the prefrontal neocortex, notably Brodman area 8, as the area for social skills and, specifically, theory of mind.⁴³ Frith⁴⁴ has suggested that memories and representations for objects or events may involve interactions between several levels of the neocortex depending on the kinds of operations

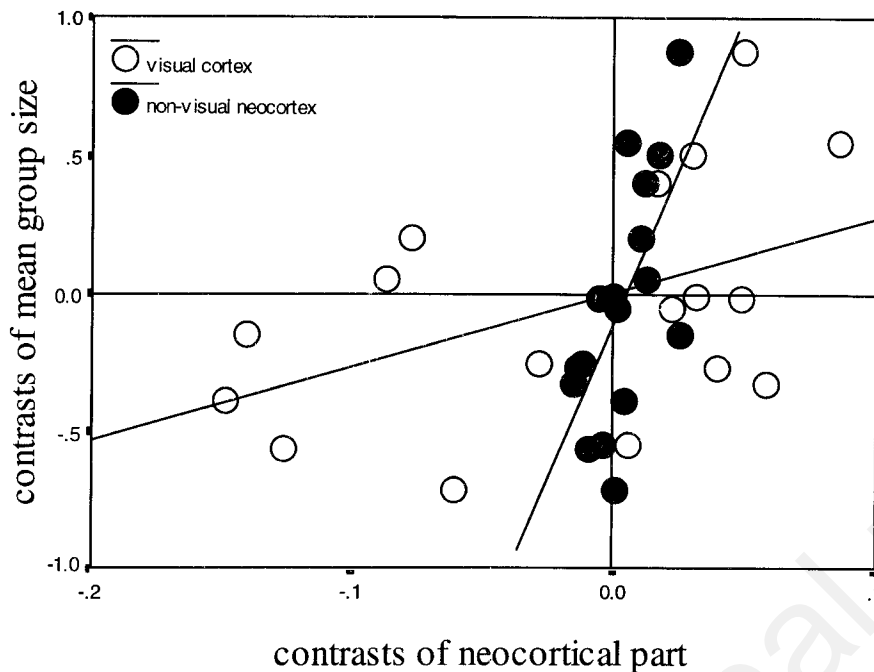


Figure 4. Independent contrasts in mean group size plotted against contrasts in the visual cortex and the volume of the rest of the neocortex (nonvisual neocortex) for individual anthropoid species. Note that the visual cortex is here defined as visual area V1; the nonvisual cortex is the non-V1 volume of the neocortex and thus includes some higher order visual processing components (e.g., visual area V2). Unfortunately, the data base of Stephan, Frahm, and Baron²⁹ does not allow us to define our measure of the nonvisual area any more finely than this. (Reprinted from Joffe and Dunbar,²⁸ Fig. 1.)

involved. These interactions could occur between the sensory and association cortices (perceiving an object), between the association and frontal cortices (remembering an object), and among all three (being aware of perceiving an object). It is worth noting in this context that although social skills are commonly disrupted by damage to the prefrontal cortex, memory for events and people is not.⁴²

It seems unlikely that emotional responses per se are the substantive constraint. Although the correct emission and interpretation of emotional cues is of singular importance in the management of social relationships,⁴⁵ there is little evidence that the subcortical areas principally associated with emotional cuing (for example, the amygdala in the limbic system) correlate in any way with social group size.²⁸ Indeed, Keverne, Martel, and Nevison⁴⁶ point out that there has been progressive reduction in the relative sizes of the “emotional” centers in the brain (the hypothalamus and septum) in favor of the “executive” centers (the neocortex and striate cortex) during primate evolution. They inter-

pret this in terms of a shift away from emotional control of behavior to more conscious, deliberate control.

The only remaining alternative is that the mechanisms involved lie in the ability to manipulate information about social relationships themselves. This claim is supported by six additional lines of evidence that point to the fundamental importance of social skills in the detailed management of social relationships.

One is the fact that close analysis of the data on group size and neocortex volume suggests that there are, in fact, distinct grades even within the anthropoid primates (Fig. 3). Apes seem to lie on a separate grade from the monkeys, which in turn lie on a separate grade from the prosimians. The slope coefficients on these separate regression lines do not differ significantly, but the intercepts do. It is as if apes require more computing power to manage the same number of relationships that monkeys do, and monkeys in turn require more than prosimians do. This gradation corresponds closely to the perceived scaling of social complexity.

