Neocortex size predicts deception rate in primates

Richard W. Byrne[*] and Nadia Corp

School of Psychology, University of St Andrews, Fife KY16 9JU, UK

Human brain organization is built upon a more ancient adaptation, the large brain of simian primates: on average, monkeys and apes have brains twice as large as expected for mammals of their size, principally as a result of neocortical enlargement. Testing the adaptive benefit of this evolutionary specialization depends on finding an association between brain size and function in primates. However, most cognitive capacities have been assessed in only a restricted range of species under laboratory conditions. Deception of conspecifics in social circumstances is an exception, because a corpus of field data is available that encompasses all major lines of the primate radiation. We show that the use of deception within the primates is well predicted by the neocortical volume, when observer effort is controlled for; by contrast, neither the size of the rest of the brain nor the group size exert significant effects. These findings are consistent with the hypothesis that neocortical expansion has been driven by social challenges among the primates. Complex social manipulations such as deception are thought to be based upon rapid learning and extensive social knowledge; thus, learning in social contexts may be constrained by neocortical size.

Keywords: primate; intelligence; deception; brain size; neocortex

1. INTRODUCTION

Neocortical enlargement appears to be an adaptive specialization of simian primates. Among orders of mammals, the primates show the largest brain sizes relative to body sizes (Martin 1990; although note that the dolphin family exceeds primates in relative brain size, see Jerison 1973; Marino 1996). In simian primates the average brain is twice the size expected from allometric scaling (Passingham 1981). However, brain enlargement must be costly, because brain tissue is metabolically expensive and fragile (Armstrong 1983; Aiello & Wheeler 1995). Correspondingly powerful adaptive benefits from brain enlargement are therefore to be expected. While analyses have often used total brain volume as a measure, in fact the neocortex and striatum have expanded most in primate evolution (Keverne *et al.* 1996), and current variation in brain size among primates is largely a reflection of neocortical differences (Stephan *et al.* 1981). Understanding the origins of this specialization therefore becomes a question of what selective pressure(s) favoured an enlarged neocortex during primate evolution. Because evolutionary history is unavailable for direct study, the usual approach is to examine the current benefits of an enlarged neocortex by seeking correlations with potential cognitive challenges in the environment.

Although several theories have been proposed that invoke benefits in environmental exploitation (Parker & Gibson 1977; Clutton-Brock & Harvey 1980; Milton 1981, 1988; Gibson & Ingold 1993), there is now some consensus that the chief benefits may be social ones. According to this 'social brain' or 'Machiavellian intelligence' hypothesis, the cognitive demands of intense social living select for increased social skill, mediated by neocortical enlargement (Humphrey 1976; Byrne & Whiten 1988; Brothers 1990; Dunbar 1992; but see also Seyfarth & Cheney 2002). Most monkeys and apes live in long-lasting groups (Smuts *et al.* 1986; Dunbar 1988), so that familiar conspecifics are major competitors for access to resources. This situation favours individuals that can offset the costs of competition by using manipulative tactics, and skilful manipulation depends on extensive social knowledge (Cheney & Seyfarth 1990). Because competitive advantage operates relative to the ability of others in the population, an 'arms race' of increasing social skill results, which is eventually brought into equilibrium by the high metabolic cost of brain tissue (Byrne 1996*a*).

In support of this idea, neocortex size has been found to vary with the species-typical mating system and social group size among haplorhine primates (Sawaguchi & Kudo 1990*a*,*b*; Dunbar 1992), whereas it correlates only weakly with their diet type and tendency towards diurnal living (Barton 1996). Further, the neocortex is an area to which the maternal genome makes a substantial developmental contribution, consistent with the importance of complex behavioural strategies within matrilines in many primate species (Keverne *et al.* 1996). These relationships favour a social origin for the neocortical enlargement of primates, on the assumption that group size and aspects of social organization correlate with the degree of intellectual challenge confronting an individual. Indirect support also comes from the finding that male rank predicts mating success less well for primate species with larger neocortices in proportion to the rest of the brain (Pawlowski *et al.* 1998): the advantages of individual rank and power appear to be offset by social skill. However, the underlying logic of the social brain hypothesis remains hypothetical, because social skill is seldom directly measured. Comparative evaluations of the relationship between aspects of brain size and direct measures of cognitive skill are lacking (although see Reader & Lefebvre 2001).

The precise nature of the neocortical adaptation of simian primates has been questioned. In primates, large brain size is associated with a visual-system enlargement (Barton *et al.* 1995; Barton 1998), particularly of the parvocellular

Proc. R. Soc. Lond. B (2004) **271**, 1693–1699
DOI 10.1098/rspb.2004.2780

1693

© 2004 The Royal Society

system, which is involved in analysis of detail and colour (Livingstone & Hubel 1988)—information that is critical in the subtle social categorization of conspecifics. This has led to a debate as to whether visual perception, rather than social skill, might underlie the relationship between social group size and neocortex size (Barton 1996; Joffe & Dunbar 1997), but the two may be intrinsically linked, if social skill depends on a sophisticated visual categorization of conspecifics' demeanour (see Barton 1998).

