Comparative Tests of Primate Cognition: Different Scaling Methods Produce Different Results

Robert O. Deaner   Charles L. Nunn   Carel P. van Schaik

Department of Biological Anthropology and Anatomy, Duke University, Durham, N.C., USA

Abstract
Although early comparative studies supported hypotheses that ecological demands selected for primate cognition, later work indicated that social demands were more important. One difference between earlier and later studies is that earlier studies scaled brain structures by (A) taking residuals from an interspecific regression of the brain structure in question on body mass, whereas later studies scaled them by (B) taking residuals from an interspecific regression of the brain structure in question on another brain structure or by (C) taking ratios of the brain structure in question to another brain structure. We conducted a series of comparative tests to explore the possibility that the different methods are responsible for the discrepancy between earlier and later studies. Specifically, we tested the ability of a social variable – group size – and an ecological variable – home range size – to explain variation in the non-V1 isocortex (isocortex minus primary visual cortex) when this structure was scaled with the three different methods. In multiple regression analysis, group size was a better predictor of the non-V1 isocortex with method (B). With methods (A) and (C), however, results were ambiguous: either home range size or group size explained more of the variation, depending on the inclusion of outliers, the use of independent contrasts, and whether home range size was scaled relative to body mass. We examine the three scaling methods and find no reasonable basis for preferring any of them. Hence, our results do not allow a distinction between social and ecological hypotheses. The general implications of our study are that (1) previous comparative studies are inconclusive and (2) further research is needed to develop a scaling method where relative measures of brain structure size are demonstrated to correspond with behavioral performance.

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Introduction

Biologists have long hypothesized that socioecological demands explain cognitive variation across primate species. There are three main hypotheses, two of which are ecological and one of which is social. The spatiotemporal mapping hypothesis emphasizes the demands of exploiting ecological resources dispersed in time and space [Allman, 1977; Clutton-Brock and Harvey, 1980; Milton, 1981]. The extractive foraging hypothesis stresses the selective impact of manually processing a variety of embedded foods [Parker and Gibson, 1977; Gibson, 1986; see also Byrne, 1997]. Finally, the social strategizing hypothesis holds that the need to predict and manipulate the behavior of conspecifics has selected for primate cognition [Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Cheney and Seyfarth, 1990].

Robert O. Deaner
Department of Biological Anthropology and Anatomy, Duke University, Box 90383
Durham, NC 27708-0383 (USA)
Tel. (919) 660-7389, Fax (919) 660-7348
E-Mail rod1@acpub.duke.edu

Table 1. Support for the three hypotheses for primate cognitive evolution

Hypothesis	Selective variable	Brain structure	Scaling method[1]	Studies
Spatiotemporal mapping	home range size	whole brain	A	Clutton-Brock and Harvey, 1980
	frugivory	whole brain	A	Clutton-Brock and Harvey, 1980
	frugivory	isocortex	B	Sawaguchi, 1992; Barton, 1996
Extractive foraging	foraging classification	whole brain	A	Gibson, 1986
Social strategizing	group size	isocortex	B	Sawaguchi, 1992; Barton and Purvis, 1994; Barton, 1996
	group size	isocortex	C	Dunbar, 1992, 1995
	group size	non-V1 isocortex	B	Joffe and Dunbar, 1997; Barton, 1998
	tactical deception	isocortex	C	Byrne, 1995

[1]   A = Taking residuals from an interspecific regression of a brain structure on body mass; B = taking residuals from an interspecific regression of a brain structure on another brain structure; C = taking ratios of a brain structure to another brain structure.

The classic approach to testing such hypotheses is to examine variation across species using the comparative method [Harvey and Pagel, 1991]. With the comparative method, one can test the evolutionary importance of a hypothesized cognitive demand by assessing whether evolutionary changes in cognition are in fact associated with evolutionary changes in that demand [Shettleworth, 1993; Balda et al., 1996; Lefebvre and Giraldeau, 1996]. Unfortunately, it is difficult to apply the comparative method to the hypotheses regarding primate cognition because classifications of species differences in cognition are notoriously contentious [Macphail, 1987, and commentaries therein]. Thus, workers have resorted to the comparative neuroanatomical approach where, instead of assessing cognition through behavioral performance, cognitive ability is assumed to correspond with the size of the whole brain or of brain structures implicated in cognitive tasks [for reviews, see Harvey and Krebs, 1990; Barton and Dunbar, 1997]. An important point, however, is that rather than considering the absolute size of the brain or brain structures, comparative neuroanatomical studies scale these structures relative to other biological variables.