The second line of evidence is that

the rates with which tactical deception are used correlate with neocortex size.²⁶ Species with large neocortex ratios make significantly more use of tactical deception, even when the differential frequencies with which these large-brained species have been studied are taken into account.

Third, Pawlowski, Dunbar, and Lowen⁴⁷ have shown that among polygamous primates the male rank correlation with mating success is negatively related to neocortex size (Fig. 5). This is just what we would predict if the lower ranking males of species with larger neocortices were able to use their greater computational capacities to deploy more sophisticated social skills, such as the use of coalitions and capitalizing on female mate choice, to undermine or circumvent the power-based strategies of the dominant animals.

. . . there is no intrinsic reason to suppose that memory per se is the issue. The social brain hypothesis is about the ability to manipulate information, not simply to remember it.

The fourth line of evidence is Joffe's⁴⁸ demonstration that adult neocortex size in primates correlates with the length of the juvenile period, but not with the length of gestation, lactation, or the reproductive life span, even though total brain size in mammals correlates with the length of the gestation period.^{49,50} This suggests that what is most important in the development of a large neocortex in primates is not the embryological development of brain tissue per se, which is associated mainly with gestation length, but rather the “software programming” that occurs during the period of social learning between weaning and adulthood.

Fifth, Kudo, Lowen, and Dunbar⁵¹ have shown that grooming clique size, a surrogate variable that indexes alli-

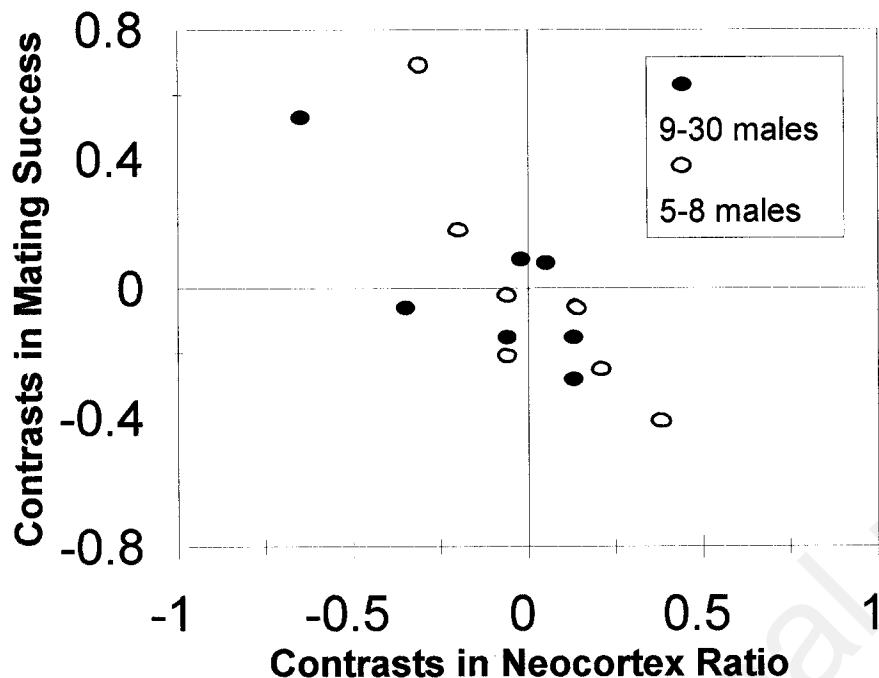


Figure 5. Independent contrasts in the Spearman rank correlation (r_s) between male rank and mating success plotted against contrasts in neocortex size for two different male cohort sizes (4 to 8, and 9 to 30 males) for individual species. The regression equations for the two cohort sizes are significantly different from $b = 0$. The species sampled are *C. apella*, *P. entellus*, *C. aethiops*, *M. fuscata*, *M. mulatta*, *M. radiata*, *M. arctoides*, *P. cynocephalus*, *P. anubis*, *P. ursinus*, and *P. troglodytes*. (Redrawn from Pawlowski, Dunbar, and Lowen,⁴⁷ Fig. 1.)

gives primate social groups their internal structure and coherence, this can be seen as a crucial basis for primate sociality.

