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Neocortex evolution in primates: the 'social brain' is for females

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According to the social intelligence hypothesis, relative neocortex size should be directly related to the degree of social complexity. This hypothesis has found support in a number of comparative studies of group size. The relationship between neocortex and sociality is thought to exist either because relative neocortex size limits group size or because a larger group size selects for a larger neocortex. However, research on primate social evolution has indicated that male and female group sizes evolve in relation to different demands. While females mostly group according to conditions set by the environment, males instead simply go where the females are. Thus, any hypothesis relating to primate social evolution has to analyse its relationship with male and female group sizes separately. Since sex-specific neocortex sizes in primates are unavailable in sufficient quantity, I here instead present results from phylogenetic comparative analyses of unsexed relative neocortex sizes and female and male group sizes. These analyses show that while relative neocortex size is positively correlated with female group size, it is negatively, or not at all correlated with male group size. This indicates that the social intelligence hypothesis only applies to female sociality.

Keywords: sexual dimorphism;
phylogenetic comparative methods; sexual selection

1. INTRODUCTION

The neocortex is the brain structure that handles the more demanding cognitive and social skills (Innocenti & Kaas 1995; Kaas 1995). Animals with large general brain sizes also tend to have disproportionally large neocortices (Finlay & Darlington 1995), but this relationship is not just simply allometric. Instead, selective processes can select for brain structures similar in function yet at different locations in the brain. In primates, for example, the visual cortex and the lateral geniculate—both involved in the visual system—have been modified through demands from frugivory on visual competence (Barton 1998; Barton & Harvey 2000; de Winter & Oxnard 2001). Hence, a single selection pressure may select for enlargement of several brain components. Nevertheless, if one wants to investigate the evolution of higher cognitive functions, the neocortex is the structure to focus on.

The social intelligence hypothesis states that relative neocortex size should be related to the degree of social complexity (Byrne & Whiten 1988). This is because more complex social networks place higher cognitive demands on individuals and thus select for larger neocortices (Sawaguchi 1992), or conversely because neocortex size places a limit on the number of social interactions an individual can keep track of and thus limits group size (Dunbar 1992; Kudo & Dunbar 2001). When studying primate sociality, however, the focus has more often been on the influence of ecological factors on group size (Emlen & Oring 1977; Altmann 1990; Lindenfors *et al.* 2004). The evolution of primate sociality has largely been seen as driven by resource defence (Wrangham 1980) or predator avoidance (van Schaik 1983). Additionally, it has been shown that ecological factors, such as the degree of frugivory, are related to neocortex size because a large part of the neocortex is involved in visual processing (Barton 1996, 1998). Also, larger brains consume more energy, placing demands for an energy-rich diet. Hence, ecology, social group size and relative neocortex size all relate to each other in a triangle of hypotheses.

An insight from research on primate sociality, however, is that social evolution in primates is driven by different processes in males and females. While female reproductive success is linked to the acquisition of resources and protection from predators, males gain from monopolizing access to females (Emlen & Oring 1977; Altmann 1990; Lindenfors *et al.* 2004). Thus, one would expect that social selection pressures on neocortex size should be different in males and females. If relative neocortex size limits group size (Dunbar 1992; Kudo & Dunbar 2001), this should limit female group size more than male group size—if nothing else, simply because there are more females than males in primate groups (Lindenfors *et al.* 2004; Nunn 1999). Also, separate dominance hierarchies are not seldom maintained for males and females in primate groups (Smuts *et al.* 1987), indicating that males should have fewer intrasexual interactions to keep track of than females.

If it is assumed that causality is reversed, in that increased social complexity is what selects for a larger relative neocortex (Sawaguchi 1992), this can still place stronger selection on neocortex size in females than in males. This because selection should be highest in the sex where the value of keeping track of social interactions is higher. Two patterns indicate that this would be females. First, most haplorhine primates are matrilocal, where females stay in the social network where they were born whereas males migrate to new social groups upon reaching adulthood (Smuts *et al.* 1987). Second, about two-thirds of haplorhine primates are polygynous (Lindenfors & Tullberg 1998), where intrasexual interactions between males to a large degree consist of competing with other males over access to females. This is not to say that males have no social interactions or even that social interactions are unimportant to males, only that the value of social interactions, and of keeping track of them, most probably is higher in primate females than in males.