More seriously, the empirical support for the social brain hypothesis has been challenged by Deaner *et al.* (2000): they argue that there is currently no reliable basis for preferring one hypothesis over the other and show that the same comparative data can be used to support both. This arises because comparing neocortex size across species is not straightforward. Primate neocortex size varies allometrically with total brain size (Passingham 1981; Deacon 1990), which itself scales with body size, as in all mammals (Jerison 1973; Martin 1990). These relationships have led to the use of several different methods for comparing brain sizes. Deaner *et al.* (2000) demonstrate that the choice of method is not neutral. When residuals from allometric scaling against another brain part are used, the data do indeed support the social brain hypothesis: the social group size correlates with neocortex size across species, whereas measures of environmental complexity do not. But if instead ratios to another brain part or residuals from allometric scaling against body size are used in the analysis, precisely which result is obtained depends on other factors, such as whether phylogenetic correction is employed or home range scaled against body size. Deaner *et al.* (2000) argue that the way forward should be an empirical one, to compare various 'scaling methods with regard to their ability to predict independently derived behavioural indicators of cognition' (Deaner *et al.* 2000, p. 50).

In support of this empirically driven approach, we here examine the relationship between neocortex size and a direct measure of social cognition, the amount that species use behavioural deception to solve social problems. We compare two alternative methods for assessing the role of the neocortex: absolute neocortex size and the ratio of neocortex size to that of the remainder of the brain. However, we do not use the third method examined by Deaner *et al.* (2000), scaling against body size. Scaling against body size is fundamentally inappropriate for measuring *cognitive potential*. This is because cognitive capacity is a matter of neural computation. Measuring the size of an animal's brain (or brain part) in relation to its body size implies acceptance of a particular hypothesis of brain function, the 'switchboard model' (Byrne 1996b) or 'traffic maintenance hypothesis' (Deaner *et al.* 2000); that is, the brain's function is to cope with sensorimotor inputs and outputs. On this basis, larger animals require proportionately larger brains, and residuals from the scaling function are indications of either overload or spare capacity. Such an assumption seems entirely unsuitable where cognition is concerned, however. For example, scaling against body size would imply that 5% extra brain mass, beyond that required for bodily maintenance, has the same cognitive 'utility' in an elephant and a mouse, despite the striking fact that the mass of neural tissue and number of neurons will be hundreds of times greater in

the elephant. Moreover, it is not implausible that cognitive ability and body mass are positively correlated (Deacon 1997), because the metabolic cost of supporting a brain of a certain size will fall less severely on a larger animal, where it will form a smaller fraction of the total metabolic needs. In this case, as Deaner *et al.* (2000, p. 49) note, 'controlling for body mass would be equivalent to controlling for cognition'. Instead, we believe that the starting point should be that the brain is (at least in part) best viewed as an 'on-board computer' (Dawkins 1982, pp. 17–18; Byrne 1996b). With this model, some measure of the absolute brain capacity available is appropriate for measuring the cognitive potential. Body metabolism will exert a significant constraint on total brain volume, as brain tissue is metabolically expensive (Armstrong 1983); account can best be taken of this by treating the total brain volume as fixed and comparing the structure of interest against another brain part rather than the size of the body. The logic here is that, for a given size of brain, species differences in the relative proportion of structures reflect differences in the extent of commitment to efficient functioning. Using another brain part as a baseline in this way may introduce problems if the comparison part itself was under active selection during the evolution of the taxa under examination; this risk can be minimized by choosing a large and relatively conservative region of the brain as a baseline. In this study we took the whole of the rest of the brain as the comparison region. (Arguments favouring the spinal cord or the brainstem instead as the comparison region can be made (Passingham 1981), but these structures have the disadvantages that they are not known for so many primate species and their small sizes would magnify any errors in measurement.) Clark *et al.* (2001) similarly noted that the use of body weight as a reference variable tends to obscure relationships of interest because of independent variation of body size.

Here, we examine two different ways of measuring neocortex utility, both consistent with the on-board computer metaphor: *absolute neocortex volume*, in which the volume of the rest of the brain is examined independently as a potential predictor of cognitive ability (as used by Barton 1996, 1998; Barton & Harvey 2000); and the *neocortex ratio* (as used by Dunbar 1992, 1995, 1998; Clark *et al.* 2001), in which the neocortex volume is divided by that of the rest of the brain and the ratio taken to reflect the degree of investment in the neocortex.