Finally, Keverne, Martel, and Nevison⁴⁶ have suggested that the neocortex and striate cortex, those areas of the primate brain that are responsible for executive function, are under maternally rather than paternally imprinted genes (i.e., genes that “know” which parent they came from), whereas the converse is true for the limbic system, those parts of the brain most closely associated with emotional behavior. They interpret this in relation to the cognitive demands of the more intense social life of females in matrilineal female-bonded societies.

IMPLICATIONS FOR HUMAN GROUPS

The fact that the relationship between neocortex size and what I will term the cognitive group size holds up so well in so many different taxonomic groups raises the obvious question of whether or not it also applies to humans. We can easily predict a value for group size in humans. Doing so, which is simply a matter of using the human neocortex volume to extrapolate a value for group size from the primate

ance size, correlates rather tightly with relative neocortex and social group size in primates, including humans (Fig. 6). The human data derive from two samples: hair-care networks among female bushmen⁵² and support cliques among adults in the United Kingdom.⁵³ What is remarkable is how closely the human data fit with the data from other primate species. Grooming cliques of this kind invariably function as coalitions in primate groups. Coalitions are functionally crucial to individuals within these groups because they enable the animals to minimize the levels of harassment and competition that they inevitably suffer when living in close proximity to others.⁵⁴ Coalitions essentially allow primates to manage a fine balancing act between keeping other individuals off their backs while at the same time avoiding driving them away altogether and thereby losing the benefits for which the groups formed in the first place. These results can thus probably be interpreted as a direct cognitive limitation on the number of individuals with which an animal can simultaneously maintain a relationship of suf-

ficient depth that they can be relied on to provide unstinting mutual support when one of them is under attack. Because this is the core process that

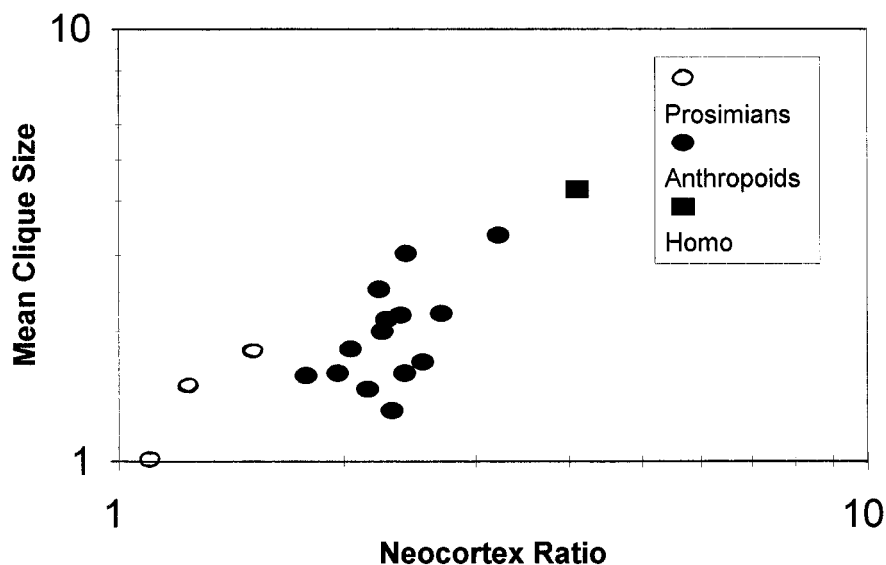


Figure 6. Mean grooming clique size plotted against mean neocortex ratio for individual primate genera. The square is *Homo sapiens*. Species sampled are *L. catta*, *L. fulvus*, *Propithecus*, *Indri*, *S. sciureus*, *C. apella*, *C. torquatus*, *A. geoffroyi*, *A. fusciceps*, *P. badius*, *P. entellus*, *P. pileata*, *P. johnii*, *C. campbelli*, *C. diana*, *C. aethiops*, *C. mitis*, *E. patas*, *M. mulatta*, *M. fuscata*, *M. arctoides*, *M. sylvana*, *M. radiata*, *P. anubis*, *P. ursinus*, *P. cynocephalus*, *P. hamadryas*, *T. gelada*, *P. troglodytes*, *P. paniscus*. (Redrawn from Kudo, Lowen, and Dunbar,⁵¹ Fig. 4a.)