The comparative neuroanatomical approach has now been widely applied to the three contending hypotheses for primate cognitive evolution. Early work found interspecific associations between relative brain size and home range size and frugivory, two variables thought to correspond with the ecological demands of spatiotemporal mapping [Clutton-Brock and Harvey, 1980; see also Harvey et al., 1980]. Similarly, investigators have shown positive interspecific correlations between frugivory and relative isocortex size [Sawaguchi, 1992; Barton, 1996]. The other ecological hypothesis, extractive foraging, was supported by a demon-

stration that, across species, relative brain size corresponds with foraging classifications [Gibson, 1986; see also Lefebvre et al., 1997]. Supporting the social strategizing hypothesis are recent studies indicating that group size [Sawaguchi and Kudo, 1990; Sawaguchi, 1992; Dunbar, 1992, 1995; Barton and Purvis, 1994; Barton, 1996] and tactical deception frequency [Byrne, 1995; see also Pawlowski et al., 1998] are positively correlated with relative isocortex size, and that group size is positively correlated with relative non-V1 isocortex size (the portion of the isocortex remaining once the primary visual cortex is substracted) [Joffe and Dunbar, 1997; Barton, 1998].

Although the three hypotheses are not mutually exclusive, a few studies have attempted to determine their relative explanatory power with multivariate analyses. The conclusion reached by these studies is that social variables are the best predictors of relative isocortex size in primates [Dunbar, 1992, 1995; Barton and Purvis, 1994; Barton, 1996]. Hence, an emerging consensus is that of the three hypotheses for the evolution of primate cognition, social strategizing is best supported [Byrne, 1995; Barton and Dunbar, 1997; Dunbar, 1998; Cummins, 1998].

In evaluating the comparative neuroanatomical evidence, however, it is seldom acknowledged that methods of scaling brain structures differ substantially among studies. In particular, early studies supporting the two ecological hypotheses scaled brain structures by (A) taking residuals from an interspecific regression of the brain structure in question on body mass [Clutton-Brock and Harvey, 1980; Gibson, 1986], whereas the later studies supporting the social strategizing hypothesis scaled brain structures by (B) taking residuals from an interspecific regression of the brain structure in question on another brain structure [Sawaguchi and Kudo,

1990; Sawaguchi, 1992; Barton and Purvis, 1994; Barton, 1996, 1998; Joffe and Dunbar, 1997] or by (C) taking ratios of the brain structure in question to another brain structure [Dunbar, 1992, 1995] (table 1).

In this paper, we investigate the possibility that support for the three hypotheses could depend on the scaling method that is used. Our investigation consists of a series of comparative tests where we assess the capacity of a social strategizing and a spatiotemporal mapping variable to explain interspecific variation in a brain structure when scaling methods (A), (B), and (C) are employed. We consider only the spatiotemporal mapping and social strategizing hypotheses because there is little data available to test the extractive foraging hypothesis [see Dunbar, 1992, 1995]. Although the implications of using different methods in comparative studies have been considered previously [e.g. Smith, 1984, 1999], the present paper represents the first attempt to directly compare the outcome of applying different scaling methods to primate brain structures.

Materials and Methods

For social strategizing and spatiotemporal mapping variables, we used group size and home range size, respectively, because they are the most widely available relevant variables [Barton and Purvis, 1994]. We took home range size and group size from Nunn and van Schaik [2000]. For the brain structure, we used the non-V1 isocortex, as it contains several structures specifically implicated in higher-order cognitive tasks (e.g. prefrontal cortex) [Joffe and Dunbar, 1997; Barton, 1998]. In considering methods (B) and (C), we used the brain minus isocortex as the brain structure for scaling [Dunbar, 1992, 1995; Barton and Purvis, 1994; Barton, 1996; Joffe, 1997; Joffe and Dunbar, 1997]. We took data on body mass and whole brain and isocortex volumes from Stephan et al. [1981] and volumes of area V1 from Frahm et al. [1984]. We were able to obtain information on all needed variables for a total of 33 species.