Equally contentious is deciding upon a valid and useful measure of animal cognition. The particular challenge for comparative analyses of cognitive skill is to find a measure that applies widely, rather than being restricted to a few species that have been studied in detail in captivity. The 'tactical' use of deception, to manipulate the behaviour of others within the social group without the use of force, has been reported in numerous primate species, spanning all major taxonomic groups (Byrne & Whiten 1985, 1990; Whiten & Byrne 1988b), but remains undocumented in other mammals under natural conditions. The frequency of using deception varies with different species (Byrne & Whiten 1992), and this variation gives a direct estimate of social problem solving; by contrast, there is, to our knowledge, no agreed experimental test of social skill (Cheney & Seyfarth 1990). Deception is often held to indicate considerable cognitive sophistication (Mitchell &

Thompson 1986; Whiten & Byrne 1988*b*); at the least, it shows very efficient learning ability and sensitivity to a wide range of subtle social discriminations (Byrne 1995, 1997; Cheney & Seyfarth 1990). A significant correlation has been found between tactical deception and neocortex size (Byrne 1993*a*), but this preliminary study suffered from a lack of control for phylogenetic independence and took no account of the possible confounding effect of social group size, which is known to correlate with neocortex volume (Dunbar 1992, 1995). In this paper, we explore whether primate social manipulation by deception is a function of opportunity and need (thus increasing with typical group size), or a function of brain capacity (thus increasing with neocortical enlargement), or both.

2. METHODS

To give an indication of cognitive skill, we used a catalogue of tactical deception in primates that incorporates all records known at the time of its publication, including some published before that date (Byrne & Whiten 1990). In the survey that formed the basis of the collation, we defined *tactical deception* as 'acts from the normal repertoire of the agent, deployed such that another individual is likely to misinterpret what the acts signify, to the advantage of the agent' (p. 3), and solicited observations that met this definition. All the records were contributed by researchers who were expert observers and highly experienced with their study species. In the current study, we restricted analysis to observations of free-ranging primates in the field, but included all types of deception that were considered by the original observers to meet our definition of tactical deception. The differing cognitive implications of various types of deception have been discussed elsewhere (see Byrne & Whiten 1991; Byrne 1993*b*, 1997, 2003).

Because the corpus of deception records was originally assembled by survey study and the data had often been recorded on an unsystematic *ad libitum* basis, the raw frequency of deception is likely to be biased by variation in opportunities for observation. We therefore corrected the frequencies for observer effort in two ways.

(i) Following the approach of Byrne & Whiten (1992), we modified the raw frequencies to take direct account of variation in observer effort. Most deceptive behaviour is subtle and thus can be detected only in highly observable and individually known animals; thus records will, in principle, derive only from long-term behavioural studies. We therefore used the number of long-running field studies current during the period of the survey (1985–1989) to correct for observation bias; these data were obtained from the 'current primate field studies supplement' regularly published by the Primate Society of Great Britain. According to the null hypothesis that frequency of report is directly proportional to the number of studies, we calculated the expected frequency of deception for each species. Deviations from this expected frequency (i.e. subtracting the expected number from the actual number of records) were taken as an index of deception frequency, which might be above or below that expected from observer effort alone.
(ii) More conventionally, we used the residuals from regression to correct for any bias in observer effort. We regressed the number of records of deception against the number of studies for each species, taking the residuals as

the corrected measure of deception frequency (with both variables log-transformed, number of records $= 0.116 + 0.911 \times$ number of studies; adjusted $r^2 = 0.306$, $F_{1,16} = 8.44$, $p < 0.01$).

Apart from observation bias, differential opportunity for effective use of deception is the principal non-adaptive alternative for explaining variations in reporting rates across species. In those species living in large groups, the tendency to use social manipulation may be greater, independently of any variation in brain capacity for doing so, because there are more chances to benefit from doing so. Furthermore, it is also possible that observers might record more deception in these large-group species, simply because they had observed more individuals. Although logically distinct, both alternatives would result in a correlation between deception frequency and group size, independent of brain properties. However, because typical group size is known to correlate with neocortical enlargement (Dunbar 1992, 1995), this might produce an indirect and perhaps spurious correlation between neocortex size and social skill. To evaluate this possibility, we included the species-typical group size as a potential predictor of deception. (The actual group size at the time of each record's original observation is not available in the database, and in most cases it could not be accurately obtained in retrospect.) The mean sizes of primate social groups were obtained from Smuts *et al.* (1986), except for the value for *Presbytis entellus*, which came from Hrdy (1977).

The volumes of the neocortex and the rest of the brain were principally obtained from published data on primate brains in Stephan *et al.* (1981), supplemented with values for the orangutan from Zilles & Rehkamper (1988). Note that more accurate values can now be obtained with brain imaging, but such data are available for fewer species. Moreover, as the values are systematically different from those obtained by traditional methods, data from the two methods cannot appropriately be combined.