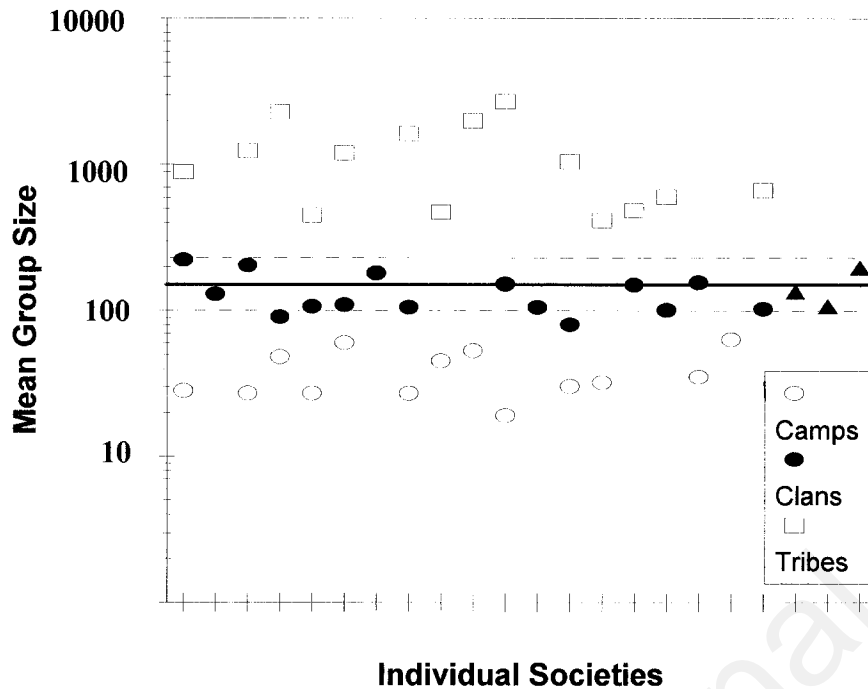


Figure 7. Mean sizes for different types of groups in traditional human societies. Individual societies are ordered along the bottom, with data for three main types of social groups (overnight camps, clans or villages, and tribes). Societies include hunter-gatherer and settled horticulturalists from Australia, Africa, Asia, and North and South America. The triangles give mean group sizes for three contemporary United States samples: mean network size from small-worlds experiments ($N = 2$),⁶⁷ mean Hutterite community size,⁶⁸ and the size of an East Tennessee mountain community.⁶⁹ The value of 150 predicted by the primate neocortex size relationship (from Fig. 1d) is indicated by the horizontal line, with 95% confidence intervals shown as dashed lines.

equation, produces a value in the order of 150. The real issue is whether humans really do go around in groups of this size.

Identifying the relevant level of grouping to measure in humans is difficult because most humans live in a series of hierarchically inclusive groups. This, in itself, is not especially unusual: Hierarchically structured groups of this kind are characteristic of primates⁵⁴ and may be typical of many mammals and birds.⁵⁵ At least in the case of the diurnal primates, it seems that, with a few notable exceptions, the various species' grouping patterns exhibit an overt level of stability at roughly the same position in the hierarchy across a wide range of taxa. Moreover, because the various layers of this hierarchy appear to be intimately related to each other, probably through being part of a series of cause-and-consequence chains,⁵¹ it would not matter which particular grouping level (for example, stable social group,

network, or grooming clique) was taken to be the grouping criterion.

The problem with respect to humans is that it is difficult to identify which of the many potential grouping levels is functionally or cognitively equivalent to the particular level of grouping that I happened to use for primates. This difficulty is particularly intrusive in this case because humans live in a dispersed social system sometimes referred to as a fission-fusion system. In order to get around this problem, I adopted the converse strategy in my original analysis,⁵⁶ asking whether there was any group size consistently characteristic of humans that was of about the requisite size and, if so, whether its intrinsic psychological characteristics were similar to those found in primate groups.

Because of the structural complexity of postagricultural societies, I considered only traditional hunter-gatherer and small-scale horticultural societies. Although census data on

such societies are limited, those that are available suggest that there is indeed a consistent group size in the region of 150 individuals (Fig. 7). Except among settled horticulturalists, where the village seems to be the relevant unit, this typically involves the set of individuals from whom overnight camps are easily and regularly formed. Such groups are not often conspicuous as physical entities (they do not often appear together in one place at one time), but they do invariably have important ritual functions for the individuals concerned. Among Australian aboriginals, for example, the relevant group is the clan, which meets from time to time in jamborees where the rituals of life (marriages and rites of passage) are enacted and tales of the old times are rehearsed to remind everyone who they are and why they hold a particular relationship to each other. Indeed, this genuinely seems to be the largest group of people who know everyone in the group as individuals at the level of personal relationships. This is essentially the definition that holds in the case of primates.