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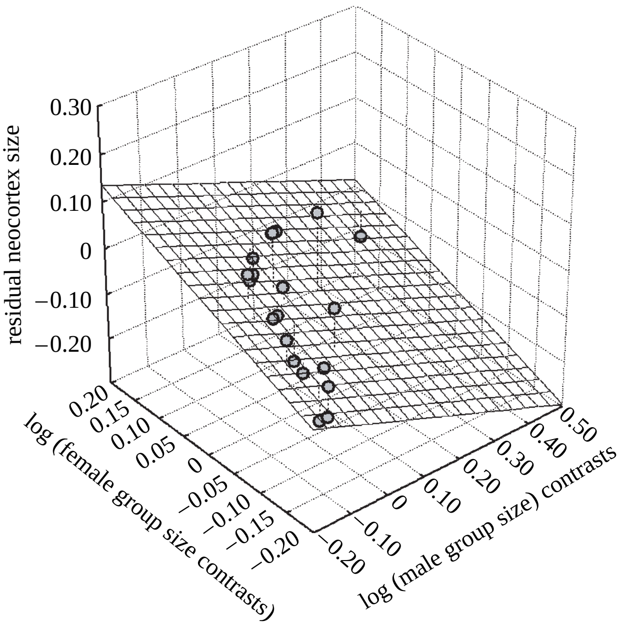

Figure 1. The relationship of relative neocortex volume and male and female group size. Relative neocortex size is for this figure calculated as residuals from a neocortex—brain size regression. Multiple regression analysis shows that relative neocortex volume scales positively with female group size and that a tendency exists for relative neocortex volume to scale negatively with male group size.

2. MATERIAL AND METHODS

Data on neocortex volumes, brain volumes, body mass, and group sizes were taken from the literature (Stephan *et al.* 1981; Smith & Jungers 1997; Nunn & Barton 2000). No information was available concerning the sexes of the animals whose brains were measured and hence the present analysis presents results concerning species-typical relative neocortex sizes. Though data exists for strepsirhine primates, these were not included here because all but four of these species were solitary.

Since the hypothesis to be investigated concerned the size of the neocortex relative to the total brain, total brain size was included as an independent variable in all regression models. Different measures of relative neocortex size produce different results (Deaner *et al.* 2000), but using the ratio of neocortex volume to total brain volume produced similar results to the approach favoured here. Residuals from neocortex—total brain volume regression were used to construct figure 1, but not in any analyses. All variables were log-transformed prior to analysis.

I used a phylogeny made with a super-tree technique combining a large number of source phylogenies (Purvis & Webster 1999). This phylogeny is a consensus tree utilizing all information published up until its construction, and it thus unites knowledge gathered from both molecular and morphological phylogenies. Hypothesis testing was done using phylogenetic independent contrasts (Felsenstein 1985) as implemented in the computer program PDAP (Garland *et al.* 1993). Diagnostics showed that branch lengths needed no adjustment (Garland *et al.* 1992).

3. RESULTS

Neocortex size is tightly correlated with total brain size ($F_{1,19}=11\,814$, $B=1.050$, $R^2=0.998$, $p\ll0.001$). Total brain size was therefore included in all further regression models. To test if the social intelligence hypothesis applies equally to males and females, I first analysed the relationship between relative neocortex size and female and male group size separately. While female group size was significantly correlated with relative neocortex volume (partial regression coefficients $t_{18}=3.078$, $B=0.021$, $p=0.006$), male group size was not (partial regression coefficients $t_{18}=1.125$, $B=0.007$, $p=0.275$). This is in spite of the fact that male and female group sizes—as also shown elsewhere with larger datasets (Nunn 1999; Lindenfors *et al.* 2004)—are highly correlated ($F_{1,19}=21.753$, $B=0.990$, $R^2=0.534$, $p=0.0002$).

