

Visual and socio-cognitive information processing in primate brain evolution

TRACEY H. JOFFE AND R. I. M. DUNBAR*

School of Life Sciences, University of Liverpool, Nicholson Building, PO Box 147, Liverpool L69 3BX, UK

SUMMARY

Social group size has been shown to correlate with neocortex size in primates. Here we use comparative analyses to show that social group size is independently correlated with the size of non-V1 neocortical areas, but not with other more proximate components of the visual system or with brain systems associated with emotional cueing (e.g. the amygdala). We argue that visual brain components serve as a social information 'input device' for socio-visual stimuli such as facial expressions, bodily gestures and visual status markers, while the non-visual neocortex serves as a 'processing device' whereby these social cues are encoded, interpreted and associated with stored information. However, the second appears to have greater overall importance because the size of the V1 visual area appears to reach an asymptotic size beyond which visual acuity and pattern recognition may not improve significantly. This is especially true of the great ape clade (including humans), that is known to use more sophisticated social cognitive strategies.

1. INTRODUCTION

A number of studies have now shown that there is a positive linear relationship between social group size and neocortex size in primates (Sawaguchi & Kudo 1990; Dunbar 1992; Sawaguchi 1992; Barton 1996; Dunbar & Joffe 1997), bats (Barton & Dunbar 1997), carnivores (Dunbar & Bever 1997) and cetaceans (Marino 1996; A. Tschudin, personal communication). This relationship is assumed to reflect the fact that the size of an animal's neocortex constrains its ability to process social information and thus maintain social relationships. Recently, a number of social variables other than group size have been correlated with neocortex size (e.g. Byrne 1993; Joffe 1997; Pawlowski *et al.* 1997), all adding support to the 'social brain' hypothesis (the claim that primates have evolved large brains and superior cognitive skills in order to operate effectively in large complex social groups: see Byrne & Whiten 1988; Brothers 1990). These findings have been further reinforced by the observation that maternal and paternal genomes may act differentially on parts of the brain associated with social skills in ways that relate directly to the species' social style (Keverne *et al.* 1996).

One problem with using the neocortex as the unit against which to correlate social variables is that it leads one to assume that the neocortex as a whole is responsible for the processing of social information. In functional terms, the neocortex is the 'thinking' part of the brain. It is implicated in association formation, planning, sensory integration, behavioural flexibility, problem solving and cognitive memory. Yet, the neocor-

tex also includes the visual cortex, an area of primary visual processing. Diurnal primates, in particular, have evolved large visual cortices, and this component alone accounts for up to 50% of the variance in primate neocortex size (Barton 1996).

Barton (1996) has suggested that the visual system may be implicated in social complexity. He has shown that there is a correlation between primate social group size and both relative parvocellular volume and cell number within the geniculo-cortical visual system. Furthermore, he has shown that variance in primary visual cortex size is associated with parvocellular rather than magnocellular specialization in primates. The parvocellular layers of the geniculo-cortical visual system are geared toward the analysis of fine detail and colour as opposed to the magnocellular layers, which are geared toward high contrast sensitivity, movement detection and the analysis of dynamic form. The correlation with social group size implies that parvocellular specialization and the analysis of colour visual stimuli are implicated in the management of social complexity.

This raises a question as to whether the apparent relationship between neocortex volume and social group size is genuinely one of social skill (as implied by the social brain hypothesis) or one of visual recognition (of either individuals or visual signals, or both). Here we use comparative methods to evaluate the relationships in anthropoid primates between group size and both relative size of the primary (striate) visual cortex (area V1) and non-V1 neocortex. In addition, we also consider relative lateral geniculate nucleus (LGN) size in order to ascertain whether the relative size of extra-neocortical visual components versus neocortical visual components may have a constraining effect on social

* Author for correspondence.

group size. Since a great deal of social behaviour involves recognition of and response to cues of others' emotional states, we also ask whether the relationship between social group size reflects the size of the brain's emotional cueing centres (the amygdala in particular), or is specific to the size of the higher order information processing centres in the neocortex. We use group size as our dependent measure here, following most previous analyses, because ultimately it is the number of relationships an animal can maintain through time that is assumed to be constrained by the processing capacities of the brain.