Comparative Methods

It is now widely recognized that, because of their shared ancestry, species do not necessarily represent independent data points in interspecific analyses [Harvey and Pagel, 1991]. Thus, methods must be employed so that only independent evolutionary events are considered. We addressed this problem of 'phylogenetic nonindependence' by using the method of independent contrasts [Felsenstein, 1985], as calculated by the CAIC computer program [Purvis and Rambaut, 1995]. This program requires a phylogeny and for this we used Purvis's [1995] composite estimate of primate phylogeny, following Nunn and van Schaik [2000] in assigning branch lengths. We log-transformed these branch lengths, however, to better meet the assumptions of CAIC [Garland et al., 1992].

Recent concerns regarding the method of independent contrasts [Price, 1997; Harvey and Rambaut, 2000] were addressed in two ways. First, we compared our results to those obtained without controlling for phylogeny (i.e. treating species as independent data points). Second, we repeated independent contrasts tests after removing outliers, which could have produced spurious patterns. We identified outliers using Mahalanobis outlier distance plots (in JMP, SAS Institute, Cary, NC, USA). We only reported the statistical details of nonphylogenetic and outlier-removed tests if they differed in significance to phylogenetic results based on all contrasts.

Statistical Analysis

In calculating regressions, we used the least squares regression technique so that residuals would be strictly uncorrelated with the independent variable [Harvey and Pagel, 1991]. Following standard practice, we forced independent contrast regression lines through the origin [Harvey and Pagel, 1991; Garland et al., 1992]. We used multiple regression to assess the capacity of group size and home range size to explain variation in scaled measures of the non-V1 isocortex. With method (A), the scaled measures were residuals from the regression, across primates, of non-V1 isocortex on body mass. With method (B), the scaled measures were residuals from the regression, across primates, of non-V1 isocortex on brain minus isocortex. Finally, with method (C) the scaled measures were the ratios of non-V1 isocortex to the brain minus isocortex.

Following previous workers, we $\log_{10}$ transformed all variables before analysis, except ratios calculated with method (C) [Dunbar, 1992, 1995; Barton and Purvis, 1994; Barton, 1996]. All probabilities reported are for two-tailed tests and statistical significance was set at $\alpha = 0.05$.

Additional Issues

In examining the effects of home range size, we repeated all analyses after controlling for body mass. We did this because Dunbar [1992] suggested that there could be 'grain effects' so that a larger animal perceives its home range differently than a smaller animal [see also Brown, 1995]. To control for body mass, we regressed home range size on body mass and calculated home range size residuals. In analyzing these residuals in conjunction with residual non-V1 isocortex, we had to deal with an additional pitfall: because both measures were regressed on body mass, any error in body mass would affect both residuals simultaneously, potentially producing spurious associations [Harvey and Krebs, 1990; Barton and Dunbar, 1997]. We avoided this problem by calculating home range size residuals from an alternative, independent set of body mass measures. We took alternative body mass measures from Smith and Jungers's [1997] table 5.

Variables other than group size and home range size might explain variation in the non-V1 isocortex [e.g. Allman et al., 1993; Barton, 1996]. However, our goal here was to determine whether comparative tests are sensitive to the use of scaling methods, not to provide a conclusive analysis of variation in the non-V1 isocortex. Preliminary work, however, showed that our conclusions were unaffected when accounting for the strepsirhine-haplorhine grade shift or evolutionary changes from nocturnality to diurnality [see Barton, 1996].

Results

The results obtained using scaling method (A) varied according to how the data were analyzed. In multiple regression with independent contrasts, home range size was superior to group size as a predictor of residual non-V1 isocortex (table 2). However, when one outlying contrast was removed

Table 2. Relations between non-V1 isocortex and group size and home range size in primates, when the non-V1 isocortex was scaled with three different methods

Scaling method[1]	n	Group size			Home range size		
		b_{group}	F-ratio	p^2	b_{home}	F-ratio	p^2
A	31	0.13	3.15	0.087	0.09	7.92	0.009**
B	31	0.08	9.07	0.005**	–0.06	0.29	0.594
C	31	0.21	5.29	0.022*	0.15	12.04	0.001**

[1] Scaling methods as in table 1.
[2] *p < 0.05; **p < 0.01.