To identify correlations that result from independent evolutionary events, we employed independent contrasts (Harvey & Pagel 1991). To derive contrasts that were independent of phylogenetic bias, we used the CAIC program, v. 2.6.8 (Purvis & Rambaut 1995) and a composite estimate of the primate phylogeny that is fully resolved to species level (Purvis 1995); branch lengths were taken from Purvis (1995). As with all comparative analyses there are a number of underlying evolutionary and statistical assumptions. The CAIC program automatically checks data to test that these assumptions are met. Thus, we found that for our analyses it was necessary to transform some of the data before independent contrasts were calculated. Volumes of the neocortex and the rest of the brain and group size were all log-transformed to meet the assumptions, while the deception index, corrected for observer effort, was transformed by square-rooting. Contrasts of the residuals of deception against the number of studies were computed directly.

3. RESULTS

There were 18 species for which both brain measurements and deception data were available, giving 17 contrasts. These spanned the entire primate radiation: three prosimian, four New World monkey, seven Old World monkey (five cercopithecine and two colobine) and four ape species.

We compared the neocortex size and the group size as predictors of the amount of deception recorded in primate

species. Four multiple regression analyses were performed to accommodate the two measures of both deception and neocortex size.

(i) Contrasts in the volumes of the neocortex and the rest of the brain, along with species' mean group size, were used as predictor variables of contrasts in tactical deception, expressed as an index corrected for observer effort (analysis 1) or as the residuals from a regression of deception frequency against the number of studies (analysis 2).

(ii) Contrasts in neocortex ratio and species' mean group size were used as predictors of contrasts in tactical deception, expressed as an index corrected for observer effort (analysis 3) or as the residuals from a regression of deception frequency against the number of studies (analysis 4).

(a) Analysis 1: tactical deception (index corrected for observer effort), neocortex volume, rest-of-brain volume and mean group size

Stepwise multiple regression through the origin showed that the deception frequency correlated with the neocortex volume (d.f. = 1,16, r^2(adj) = 0.269, β = 0.559, t = 2.695, p = 0.016). In stepwise regression, once the correlation with the neocortex volume had been removed, neither the volume of the rest of the brain nor the group size emerged as significant predictors. Even when group size was entered first into a multiple regression, it failed to predict the frequency of deception (d.f. = 1,16, β = 0.010, t = 0.40, p = 0.969).

(b) Analysis 2: tactical deception (residuals from regression on observer effort), neocortex volume, rest-of-brain volume and mean group size

Stepwise multiple regression through the origin showed that the deception frequency correlated with the neocortex volume (d.f. = 1,16, r^2(adj) = 0.316, β = 0.597, t = 2.977, p = 0.009; figure 1); neither of the two remaining variables accounted significantly for the remaining variation in deception. Even when group size was entered first into a multiple regression, it failed to predict the frequency of deception (d.f. = 1,16, β = −0.065, t = −0.259, p = 0.799).

(c) Analysis 3: tactical deception (index corrected for observer effort), neocortex ratio and mean group size

Stepwise multiple regression through the origin showed that the deception frequency correlated with the neocortex ratio (d.f. = 1,16, r^2(adj) = 0.517, β = 0.738, t = 4.379, p < 0.0001). Group size did not emerge as a significant predictor (see analysis 1 for the effect of entering group size first in the regression).

(d) Analysis 4: tactical deception (residuals), neocortex ratio and mean group size