2. METHODS

Mean group sizes were taken from Dunbar (1992). All brain component volumes for anthropoid primates were taken from Stephan *et al.* (1981). Data were not available for the extrastriate visual cortex (area V2) which also forms part of the neocortex. We have, therefore, used the primary (striate) visual cortex (area V1) as a marker for visual neocortex size as a whole. This should not seriously effect calculations of relative non-V1 neocortex size since the sizes of visual subsystems have been shown to correlate in anthropoid primates (Barton 1996). Non-V1 neocortex volume was calculated as neocortex volume minus primary visual cortex volume. To avoid terminological confusion, we refer to this as NVC.

Ever since Jerison's (1973) seminal analyses, it has been conventional to remove the effects of body size from comparative analyses of brain evolution on the grounds that it is the brain volume over and above that needed to manage the body system that is of interest. Because body size has been shown to change independently of brain size (Willner 1989; Deacon 1990), changes in brain component size need to be considered in terms of brain size itself (see also Dunbar 1992). Because 50–80% of total brain size is accounted for by the neocortex in primates, we calculated residuals on the 'rest of the brain' (i.e. total brain volume—neocortex volume) in order to control for changes in absolute brain component size independent of neocortex size and body size. Non-V1 neocortex, V1 and amygdala component volumes were calculated as reduced major axis linear regression residuals on (total brain volume—neocortex volume).

To control for phylogenetic relatedness, we use the method of independent contrasts recommended by Harvey & Pagel (1991), without taking branch length into account. All values were \log_{10} -transformed prior to analysis. All statistical tests are two-tailed and regressions are set through the origin for all contrasts analyses.

Table 1 lists brain volume, NVC, primary visual cortex (area V1) volume, LGN volume, amygdala volume and group size for the anthropoid primate species used in the analysis. Strepsirrhine primates were not included in the sample because many of these are characterized by a nocturnal lifestyle, and this is thought to have had its own influence on brain evolution (Barton & Dunbar 1997). In addition, *Tarsier*

Table 1. *Data for variables used in the analysis*

species	brain volume ^a	NVC ^c	primary visual cortex (area V1) volume	LGN volume	amygdala volume	group size ^b
<i>Callithrix jacchus</i>	7241	3679	692	25.7	113	8.5
<i>Cebuella pygmaea</i>	4302	—	—	—	—	6.0
<i>Sanguinus oedipus</i>	9537	4891	1003	33.0	—	5.2
<i>Sanguinus tamarin</i>	9569	4806	1077	36.8	—	—
<i>Callimico goeldi</i>	10 510	—	—	—	—	7.3
<i>Aotus trivirgatus</i>	16 195	8806	1144	36.0	201	3.8
<i>Callicebus moloch</i>	17 944	9661	1502	53.2	—	3.3
<i>Pithecia monacha</i>	32 867	18 874	2154	72.3	—	3.6
<i>Alouatta sp.</i>	49 009	29 286	2374	85.7	413	8.2
<i>Ateles geoffroyi</i>	101 034	66 118	4738	151.0	—	17.0
<i>Lagothrix lagotricha</i>	95 503	59 585	6288	149.0	—	23.4
<i>Cebus sp.</i>	66 939	41 739	4690	137.0	502	18.1
<i>Saimiri sciurius</i>	22 572	13 215	2326	62.9	227	32.5
<i>Macaca mulatta</i>	87 896	56 896	6586	158.0	—	39.6
<i>Cercocebus albigena</i>	97 603	61 902	6831	182.0	—	15.4
<i>Papio anubis</i>	190 957	—	—	—	—	51.2
<i>Cercopithecus ascanius</i>	63 505	40 014	5152	147.0	601	29.7
<i>Cercopithecus mitis</i>	70 564	44 659	5274	150.0	—	33.0
<i>Miopithecus talapoin</i>	37 776	23 381	3046	116.0	—	65.5
<i>Erythrocebus patas</i>	103 167	—	—	—	—	28.1
<i>Pygathrix nemaeus</i>	72 530	—	—	—	—	—
<i>Nasalis larvatus</i>	92 797	—	—	—	—	14.4
<i>Procolobus badius</i>	73 818	46 922	3984	128.0	479	35.0
<i>Hylobates lar</i>	97 505	—	—	—	—	3.4
<i>Gorilla gorilla</i>	470 359	326 259	15 185	384.0	—	7.0
<i>Pan troglodytes</i>	382 103	276 901	14 691	356.0	—	53.5
<i>Homo sapiens</i>	1 251 847	983 659	22 866	416.0	3015	—