Table 3. Relations between non-V1 isocortex and group size and residual home range in primates, when the non-V1 isocortex was scaled with three different methods[1]

Scaling method	n	Group size			Residual home range size		
		b_{group}	F-ratio	p	$b_{residual}$	F-ratio	p
A	31	0.07	1.12	0.299	0.19	24.37	<0.0001**
B	31	0.07	6.69	0.015*	0.01	0.05	0.83
C	31	0.31	7.08	0.011*	0.05	0.50	0.487

[1] Footnotes as in table 2.

and when the test was performed nonphylogenetically, group size explained more of the variation (outlier removed: F_{group} = 8.14, d.f. = 1,29, p = 0.008; F_{home} = 2.32, d.f. = 1,29, p = 0.139; nonphylogenetic: F_{group} = 10.58, d.f. = 1,31, p = 0.003; F_{home} = 0.18, d.f. = 1,31, p = 0.674). With regard to grain effects, in multiple regression residual home range size was better than group size as a predictor of residual non-V1 isocortex (table 3). The same result was obtained when outliers were removed and when the test was repeated nonphylogenetically.

With scaling method (B), in multiple regression with independent contrasts, group size explained more variation in residual non-V1 isocortex than either home range size (table 2) or residual home range size (table 3). The same results were obtained when outliers were removed and when analyses were repeated nonphylogenetically.

The results obtained with method (C) varied according to how the data were analyzed. In multiple regression with independent contrasts, home range size was superior to group size as a predictor of non-V1 isocortex ratio (table 2). The same result was obtained when outlying contrasts were removed. However, when the test was performed nonphylogenetically, group size explained more of the variation (F_{group} = 18.14, d.f. = 1,31, p = 0.0002; F_{home} = 13.02, d.f. =

1,31, p = 0.001). Regarding grain effects, group size was superior to residual home range size as a predictor of non-V1 isocortex ratio (table 3) in multiple regression. The same result was obtained when outliers were removed and when the test was repeated nonphylogenetically.

Discussion

Our analyses demonstrate that the choice of scaling method can affect the results of a comparative neuroanatomical test. With method (B), group size was better than home range size as a predictor of the non-V1 isocortex. With methods (A) and (C), however, either group size or home range size was the better predictor, depending on the inclusion of outliers, the use of independent contrasts, and whether home range size was corrected for body mass. These results raise the question of which scaling method is most appropriate. In particular, unless method (B) is demonstrably preferable, group size should not be considered a better predictor of the non-V1 isocortex than home range size. Our results may also indicate that both home range size and group size influence cognitive evolution in primates. This conclusion is complicated, however, by intercorrela-

tions between the two independent variables (r = 0.56, d.f. = 31, p < 0.001) and the resulting problems of collinearity [see Wetherill et al., 1986; Mitchell-Olds and Shaw, 1987).

The justification for scaling brain structures relative to other biological variables has been based on what can be termed the 'traffic maintenance' hypothesis. According to this hypothesis, larger animals will generally require larger nervous systems (including brains and brain structures) to coordinate the actions of their larger bodies while also achieving a given level of cognitive processing. Researchers who explicitly or implicitly base their scaling method on traffic maintenance therefore seek to statistically remove the 'traffic portion' of the brain (or brain structure), thus allowing comparisons of only the 'cognitive portion' [Dubois, 1897; Lashley, 1949; Jerison, 1973, 1977; Passingham, 1975; Hofman, 1982; Fox and Wilczynski, 1986; Byrne, 1995; Aboitiz, 1996; Deacon, 1997].

Unfortunately, it remains unclear how to control for neural traffic in cross-species studies. The only specific hypothesis which has been offered is that whole brain size must increase to the 2/3 power of body mass in order to maintain equivalent communication with the body surface (which scales to the 2/3 power of body mass) [Jerison, 1973, 1977; see also Dubois, 1897]. Several lines of evidence contradict this idea, however. First, a variety of studies have failed to find a constant density of surface effectors and receptors across species [reviewed in Armstrong, 1985]. Second, the density of effectors and receptors (and their representation in the brain) varies widely across the body surface [Allman, 1999]. Finally, empirical evidence suggests that the brain scales closer to the 3/4 power of body mass rather than to the 2/3 power [Martin, 1981; Armstrong, 1985; but see Harvey and Pagel, 1991; Barton, 1999].