Stepwise multiple regression through the origin showed that the deception frequency correlated weakly with the neocortex ratio (d.f. = 1,16, r^2(adj) = 0.241, β = 0.535, t = 2.53, p = 0.022; figure 2). The group size did not
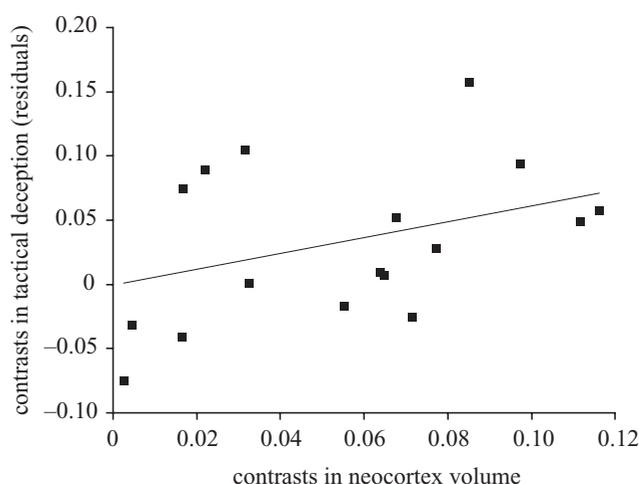
Figure 1. Correlation between deception usage and volume of the neocortex in primates. Independent contrasts were used to avoid a taxonomic bias. The frequency of within-group tactical deception was corrected for bias in observation effort, by using the residuals of the regression of deception against the number of studies.
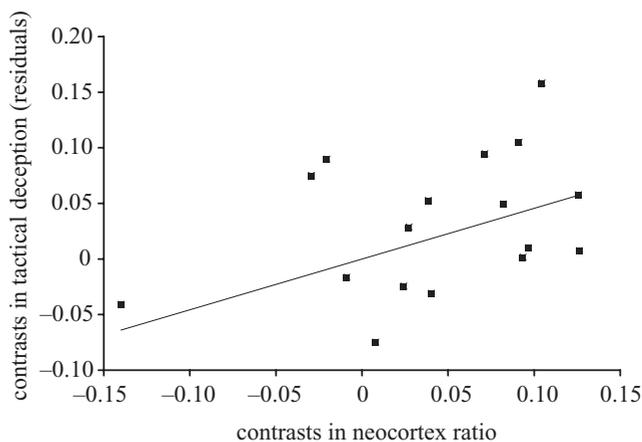

Figure 2. Correlation between deception usage and neocortex ratio in primates. Independent contrasts were used to avoid a taxonomic bias. The frequency of within-group tactical deception was corrected for bias in observation effort, by using the residuals of the regression of deception against the number of studies.

emerge as a significant predictor (see analysis 2 for the effect of entering group size first in the regression).

4. DISCUSSION

Our analysis shows that the size of the neocortex in a modern primate species predicts the extent to which individuals of that species use deceptive tactics for social manipulation. This finding is robust and not dependent on the particular measure of neocortex size used (absolute volume or volumetric fraction of the brain) or on the way data on deception were corrected for observer effort (adjusted according to the frequency of long-term studies during the period of data collection, or expressed as residuals from scaling against the number of long-term studies). Moreover, the relationship appears to be a rather direct one between neocortical size and deception usage.

Absolute neocortex volume was a reliable predictor in all analyses, whereas neither the volume of the rest of the brain nor the typical size of a species' social group emerged as a significant predictor of deception in any of them. These findings eliminate concerns that this neocortex–deception relationship was mediated by correlation with either overall brain size (as a by-product of underlying selection upon total brain size; see Finlay *et al.* 2001) or the varying opportunities for deception that exist in social groups of different sizes (i.e. because an individual in a larger social group has more chances to effect successful deceptions, or because observers of larger groups have more opportunities to see deception carried out).

The lack of a significant correlation between the use of deception and social group size, even when group size was entered first into the multiple regression, seems at first sight surprising, given the well-established correlation between neocortex size and social group size in primates, as well as in carnivores, dolphins and bats (Dunbar 1992; Marino 1996; Barton & Dunbar 1997). However, the findings should not be taken as conflicting. Those analyses used much larger sets of data, with consequently greater power. Comparison with our results suggests that the relationship between neocortex size and deception usage is a relatively strong one, consistent with the idea that it reflects a direct constraint of neocortex size on the ability to deploy cognitive problem solving in the social arena. This contrasts with the weaker indirect relationship between neocortex size and social group size, thought to reflect the limit of social complexity that can be managed by a primate with a particular neocortex volume, that is the social complexity itself limited by the cognitive ability of the species. The typical group size of a species is a function of many factors, some competing with others and all averaged over wide variations in living conditions (e.g. local changes in population growth or decline, individual histories of group fission or fusion, opportunities for one or both sexes to move between groups, differing predation pressure, etc.). That any correlation can be found between neocortex size and species-typical group size shows that brain parameters can have profound effects on social-grouping tendencies in natural environments. Our results therefore support rather than question theories that link evolutionary development of the neocortex with increased complexity of social living (e.g. Humphrey 1976; Byrne & Whiten 1988; Brothers 1990; Dunbar 1993, 1998; Byrne 1996*a*). Although current function does not necessarily signal evolutionary origin and other accounts are possible, it is plausible that a major adaptive function of increased neocortical volume in primate evolution was that it enabled more sophisticated and elaborate social manipulations.