^a Brain volumes from Stephan *et al.* (1981) in mm³.

^b Mean group sizes from Dunbar (1992).

^c NVC = neocortex volume minus primary visual cortex (area V1) volume.

was excluded from these analyses because of its nocturnal habit and uncertainty about its social group size.

3. RESULTS

Figure 1 plots contrasts in social group size against relative NVC contrasts, primary (striate) visual cortex volume contrasts and LGN volume contrasts. All regressions are through the origin and all are significant (non-V1 neocortex: $r^2 = 0.61$, $F = 24.987$, d.f. = 1,16, $p = 0.000$; primary visual cortex: $r^2 = 0.309$, $F = 7.162$, d.f. = 1,16, $p = 0.021$; LGN: $r^2 = 0.337$, $F = 8.128$, d.f. = 1,16, $p = 0.016$). A stepwise regression analysis shows that the best-fit predictor of social group size is NVC, where NVC contrasts account for 61% of the variance in group size, while visual component contrasts do not contribute significantly to the equation. The reduced major axis regression equation is as follows:

$$\text{contrast in } \log_{10}(G) = -0.128 + 8.8 \text{ contrast in } \log_{10}(\text{NVC}),$$

where G = mean group size and NVC = non-V1 neocortex volume RMA residuals on the 'rest of the brain' (i.e. total brain - volume neocortex volume) (with all volumes \log_{10} -transformed). Partial correlation analysis confirms that group size contrasts and NVC contrasts are significantly correlated when primary visual cortex and LGN volume contrasts are held constant ($p = 0.001$). However, when NVC contrasts are held constant, partial correlations between group size and visual component contrasts are no longer significant ($p = 0.735$ for the primary visual cortex and $p = 0.585$ for the LGN).

The distributions in figure 1 suggest an important difference between V1 and non-V1 cortical segments. The regression coefficient between V1 cortex contrasts and group size contrasts is much weaker than that for the non-V1 cortex contrasts: the regression slope for the V1 cortex is significantly lower than that for the non-V1 neocortex ($t = 2.676$, d.f. = 18, $p = 0.021$), and the fit to the regression is much poorer because the data are considerably more scattered ($r^2 = 0.61$ versus $r^2 = 0.31$, respectively).

One reason for this is suggested by the plot of absolute visual cortex (V1) volume against absolute non-V1 cortex volume (figure 2). There is a significant quadratic relationship between the two variables:

$$\log_{10}(PVC) = -1.209 + 1.442 \log_{10}(NVC) - 0.085 (\log_{10}(NVC))^2$$

($r^2 = 0.97$, $F = 265.05$, d.f. = 1,17, $p < 0.0001$), where PVC is absolute primary visual cortex (V1) volume and NVC is absolute non-V1 cortex volume. This suggests that visual cortex may reach an absolute upper limit for the visual system elements beyond which little improvement in system performance is gained by further increments in size, but that this is not the case for the non-V1 neocortex elements. The LGN also forms this asymptotic relationship with NVC.