Table 1. Multiple regression of relative neocortex volume on male and female group size.
(Full model $F_{3,17}=6574.7$, $R^2=0.999$, $p\ll0.001$.)

	B	*t*(18)	*p*-level
total brain size	1.035	118.158	0.000
male group size	−0.014	−1.940	0.069
female group size	0.037	3.552	0.002

A multiple regression model including both male and female group size showed that relative neocortex volume was significantly correlated with female group size, while only a tendency of a correlation ($p=0.069$) was found with male group size (figure 1; table 1). Somewhat surprisingly, the latter tendency was negative. Given the correlation between male and female group size, one could expect collinearity problems in the multiple regression analysis, but tolerance values of 0.366 for male group size and 0.344 for female indicated that this posed no problem. Thus, male group size, despite being closely tied to female group size (Nunn 1999; Lindenfors *et al.* 2004), is not correlated with neocortex size by itself, and is even indicated to have a negative influence on relative neocortex size after accounting for female group size.

If neocortex size scales positively with female group size and negatively with male group size, this could indicate that the underlying process is not selection from increasing social demands, but instead involves sexual selection on males (Sawaguchi 1997), which is expected to be more intense in species where more females and fewer males are included in a social group (Darwin 1871). A large neocortex would in this scenario be beneficial to males by e.g. making them able to outsmart other males in intrasexual competition, or due to female choice, where females then simply would prefer more ‘cerebral’ males. To investigate this possibility, I included body mass dimorphism as a surrogate measure of sexual selection in the statistical models. Dimorphism did not correlate significantly with relative neocortex volume either when including only brain size (partial regression coefficients $t_{18}=-1.748$, $B=-0.031$, $p=0.098$), or when also including female group size (partial regression coefficients of dimorphism $t_{17}=-1.255$, $B=-0.020$, $p=0.226$).

Using the Akaike information criterion (AIC; Quinn & Keough 2002) for selecting between different multiple regression models—initially including total brain size, male and female group size, male and female body mass, and body mass dimorphism as independent variables in the model—showed that the best regression model should include only total brain size and female group size (table 2;

Table 2. Multiple regression of relative neocortex volume on total brain size and female group size.
(Full model $F_{2,18}=8547.8$, $R^2=0.999$, $p \ll 0.001$.)

	B	*t*(18)	*p*-level
total brain size	1.043	125.083	0.000
female group size	0.021	3.079	0.006

AIC = −126.101). The AIC statistic only differed slightly with that also including male group size (table 1; AIC = −126.514) while the gap was wider to other alternative models.

4. DISCUSSION

The comparative analysis presented here indicates that brain evolution proceeds in accordance with the social demands of females, because the size of the neocortex in both sexes is larger in species with larger female social networks. In this scenario, large relative neocortex size in males could be the result of a genetic correlation between the sexes, or of the possible importance for both sexes of keeping track of female social interactions. Note, however, that at present no data exist to examine if neocortex size differs between the sexes in primates.

Nevertheless, sex-specific predictions can be made from the results presented here. For example, relative neocortex size should be larger in females than in males in more social primate species. Also, females in social species should be expected to be relatively better than males at tasks relating to sociality.

Other hypotheses exist regarding the evolution of relative neocortex size, primarily concerning the relationship with diet (Barton 1996, 1998). These hypotheses propose that frugivory selects for a larger neocortex through higher demands placed on the visual system. Though it has been shown that diet also influences neocortex size, it is highly unlikely that this influence is sex-specific. On the other hand, sex-specific factors beside group sizes may be of importance for neocortex evolution. It has been shown in terrestrial carnivores that degree of maternal care correlates with larger female total brain size (Gittleman 1994). Further sex-specific data on different brain structures in primates and other mammals could shed light on such questions.

There is no *a priori* reason to suspect that the pattern reported here only applies to primates. In any animal that is social, it is important for an individual's well-being and—in extreme cases—survival, to keep track of social interactions and dominance hierarchies. Where opportunities exist for males to monopolize females, however, the advantages of doing so would quickly outweigh the advantages of keeping track of more fine-tuned social interactions. Intramale competition could thus counter the evolution of neocortex size by making selection for larger neocortices female-specific.

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