A more extensive exploration of human groups in other contexts suggests that groupings of this size are widespread and form an important component of all human social systems, being present in structures that range from business organizations to the arrangement of farming communities.⁵⁶ Estimates of community size for two traditional farming communities in the United States, Hutterites and an East Tennessee mountain community, and of actual social network sizes (from small-worlds experiments) (shown as triangles on the right side of Fig. 7) fit very closely within the relevant range of group sizes.

It is easy, of course, to play the numerologist in this context by finding groups that fit whatever group size one wishes to promote. The important feature to note here, however, is that the various human groups that can be identified in any society seem to cluster rather tightly around a series of values (5, 12, 35, 150, 500, and 2,000) with virtually no overlap in the variance around these characteristic values. They seem to represent points of stability or clustering in the degrees of familiarity within the broad range of

Box 2. A Beginner's Guide to Intensionality

Computers can be said to know things because their memories contain information; however, it seems unlikely that they know that they know these things, in that we have no evidence that they can reflect on their states of "mind." In the jargon of the philosophy of mind, computers are zero-order intensional machines. Intensionality (with an -s) is the term that philosophers of mind use to refer to the state of having a state of mind (knowing, believing, thinking, wanting, understanding, intending, etc).

Most vertebrates are probably capable of reflecting on their states of

mind, at least in some crude sense: they know that they know. Organisms of this kind are first-order intensional. By extension, second-order intensional organisms know that someone else knows something, and third-order intensional organisms know that someone else knows that someone else knows something. In principle, the sequence can be extended reflexively indefinitely, although, in practice, humans rarely engage in more than fourth-order intensionality in everyday life and probably face an upper limit at sixth-order ("Peter knows that Jane believes that Mark thinks that Paula

wants Jake to suppose that Amelia intends to do something").

A minimum of fourth-order intensionality is required for literature that goes beyond the merely narrative ("the writer wants the reader to believe that character A thinks that character B intends to do something"). Similar abilities may be required for science, since doing science requires us to ask whether the world can be other than it is (a second-order problem at the very least) and then ask someone else to do the same (an additional order of intensionality).

human relationships, from the most intimate to the most tenuous.

COGNITIVE MECHANISMS

The suggestion that the mechanisms involved in these processes may be concerned with social skills raises the issue alluded to by the original Machiavellian intelligence hypothesis, namely to what extent cognitively sophisticated mechanisms conferring the ability to "mind-read" might be involved. Tactical deception, in its strong sense, implies the ability to hold false beliefs and, thus, the presence of the ability known as "theory of mind" (ToM). Of course, tactical deception as practiced by primates on a daily basis may not, as Byrne²⁶ himself has pointed out, be quite as sophisticated as first impressions suggest. A more conventional behaviorist account based on simple associative learning can invariably be given for almost all examples reported in the literature.

Nonetheless, convincing evidence suggests that humans at least do use ToM in executing some of their more manipulative social activities. And while we may not wish to attribute full ToM to all primates, at least circumstantial evidence suggests that basic ToM is present in great apes and that monkeys may aspire to a level that Byrne²⁶ has described as level 1.5 intentionality (full ToM being level 2 intentionality) (see Box 2). The difference has been summed up rather

graphically by Cheney and Seyfarth's⁵⁷ observation that apes seem to be good psychologists in that they are good at reading minds, whereas monkeys are good ethologists in that they are good at reading behavior—or at least at making inferences about intentions in the everyday sense, even if not in the

. . . apes seem to be good psychologists in that they are good at reading minds, whereas monkeys are good ethologists in that they are good at reading behavior . . .

philosophical sense of belief states.

Evidence that chimpanzees aspire to at least a basic form of ToM is provided by their performance on experimental false-belief tasks.^{58–61} These studies have attempted to develop analogues of the classic false-belief tasks used with children.⁶² Though it is clear that chimpanzees do not perform to the level at which fully competent children perform, O'Connell's⁶¹ experiments at least suggest that they can perform at the level of children who

stand on the threshold of acquiring ToM. More importantly, chimpanzees do better than autistic adults, one of whose defining features is the lack of ToM, on the same tests.