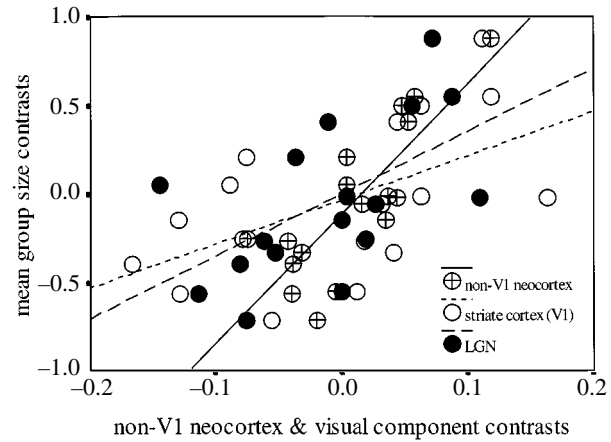


Figure 1. Contrasts in mean group size plotted against contrasts in primary visual cortex (area V1), LGN and non-V1 neocortex for individual species. Regression lines are reduced major axis regressions through the origin. Source: table 1.

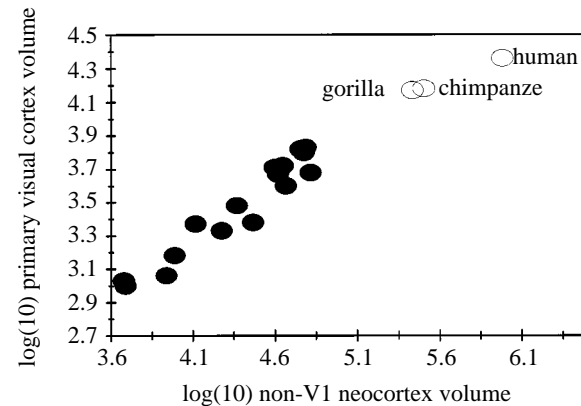


Figure 2. Absolute visual cortex (area V1) volume plotted against absolute non-V1 neocortex volume. Source: table 1.

There is no significant difference between neocortical and extraneocortical visual components as they relate to social group size. Both the regression slopes and coefficients are of similar magnitude in the primary visual cortex and LGN contrasts ($t = 2.676$, $r^2 = 0.309$, d.f. = 18, $p = 0.021$ and $t = 2.851$, $r^2 = 0.337$, d.f. = 18, $p = 0.016$, respectively). To be sure there were no confounded effects, we reanalysed the visual system data for the combined volume of LGN plus primary visual cortex; the results were the same as those obtained for each component separately.

Figure 3 shows that there is no relationship between amygdala volume contrasts and social group size contrasts ($r^2 = 0.002$, $F = 0.008$, $n = 6$, $p = 0.769$). Corticomedial and basolateral parts of the amygdala were also evaluated separately, and no relationship between group size contrasts and contrasts in the volumes of those parts was found. This suggests that the major neuronal systems involved in emotional behaviour are not specifically involved in the management of large social groups (however important the information they may provide at the input end).

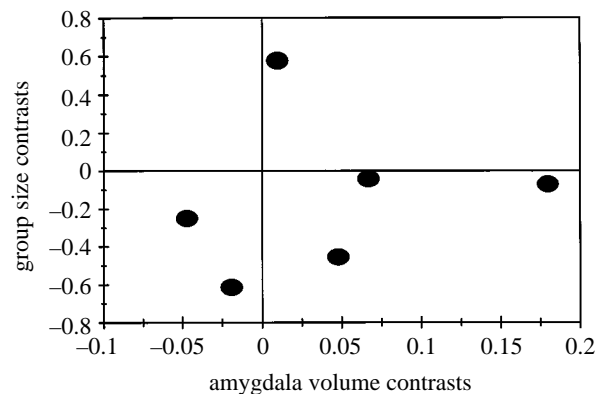


Figure 3. Contrasts in mean group size plotted against contrasts in amygdala volume for individual species. Source: table 1.

4. DISCUSSION

Although visual processing components are not independently correlated with social group size when controlling for the effects of the non-VI neocortex, these components (the primary visual cortex in particular) have coevolved with the neocortex and may form part of a functional system implicated in managing social group size in anthropoid primates. The relationship between neocortex volume and social group size does appear, however, to be one of genuine social skill rather than one of visual recognition or emotional cueing, as evinced by the significant relationship between NVC and social group size.