Because there is no established procedure for controlling neural traffic, none of the three commonly used scaling methods can be theoretically justified. Nevertheless, it is worthwhile to clarify how each method attempts to control for neural traffic and to consider each method's potential strengths and weaknesses. We pay particular attention to method (A) because it has fallen out of favor [Dunbar, 1992].

Method (A)

Method (A) assumes that neural traffic is controlled by taking residuals from an interspecific regression of a brain structure on body mass. Although some investigators have calculated regressions from taxa of a 'basal' group [e.g. Bauchot and Stephan, 1966, 1969; Stephan et al., 1988; see also Gibson, 1986], in most recent studies, regressions are based on all taxa in the study [e.g. Clutton-Brock and Har-

vey, 1980; Gittleman, 1986; Krebs et al., 1989; present study]. Using body mass as an index of neural traffic is reasonable as it is widely available and highly correlated with the spinal cord [MacLarnon, 1996] and other neural structures [Stephan et al., 1988] that might contribute to neural traffic. Furthermore, method (A) is advantageous because it statistically controls for variation in body mass, arguably the best single measure of body size [Smith, 1993]. Thus, spurious correlations cannot arise between brain structures and socioecological variables because both measures are related to body size.

Two main criticisms have been leveled against method (A). First, some researchers have suggested that when evolutionary changes in body size occur, corresponding changes in brain size do not occur immediately, but only after a substantial evolutionary delay [Lande, 1979; Martin and Harvey, 1985; Deason, 1990]. If this 'lag hypothesis' is correct, measures of body mass will introduce pronounced error, potentially obscuring adaptive patterns [Dunbar, 1992, 1998; Barton and Purvis, 1994; Barton and Dunbar, 1997]. However, there is no evidence supporting the long-term persistence of evolutionary brain size lag [Pagel and Harvey, 1989; Barton, 1998], even from a recent study specifically designed to detect it [Deaner and Nunn, 1999].

The second criticism raised against method (A) is that body mass is a biased estimator of neural traffic. The hypothesis suggested in primates is that the relatively small brains of folivorous primates may falsely indicate reduced cognitive capability because body size is effectively overestimated for animals with large guts [Clutton-Brock and Harvey, 1980; Sawaguchi, 1992; Byrne, 1995; Barton and Dunbar, 1997; see also Hofman, 1982; Marino, 1998]. This idea is plausible because diet is related to the size of the digestive tract [Chivers and Hladik, 1980], a system of organs which may have relatively few connections to the central nervous system [Loewy, 1990].

Nevertheless, several lines of evidence contradict the idea that large guts produce negatively biased estimates of neural traffic. First, Clutton-Brock and Harvey [1980] carried out analyses of relative brain mass with both body mass and body length as scaling variables and found that, regardless of which scaling variable was used, frugivores have larger brains than folivores [for similar analyses in other taxa, see Roth and Thorington, 1982; Gittleman, 1986]. Because increased gut size will not necessarily be reflected in body length, differences in brain mass relative to body length cannot be readily attributed to gut size [Clutton-Brock and Harvey, 1980]. Second, there is no evidence that folivores have small spinal cords relative to their bodies, as might be expected if their effective body size (i.e. neural

traffic) was overestimated by their large guts. In fact, in MacLarnon's [1996] sample, one of the most folivorous primates, the dusky leaf monkey, *Presbytis obscurus,* has the largest spinal cord for its body mass.

Finally, we have directly tested two predictions of the hypothesis that variation in the primate digestive tract leads to biased estimates of peripheral traffic: (1) measures of residual brain mass should differ depending on whether the brain is regressed on body mass or on body mass minus total gut mass and (2) measures of residual brain mass should correlate with percentage of fruit in the diet when brain mass is regressed on body mass [e.g. Clutton-Brock and Harvey, 1980], but not when brain mass in regressed on body mass minus total gut mass. Contrary to these predictions, brain mass residuals were virtually identical whether calculated from the regression of brain mass on body mass or from the regression of brain mass on body mass minus total gut mass ($r = 0.99$, d.f. = 14, $p < 0.0001$). Similarly, brain mass residuals were correlated with percentage frugivory when brain mass was regressed on either body mass ($r = 0.63$, d.f. = 14, $p = 0.01$) or on body mass minus total gut mass [$r = 0.64$, d.f. = 14, $p = 0.01$; all results based on independent contrasts; gut data from Chivers and Hladik, 1980; brain data from Stephan, unpublished, see Deaner and Nunn, 1999; frugivory data from CLN, unpublished, for methods of data collection see Nunn and van Schaik, 2000]. We suspect that total gut mass does not affect measures of residual brain size because gut mass composes only a small portion of total body mass (e.g. 2–7%).