All the major taxonomic groups of primates, including prosimians and both Old and New World monkeys, were included in this examination, so we have no reason to suppose that this result is particularly associated with simian primates or with great apes in particular. This is important, because it gives a clue as to cognitive mechanism. Within-group behavioural deception is necessarily a rather complicated form of social manipulation: its use depends on knowing other group members as individuals and remembering their differing social attributes and histories of interaction (Whiten & Byrne 1988*a*,*b*). However, the only sign that primate deception is based on any understanding of mechanism or involves representing the mental states of others comes from a few records from great apes: all data from monkeys and prosimians and most of those from lesser and great apes can be understood as the product of learning (Byrne & Whiten 1991; Byrne 1997). Therefore, just as with other aspects of social complexity and sophistication that are widespread in non-human primates, it is likely that most primate tactical deception is a function of rapid and extensive learning in social contexts (Seyfarth *et al.* 1986; Byrne 1996*a*), without the deeper understanding of mechanism that would be implied by having a theory of mind (Premack & Woodruff 1978; Karmiloff-Smith 1993; Lewis & Mitchell 1994; Sperber 2000). Our results imply that primates' efficient learning ability is dependent upon neocortical enlargement, and encourage accounts of brain structure that point to mosaic evolution, in the sense that different brain systems evolve somewhat independently in response to selective pressures whose effects fall unevenly on different brain parts (Barton & Harvey 2000; Clark *et al.* 2001; de Winter & Oxnard 2001).

Finding a specific relationship between social sophistication and neocortical specialization should not, however, be taken to mean that total brain size and body size are of no account in understanding cognitive evolution. It may be no coincidence that the primate species with the largest absolute brain sizes are also those in which there is increasing evidence of deeper understanding and cognitive sophistication (Gallup 1970; Boesch 1991; Byrne & Whiten 1992; Parker *et al.* 1994; Boysen *et al.* 1996; Hare *et al.* 2000, 2001). Both absolute neocortical volume and neocortical ratio increase allometrically with the total brain volume, and there are evidently developmental constraints that limit the extent to which any cortical structure can vary within the envelope of the total brain volume (Finlay & Darlington 1995; Finlay *et al.* 2001). Also, because brain tissue is metabolically expensive, similar constraints will apply to the brain volume at a given body size (Milton 1988; Aiello & Wheeler 1995). For these reasons, cognitive potential and total body mass may correlate (Deacon 1997). Evolving a larger body may even be one viable evolutionary strategy to respond to environmental challenges that demand enhanced cognition, because it releases developmental and metabolic constraints on neocortical volume. In primates, where the main differences in brain size are owing to differing sizes of the neocortex (Stephan *et al.* 1981), differences in the volume fraction of the brain taken up by the neocortex and in encephalization quotient (Dunbar 1992; Jerison 1973) may reflect differences in recent strong selection driven by cognitive needs. However, the strong allometric relationships across mammals as a whole suggest that, in the long term, such deviations tend to return to an equilibrium determined by body size and metabolic intake. This picture is consistent with the evidence that more insightful cognitive processing is found in non-human great apes, where larger body size has allowed very much larger brains than any other primate, even without a major dietary shift (Byrne 1998, 2000), and specifically in ancestral humans, whose richer diet allowed a further increase in brain size (Foley 1987).

We thank Robert Barton for useful discussions on the topic over many years, David Perrett and Jeff Graves for constructive comments on previous drafts of this paper, Simon Reader for help with tracking down brain volume data, and Andrew Purvis for technical advice on this analysis and for allowing us to use the CAIC program.

REFERENCES

Aiello, L. & Wheeler, P. 1995 The expensive tissue hypothesis. *Curr. Anthropol.* **36**, 199–221.

Armstrong, E. 1983 Relative brain size and metabolism in mammals. *Science* **220**, 1302–1304.

Barton, R. A. 1996 Neocortex size and behavioural ecology in primates. *Proc. R. Soc. Lond.* B **263**, 173–177.

Barton, R. A. 1998 Visual specialisation and brain evolution in primates. *Proc. R. Soc. Lond.* B **265**, 1933–1937. (DOI 10.1098/rspb.1998.0523.)

Barton, R. A. & Dunbar, R. I. M. 1997 Evolution of the social brain. In *Machiavellian intelligence. II. Extensions and evaluations* (ed. A. Whiten & R. W. Byrne), pp. 240–263. Cambridge University Press.

Barton, R. A. & Harvey, P. H. 2000 Mosaic evolution of brain structure in mammals. *Nature* **405**, 1055–1058.

Barton, R. A., Purvis, A. & Harvey, P. H. 1995 Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Phil. Trans. R. Soc. Lond.* B **348**, 381–392.

Boesch, C. 1991 Teaching among wild chimpanzees. *Anim. Behav.* **41**, 530–532.

Boysen, S. T., Berntson, G. G., Mannan, M. B. & Cacioppo, J. T. 1996 Quantity based interference and symbolic representations in chimpanzees (*Pan troglodytes*). *J. Exp. Psychol. Anim. Behav. Processes* **22**, 76–86.

Brothers, L. 1990 The social brain: a project for integrating primate behavior and neurophysiology in a new domain. *Concepts Neurosci.* **1**, 27–51.