That mind-reading, the basis of ToM, is difficult to do has been shown by experiments on normal adults tested on "advanced" ToM tasks, up to fifth-order intentionality.⁶² These data suggest that normal humans find tasks of greater than fourth-order intentionality exceedingly hard to do. The high error rates at these levels do not reflect a memory retention problem: All subjects pass the tests that assess memory for the story line. Moreover, the same subjects show considerable competence on reasoning tasks that involve causal chains of up to the sixth order. The difficulty seems genuinely to be something to do with operating with deeply embedded mental states.

One possibly significant observation in this context is that the visual and nonvisual components of the primate neocortex do not increase isometrically. Although initially there is a more or less linear increase in the visual area V1 with increasing size of the rest of the neocortex, this drops off within the great ape clade. From gorillas through humans, increases in the size of the visual area progress more slowly than do increases in the size of the rest of the neocortex.²⁸ We interpret this as implying that beyond a certain point the acuity of the visual system does

not increase linearly with size. Because the total size of the neocortex is limited by embryological and energetic factors, this means that disproportionately more capacity can be dedicated to nonvisual areas of the neocortex once the volume is above the crucial threshold. This might explain why apes appear to be capable of the additional cognitive processing associated with mind reading, whereas monkeys are not. It might also explain why humans are better at it than apes.

For humans, one important aspect of ToM concerns its relevance to language, a communication medium that crucially depends on understanding interlocutors' mental states or intentions. The kinds of metaphorical uses of language that characterize not only our rather telegraphic everyday exchanges (in which "you know what I mean?" is a common terminal clause) but also lies at the very heart of the metaphorical features of language. As studies of pragmatics have amply demonstrated,⁶³ a great deal of linguistic communication is based on metaphor: Understanding the intentions behind a metaphor is crucial to successful communication. Failure to understand these intentions commonly results in confusion or inappropriate responses. Indeed, without these abilities it is doubtful whether literature, notably poetry, would be possible. Our conversations would be confined to the banally factual; those fine nuances of meaning that create both the ambiguities of politeness and the subtleties of public relations would not be possible.⁶⁴