To summarize, the commonly cited criticisms of method (A) are weak. Nevertheless, method (A) still remains of questionable validity because there is no evidence that controlling for body mass yields measures that correspond with cognitive ability. In fact, it is plausible that cognition and body mass are positively correlated [Deacon, 1997]. If so, controlling for body mass would be equivalent to controlling for cognition, the actual variable of interest [see Harvey and Pagel, 1991].

Method (B)

Method (B) assumes that neural traffic is controlled by taking residuals from an interspecific regression of a brain structure on another brain structure. As seen in method (A), regressions can be based on taxa of a 'basal' group [see Portmann and Stingelin, 1961] but usually are based on the taxa included in the study [e.g. Krebs et al., 1989; DeVoogd et al., 1993; Barton and Purvis, 1994; Barton, 1996; Joffe and Dunbar, 1997; Barton, 1998; present study]. Using another brain structure to estimate neural traffic is reasonable if the scaling brain structure has connections to the
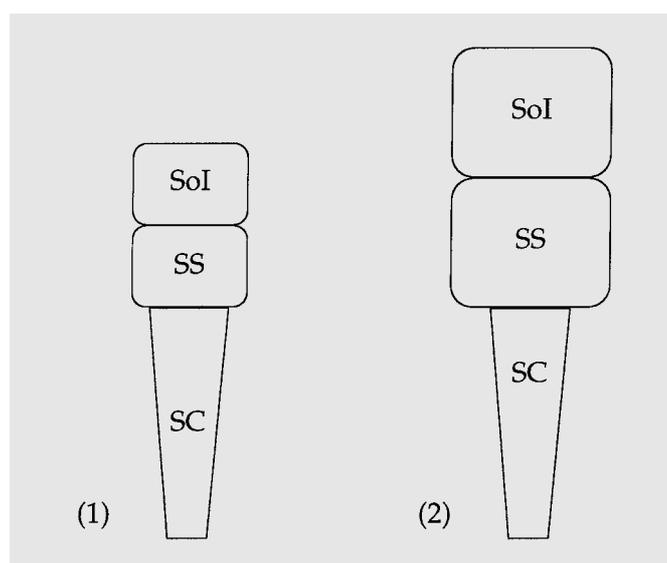

Fig. 1. The masking problem. Here two hypothetical nervous systems are shown. The structure of interest (SoI) and the scaling structure (SS) are smaller in (1) than in (2). However, the spinal cord (SC) is the same size in both systems. With methods (B) and (C), SoI's processing is estimated relative to SS and could be estimated equal in both systems. However, if SoI's processing is estimated relative to SC, it is estimated greater in (2) than in (1). Thus, variation in the scaling structure may mask variation in the structure of interest.

brain structure of interest. Because most brain structures are highly correlated with body mass [Stephan et al., 1988], method (B) can be expected to avoid the problem of spurious correlations between brain measures and ecological variables (see above).

There is, however, a potentially serious drawback with method (B): selection for increased size in the scaling structure could mask selection for increased size in particular brain structures (fig. 1) [see Barton and Dunbar, 1997; Barton, 1998]. In other words, the scaling structure might provide a biased estimate of neural traffic if the same selective pressure that affected the brain structure of interest has affected its size. For instance, extractive foraging requires both higher order planning to organize novel behavioral sequences and complex manual motor coordination to execute them [see Gibson, 1990; Byrne, 1997]. Extractive foraging thus may select for an enlarged isocortex (for planning) as well as an enlarged cerebellum (for motor execution). Hence, if an extractive forager's isocortex is scaled relative to its cerebellum, selection for an enlarged isocortex might be masked. Masking could also be a problem if there are multiple, correlated cognitive demands: if one demand

affects the scaling structure, the effects of the other demand on the brain structure of interest might be obscured.