Byrne, R. W. 1993*a* Do larger brains mean greater intelligence? *Behav. Brain Sci.* **16**, 696–697.

Byrne, R. W. 1993*b* A formal notation to aid analysis of complex behaviour: understanding the tactical deception of primates. *Behaviour* **127**, 231–246.

Byrne, R. W. 1995 *The thinking ape: evolutionary origins of intelligence*. Oxford University Press.

Byrne, R. W. 1996*a* Machiavellian intelligence. *Evol. Anthropol.* **5**, 172–180.

Byrne, R. W. 1996*b* Relating brain size to intelligence in primates. In *Modelling the early human mind* (ed. P. A. Mellars & K. R. Gibson), pp. 49–56. Cambridge: Macdonald Institute for Archaeological Research.

Byrne, R. W. 1997 What's the use of anecdotes? Attempts to distinguish psychological mechanisms in primate tactical deception. In *Anthropomorphism, anecdotes, and animals: the emperor's new clothes?* (ed. R. W. Mitchell, N. S. Thompson & L. Miles), pp. 134–150. SUNY Series in Philosophy and Biology. New York: SUNY Press.

Byrne, R. W. 1998 Cognition in great apes. In *Brain and cognition in monkeys, apes and man* (ed. A. D. Milner), pp. 228–244. Oxford University Press.

Byrne, R. W. 2000 The evolution of primate cognition. *Cogn. Sci.* **24**, 543–570.

Byrne, R. W. 2003 Novelty in deception. In *Animal innovation* (ed. K. Laland & S. Reader), pp. 237–259. Oxford University Press.

Byrne, R. W. & Whiten, A. 1985 Tactical deception of familiar individuals in baboons (*Papio ursinus*). *Anim. Behav.* **33**, 669–673.

Byrne, R. W. & Whiten, A. 1988 *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford: Clarendon.

Byrne, R. W. & Whiten, A. 1990 Tactical deception in primates: the 1990 database. *Primate Rep.* **27**, 1–101.

Byrne, R. W. & Whiten, A. 1991 Computation and mindreading in primate tactical deception. In *Natural theories of mind* (ed. A. Whiten), pp. 127–141. Oxford: Blackwell.

Byrne, R. W. & Whiten, A. 1992 Cognitive evolution in primates: evidence from tactical deception. *Man* **27**, 609–627.

Cheney, D. L. & Seyfarth, R. M. 1990 *How monkeys see the world: inside the mind of another species*. University of Chicago Press.

Clark, D. A., Mitra, P. P. & Wang, S. S. H. 2001 Scalable architecture in mammalian brains. *Nature* **411**, 189–192.

Clutton-Brock, T. H. & Harvey, P. H. 1980 Primates, brains and ecology. *J. Zool.* **190**, 309–323.

Dawkins, R. 1982 *The extended phenotype*. Oxford: Freeman.

Deacon, T. W. 1990 Fallacies of progression in theories of brain-size evolution. *Int. J. Primatol.* **11**, 193–236.

Deacon, T. W. 1997 *The symbolic species: the co-evolution of language and the brain*. New York: Norton.

Deaner, R. O., Nunn, C. L. & Van Schaik, C. P. 2000 Comparative tests of primate cognition: different scaling methods produce different results. *Brain Behav. Evol.* **55**, 44–52.

de Winter, C. & Oxnard, C. E. 2001 Evolutionary radiations and convergences in the structural organization of mammalian brains. *Nature* **409**, 710–714.

Dunbar, R. I. M. 1988 *Primate social systems*. London: Croom Helm.

Dunbar, R. I. M. 1992 Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* **20**, 469–493.

Dunbar, R. I. M. 1993 Coevolution of neocortical size, group size and language in humans. *Behav. Brain Sci.* **16**, 681–735.

Dunbar, R. I. M. 1995 Neocortex size and group size in primates: a test of the hypothesis. *J. Hum. Evol.* **28**, 287–296.

Dunbar, R. I. M. 1998 The social brain hypothesis. *Evol. Anthropol.* **6**, 178–190.

Finlay, B. L. & Darlington, R. B. 1995 Linked regularities in the development and evolution of mammalian brains. *Science* **268**, 1578–1584.

Finlay, B. L., Darlington, R. B. & Nicastro, N. 2001 Developmental structure in brain evolution. *Behav. Brain Sci.* **24**, 263–308.

Foley, R. 1987 *Another unique species: patterns in human evolutionary ecology*. Harlow, UK: Longman.

Gallup Jr, G. G. 1970 Chimpanzees: self-recognition. *Science* **167**, 86–87.

Gibson, K. R. & Ingold, T. 1993 *Tools, language and cognition in human evolution*. Cambridge University Press.

Hare, B., Call, J., Agnetta, B. & Tomasello, M. 2000 Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* **59**, 771–785.