REFERENCES

- 1 Clutton-Brock TH, Harvey PH (1980) Primates, brains and ecology. *J Zool Lond* 190:309–323.
- 2 Aiello LC, Wheeler P (1995) The expensive tissue hypothesis. *Curr Anthropol* 36:184–193.
- 3 Parker ST, Gibson KR (1977) Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in great apes and cebus monkeys. *J Hum Evol* 6:623–641.
- 4 Gibson KR (1986) Cognition, brain size and the extraction of embedded food resources. In Else J, Lee PC (eds), *Primate Ontogeny, Cognition and Social Behaviour*, pp 93–104. Cambridge: Cambridge University Press.
- 5 Whiten A, Byrne R (1988) Tactical deception in primates. *Behav Brain Sci* 12:233–273.
- 6 Byrne R, Whiten A (eds) (1988) *Machiavellian Intelligence*. Oxford: Oxford University Press.
- 7 Harcourt AH (1988) Alliances in contests and social intelligence. In Byrne R, Whiten A (eds), *Machiavellian Intelligence*, pp 142–152. Oxford: Oxford University Press.
- 8 Harcourt AH (1989) Sociality and competition in primates and non-primates. In Standen V, Foley R (eds), *Comparative Socioecology*, pp 223–242. Oxford: Blackwell Scientific.
- 9 Brothers L (1990) The social brain: A project for integrating primate behaviour and neurophysiology in a new domain. *Concepts Neurosci* 1:27–251.
- 10 Barton RA, Dunbar RLM (1997) Evolution of the social brain. In Whiten A, Byrne R (eds), *Machiavellian Intelligence*, Vol. II. Cambridge: Cambridge University Press.
- 11 Finlay BL, Darlington RB (1995) Linked regularities in the development and evolution of mammalian brains. *Science* 268:1678–1684.
- 12 Martin RD (1981) Relative brain size and metabolic rate in terrestrial vertebrates. *Nature Lond* 293:57–60.
- 13 Martin RD (1983) Human brain evolution in an ecological context. 52nd James Arthur Lecture, American Museum of Natural History, New York.
- 14 Hofman MA (1983) Evolution of the brain in neonatal and adult placental mammals: A theoretical approach. *J Theoret Biol* 105:317–322.
- 15 Pagel M, Harvey PH (1988) How mammals produce large-brained offspring. *Evolution* 42:948–957.
- 16 Boesch C, Boesch H (1984) Mental map in chimpanzees. *Primates* 25:110–170.
- 17 MacLean PD (1982) On the origin and progressive evolution of the triune brain. In Armstrong E, Falk D (eds), *Primate Brain Evolution*, pp 291–310. New York: Plenum Press.
- 18 Joffe T, Dunbar RIM (n.d.). Primate brain system evolution. *Brain Behav Evol*, submitted for publication.
- 19 Passingham RE (1982) *The Human Primate*. San Francisco: Freeman.
- 20 Jersson HJ (1973) *Evolution of the Brain and Intelligence*. New York: Academic Press.
- 21 Dunbar RIM (1989) Environmental determinants of intraspecific variation in body weight in baboons. *J Zool Lond* 220:167–169.
- 22 Willner LA (1989) Sexual Dimorphism in Primates. Ph.D. thesis, University of London.
- 23 Deacon TW (1990) Fallacies of progression indices in theories of brain-size evolution. *Int J Primatol* 12:193–236.
- 24 Dunbar RIM (1992) Neocortex size as a constraint on group size in primates. *J Hum Evol* 20:469–493.
- 25 Dunbar RIM, Joffe TH (n.d.). Neocortex size and social group size in prosimians. *Primates*, submitted for publication.
- 26 Byrne RB (1995) *The Thinking Primate*. Oxford: Oxford University Press.
- 27 Barton RA (1995) Neocortex size and behavioural ecology in primates. *Proc R Soc Lond B*, 263:173–177.
- 28 Joffe TH, Dunbar RIM (1997) Visual and socio-cognitive information processing in primate brain evolution. *Proc R Soc Lond B*, 264:1303–1307.
- 29 Stephan H, Frahm H, Baron G (1981) New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatol* 35:1–29.
- 30 Sawaguchi T, Kudo H (1990) Neocortical development and social structure in primates. *Primates* 31:283–290.
- 31 Barton RA, Purvis A (1994) Primate brains and ecology: Looking beneath the surface. In Anderson JR, Thierry B, Herrenschmidt N (eds), *Current Primatology*, pp 1–12. Strasbourg: University of Strasbourg Press.
- 32 O'Keefe J, Nadel L (1978) *The Hippocampus as a Cognitive Map*. Oxford: Oxford University Press.
- 33 Krebs JH, Sherry DF, Healy SD, Perry VH, Vaccarino AL (1989) Hippocampal specialisation of food-storing birds. *Proc Natl Acad Sci USA* 86:1488–1492.
- 34 Aiello LC, Dunbar RIM (1993) Neocortex size, group size and the evolution of language. *Curr Anthropol* 34:184–193.
- 35 Dunbar RIM (1995) Neocortex size and group size in primates: A test of the hypothesis. *J Hum Evol* 28:287–296.
- 36 Bearder SK (1987) Lorises, bushbabies and tarsiers: Diverse societies in solitary foragers. In Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T (eds), *Primate Societies*, pp 12–24. Chicago: Chicago University Press.
- 37 Dunbar RIM, Bever J (n.d.). Neocortex size determines group size in carnivores and insectivores. *Ethology*, in press.
- 38 Gittleman JH (1986) Carnivore brain size, behavioural ecology and phylogeny. *J Mammal* 67:23–36.
- 39 Marino L (1996) What can dolphins tell us about primate evolution? *Evol Anthropol* 5:81–86.
- 40 Tschudin A (1996) The Use of Neuroimaging in the Assessment of Brain Size and Structure in Odontocetes. MSc thesis, University of Natal (Durban).
- 41 Barton RA, Purvis A, Harvey PH (1995) Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Philos Trans R Soc B* 348:381–392.
- 42 Kolb B, Wishaw LO (1996) *Fundamentals of Human Neuropsychology*. San Francisco: Freeman.
- 43 Fletcher P, Happé F, Frith U, Baker SC, Dolan RJ, Frakowiak RJS, Frith CD (1996) Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition* 00:000–000.
- 44 Frith C (1996) Brain mechanisms for "having a theory of mind." *J Psychopharmacol* 10:9–16.
- 45 Armstrong E, Clarke MR, Hill EM (1987) Relative size of the anterior thalamic nuclei differentiates anthropoids by social system. *Brain Behav Evol* 30:263–271.
- 46 Keverne EB, Martel FL, Nevison CM (1996) Primate brain evolution: Genetic and functional considerations. *Proc R Soc Lond B* 262:689–696.
- 47 Pawlowski B, Dunbar R, Lowen C (n.d.). Neocortex size, social skills and mating success in primates. *Behaviour*, in press.
- 48 Joffe TH (1997) Social pressures have selected for an extended juvenile period in primates. *J Hum Evol*, in press.
- 49 Bennett PM, Harvey PH (1985) Brain size, development and metabolism in birds and mammals. *J Zool Lond* 207:491–509.
- 50 Marino L (1997) The relationship between gestation length, encephalisation and body weight in odontocetes. *Marine Mammal Sci* 14:143–148.
- 51 Kudo H, Lowen S, Dunbar RIM (n.d.). Neocortex size and social network size in primates. *Behaviour*, submitted for publication.
- 52 Sugawara K (1984) Spatial proximity and bodily contact among the central Kalahari San. *Afr Studies Monogr* 3.
- 53 Dunbar RIM, Spoor M (1995) Social networks, support cliques and kinship. *Hum Nature* 6:273–290.
- 54 Dunbar RIM (1988) *Primate Social Systems*. London: Chapman & Hall.
- 55 Dunbar RIM (1989) Social systems as optimal strategy sets. In Standen V, Foley R (eds), *Comparative Socioecology*, pp 141–149. Oxford: Blackwell Scientific.