Because there is no established measure of actual neural traffic, demonstrating the existence of the masking problem is difficult. If we assume, however, that body mass provides a reasonable estimate of neural traffic (see above), then we can regress the scaling structure on body mass and test whether the residuals are associated with a putative cognitive demand. If so, we would have evidence that the scaling structure has undergone selection relative to an alternative estimate of neural traffic. To investigate if the common scaling structure in primate studies – brain minus isocortex – provides a potentially biased measure of neural traffic, we regressed brain minus isocortex on body mass and tested if the residuals were correlated with home range size or group size. In both cases there was a positive correlation (home range: $r = 0.66$, d.f. = 30, $p < 0.001$; group size: $r = 0.36$, d.f. = 30, $p < 0.05$; based on independent contrasts). Thus, masking is a potentially serious problem with method (B).

Method (C)

Method (C) is an approach which attempts to control neural traffic by taking a ratio of one brain structure to another [Passingham, 1975; see Krompecher and Lipák, 1966]. Recent primate studies using method (C) have taken a ratio of the isocortex [Dunbar, 1992, 1995; Byrne, 1995; Pawlowski et al., 1998] or the non-V1 isocortex [Joffe, 1997] to the brain minus the isocortex. Similar to method (B), method (C) introduces the possibility that selection for increased size in the scaling structure will mask selection for increased size in the brain structure of interest.

The most notable property of the ratio measures produced by method (C) is that they are usually correlated with body size. For instance, we found that across primates there is a strong positive correlation between body mass and the ratio of non-V1 isocortex to the brain minus the isocortex ($r = 0.60$, d.f. = 30, $p < 0.0001$; based on independent contrasts).

On one hand, the correlation between body mass and the ratio measures produced by method (C) is desirable if cognition and body mass are indeed positively correlated. On the other hand, employing measures that are positively correlated with body mass may result in spurious correlations between the measures and socioecological variables that are also correlated with body mass [Gould, 1966; Passingham, 1975; Packard and Boardman, 1987; Deacon, 1993; Barton, 1993]. Previous studies indicate that body mass is correlated with home range size [Milton and May, 1976; Clutton-Brock and Harvey, 1977; Nunn and van Schaik, 2000] and group size [Clutton-Brock and Harvey, 1977; Nunn and van

Schaik, 2000; but see Barton, 1996], indicating a potential for spurious correlations.

Conclusions

Our discussion indicates that there is no theoretical or empirical basis for preferring any of the methods examined here, the oft-cited problems of method (A) are overstated, and methods (B) and (C) each have potential pitfalls. Because method (B) is not preferable to methods (A) and (C), our comparative tests do not provide more support for the social strategizing hypothesis than the spatiotemporal mapping hypothesis. More generally, our tests indicate that it is premature to conclude that previous neuroanatomical studies [Dunbar, 1992, 1995; Barton and Purvis, 1994; Barton, 1996] have successfully differentiated between the three hypotheses for primate cognitive evolution [cf. Byrne, 1995; Barton and Dunbar, 1997; Dunbar, 1998; Cummins, 1998].

Definitive tests of primate cognitive evolution require a valid scaling method. In the absence of theoretical principles, progress will be made when investigators compare a variety of scaling methods with regard to their ability to predict independently derived behavioral indicators of cognition. The pool of potential scaling methods should include those which have been previously used [e.g. (A), (B), (C)] but should also include novel approaches that give more consideration to the neural traffic relevant to the particular brain structure in question. Obtaining behavioral indicators of cognition will be difficult, but it might be possible to combine interspecific data on standardized tasks [Passingham, 1975; Riddell and Corl, 1977; Rumbaugh et al., 1996]. If it can be shown that one scaling method repeatedly provides a close correspondence with behavioral performance, future comparative neuroanatomical studies will be more conclusive.

Finally, even if a valid scaling method is developed, the sensitivity of our results to other methodological decisions suggests that distinguishing between socioecological hypotheses will still be challenging. The main problem could be that multiple regression models are highly fragile because the independent variables – group size and home range size – are significantly intercorrelated (see above). This problem of collinearity has yet to be addressed in studies of primate cognitive evolution [see Wetherill et al., 1986; Mitchell-Olds and Shaw, 1987]. Besides suggesting that statistically distinguishing between these variables will be difficult, this correlation indicates that socioecological demands might often evolve in tandem (e.g. using a larger home range leads to living in larger groups, and vice-versa). If true, attempts to identify the preeminence of a single demand may be misguided.

Acknowledgments

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