As noted previously, Barton (1996) found a significant positive linear relationship between parvocellular volume and cell number in the geniculo-cortical visual system. Although he measures relative parvocellular volume against the 'rest of the brain' in much the same way as we have here, he does not factor out the relative contribution of the visual cortex to the neocortex as a whole (up to 50% of neocortex volume is comprised of primary visual cortex). His results may therefore reflect the fact that the covariance between brain parts results in confounded relationships. However, the fact that the variance in interspecific primary visual cortex volume in primates is associated with parvocellular specialization (Barton 1996) sheds some light on the positive (although non-significant) relationship that we find between primary visual cortex (VI) volume and social group size (see figure 1). There is evidence to suggest that diurnal (parvocellular specialized) primates, in particular, rely on detailed visual analysis in order to process socio-visual stimuli. Visual displays, grimacing, postural-gestural displays and facial displays all serve to relay social information (Fridlund 1994). In fact, facial perception and discrimination of facial features is quite specialized in non-human primates (Rosenfeld & Van Hoesen 1979) and particularly in humans. Many anthropoid primates show a variety of highly differentiated facial displays, including, the grimace or 'silent bared-teeth face' (van Hooff 1969; c.f. human 'fear' or 'surprise' faces), the tense-mouth display (human 'anger' faces), and the play face in which the mouth is opened wide with the lip corners barely retracted (the human amusement smile).

Furthermore, neocortical cells appear to be implicated in the processing of these facial gestures. Electrophysiological evidence from single unit recordings on monkeys demonstrates that neocortical cells in these animals are sensitive to still photographs of their own species' face (Bruce *et al.* 1981; Gross *et al.* 1972; Perrett *et al.* 1982). Moreover, 'face cell' studies in rhesus macaques indicate that neocortical cells respond selectively to head orientation, gaze direction, face identity and certain facial displays (Perrett *et al.* 1985; Perrett *et al.* 1987; Hasselmo *et al.* 1986).

The non-VI neocortex may therefore be implicated in the encoding and processing of socio-visual stimuli, while the primary visual cortex may act as an input 'device' for detailed fine-tuned visual stimuli which carry social information. In combination, these neocortical components may make up a functional system that has evolved in response to social pressures, particularly among diurnal frugivorous primates that are parvocellularly specialized. Moreover, the relative importance of the input versus the processing components of this system may depend upon the species in question. As shown by figure 2, absolute primary visual cortex size appears to reach an asymptotic size in the larger-brained species. This may be an indication that the social information processing system in hominines (in particular) is biased in favour of the non-VI neocortex over the primary visual cortex. This might suggest that the functional efficiency of visual cue processing reaches an upper limit beyond which further increases in computing power do not add measurably to the effectiveness of the visual recognition system. Where social interactions are highly complex, selection may favour a relatively larger processing or encoding component over the input component. This would not be surprising given the superior socio-cognitive skills of the great apes and humans, particularly in the areas of tactical deception and 'theory of mind' (Byrne 1995) which require the processing and integration of complex strings of socio-visual information.

The fact that both LGN and primary visual cortex (VI) volume contrasts form similar regressions with group size contrasts (and both show asymptotic relationships to non-VI neocortex size in terms of their absolute volumes) suggests that the 'input' of socio-visual information is not confined to higher cognitive brain areas (i.e. visual cortex). Rather, it is the encoding and processing of such information that is confined to the non-visual neocortex.

Finally, it should be noted that the non-VI neocortex also consists of a number of areas with other kinds of functions (the motor cortex, somatosensory cortex and auditory cortex, for example, as well as other components of the visual system). Given that the visual cortex does not seem to be involved in the maintenance of social group size directly, it seems unlikely that these areas will be any more intimately implicated. Our difficulty at this point is that we do not have sufficiently detailed data on the sub-components of the neocortex or the visual cortex as a whole to undertake a more detailed analysis. Until more detailed information on the volumes of each neocortical component is available, the non-VI neocortex is the most

refined measure for the 'social information processing' part of the brain that we can aspire to. This limitation notwithstanding, the present analyses at least allow us to begin to differentiate between neocortical 'software' and 'hardware' units and their functional relationships to social behaviour.

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Received 28 May 1997; accepted 1 June 1997