Hare, B., Call, J. & Tomasello, M. 2001 Do chimpanzees know what conspecifics know? *Anim. Behav.* **61**, 139–151.

Harvey, P. H. & Pagel, M. 1991 *The comparative method in evolutionary biology*. Oxford University Press.

Hrdy, S. B. 1977 *The langurs of Abu*. Cambridge MA: Harvard University Press.

Humphrey, N. K. 1976 The social function of intellect. In *Growing points in ethology* (ed. P. P. G. Bateson & R. A. Hinde), pp. 303–317. Cambridge University Press.

Jerison, H. J. 1973 *Evolution of the brain and intelligence*. New York: Academic.

Joffe, T. H. & Dunbar, R. I. M. 1997 Visual and socio-cognitive information processing in primate brain evolution. *Proc. R. Soc. Lond.* B **264**, 1303–1307. (DOI 10.1098/rspb.1997.0180.)

Karmiloff-Smith, A. 1993 *Beyond modularity: a developmental perspective on cognitive science*. Cambridge, MA: Bradford/MIT.

Keverne, E. B., Martel, F. L. & Nevison, C. M. 1996 Primate brain evolution: genetic and functional considerations. *Proc. R. Soc. Lond.* B **263**, 689–696.

Lewis, C. & Mitchell, P. 1994 *Origins of an understanding of mind*. Hove, UK: Lawrence Erlbaum.

Livingstone, M. S. & Hubel, D. H. 1988 Segregation of form, color, movement and depth: anatomy, physiology and perception. *Science* **240**, 740–749.

Marino, L. 1996 What can dolphins tell us about primate evolution? *Evol. Anthropol.* **5**, 81–85.

Martin, R. D. 1990 *Primate origins and evolution*. London: Chapman & Hall.

Milton, K. 1981 Distribution patterns of tropical plant foods as a stimulus to primate mental development. *Am. Anthropol.* **83**, 534–548.

Milton, K. 1988 Foraging behaviour and the evolution of primate intelligence. In *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans* (ed. R. W. Byrne & A. Whiten), pp. 285–305. Oxford: Clarendon.

Mitchell, R. W. & Thompson, N. S. 1986 *Deception: perspectives on human and nonhuman deceit*. Albany, New York: SUNY Press.

Parker, S. T. & Gibson, K. R. 1977 Object manipulation, tool use, and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *J. Hum. Evol.* **6**, 623–641.

Parker, S. T., Mitchell, R. W. & Boccia, M. L. 1994 *Self-awareness in animals and humans: developmental perspectives*. Cambridge University Press.

Passingham, R. E. 1981 Primate specializations in brain and intelligence. *Symposia Zool. Soc. Lond.* **46**, 361–388.

Pawlowski, B., Lowen, C. B. & Dunbar, R. I. M. 1998 Neocortex size, social skills and mating success in primates. *Behaviour* **135**, 357–368.

Premack, D. & Woodruff, G. 1978 Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* **1**, 515–526.

Purvis, A. 1995 A composite estimate of primate phylogeny. *Phil. Trans. R. Soc. Lond.* B **348**, 405–421.

Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Mackintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11**, 247–251.

Reader, S. M. & Lefebvre, L. 2001 Social learning and sociality. *Behav. Brain Sci.* **24**, 353–355.

Sawaguchi, T. & Kudo, H. 1990a Neocortical development and social structure in primates. *Primates* **31**, 283–289.

Sawaguchi, T. & Kudo, H. 1990b Relative brain size, stratification and social structure in primates. *Primates* **31**, 257–272.

Seyfarth, R. M. & Cheney, D. L. 2002 What are big brains for? *Proc. Natl Acad. Sci. USA* **99**, 4141–4142.

Seyfarth, R. M., Smuts, B. B. & Cheney, D. 1986 Social relationships and social cognition in nonhuman primates. *Science* **234**, 1361–1366.

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. 1986 *Primate societies*. University of Chicago Press.

Sperber, D. 2000 *Metarepresentation: a multidisciplinary perspective*. Oxford University Press.

Stephan, H., Frahm, H. & Baron, G. 1981 New and revised data on the brain structures in insectivores and primates. *Folia Primatologica* **35**, 1–29.

Whiten, A. & Byrne, R. W. (eds) 1988a The manipulation of attention in primate tactical deception. In *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans*, pp. 211–223. Oxford: Clarendon.

Whiten, A. & Byrne, R. W. 1988b Tactical deception in primates. *Behav. Brain Sci.* **11**, 233–273.

Zilles, K. & Rehkamper, G. 1988 The brain, with special reference to the telencephalon. In *Orang-utan biology* (ed. J. H. Schwartz), pp. 157–176. Oxford University Press.