- 56** Dunbar RIM (1993) Coevolution of neocortical size, group size and language in humans. *Behav Brain Sci* 11:681–735.
- 57** Cheney DL, Seyfarth RM (1990) *How Monkeys See the World*. Chicago: Chicago University Press.
- 58** Povinelli DJ, Nelson KE (1990) Inferences about guessing and knowing in chimpanzees. *J Comp Psychol* 104:203–210.
- 59** Povinelli DJ (1994) What chimpanzees (might) know about the mind. In Wrangham R, McGrew W, de Waal F, Heltne P (eds), *Chimpanzee Cultures*, pp 285–300. Cambridge: Harvard University Press.
- 60** O'Connell SM (1996) Theory of Mind in Chimpanzees. Ph.D. thesis, University of Liverpool.
- 61** Perner J, Wimmer D (1985) "John thinks that Mary thinks that. . ." Attribution of second-order beliefs by 5 and 10 year-old children. *J Exp Child Psychol* 39:437–471.
- 62** Kinderman P, Dunbar RIM, Bentall RP (n.d.) Theory of mind deficits and causal attributions. *Br J Psychol*, in press.
- 63** Desalles J-L (n.d.) Altruism, status and the origin of relevance. In Hurford JR, Studdert-Kennedy M, Knight C (eds), *Evolution of Language*. Cambridge: Cambridge University Press.
- 64** Dunbar RIM (1997) *Grooming, Gossip and the Evolution of Language*. Cambridge: Harvard University Press.
- 65** Harvey PH, Krebs JR (1990) Comparing brains. *Science* 249:150–156.
- 66** Stephan H (1972) Evolution of primate brains: A comparative anatomical investigation. In Tuttle R (ed), *Functional and Evolutionary Biology of Primates*, pp 165–174. Chicago: Aldine-Atherton.
- 67** Killworth PD, Bernard HR, McCarty C (1984) Measuring patterns of acquaintanceship. *Curr Anthropol* 25:391–397.
- 68** Mange A, Mange E (1980) *Genetics: Human Aspects*. W.B. Saunders.
- 69** Bryant FC (1981) *We're All Kin: A Cultural Study of a Mountain Neighbourhood*. Knoxville: University of Tennessee Press.
- 70** Gould SJ (1975) Allometry in primates, with emphasis on scaling and the evolution of the brain. *Contrib Primatol* 5:244–292.
- 71** Jolly A (1969) Lemur social behaviour and primate intelligence. *Science* 163:501–506.
- 72** Humphrey NK (1976) The social function of intellect. In Bateson PPG, Hinde RA (eds) *Growing Points in Ethology*, pp 303–317. Cambridge: Cambridge University Press.
- 73** Armstrong E (1985) Relative brain size in monkeys and prosimians. *Am J Phys Anthropol* 66:263–273.