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SHORT COMMUNICATION

Neocortical Development and Social Structure in Primates

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ABSTRACT. The relationships between the relative size of the neocortex and differences in social structures were examined in prosimians and anthropoids. The relative size of the neocortex (RSN) of a given congeneric group in each superfamily of primates was measured based on the allometric relationships between neocortical volume and brain weight for each superfamily, to control phylogenetic affinity and the effects of brain size. In prosimians, "troop-making" congeneric groups (N = 3) revealed a significantly larger RSN than solitary groups (N = 6), and there was a significant, positive correlation between RSN and troop size. In the case of anthropoids, polygynous/frugivorous groups (N = 5) revealed a significantly larger RSN than monogynous/frugivorous groups (N = 8). Furthermore, a significant, positive correlation between RSN and troop size was found for frugivorous congeneric groups of the Ceboidea. These results suggest that neocortical development is associated with differences in social structure among primates.

Key Words: Neocortex; Relative size; Allometry; Congeneric group; Social structure; Monogyny; Polygyny; Primates.

INTRODUCTION

Since the neocortex, which is associated with higher brain functions, has become highly developed during the course of primate evolution and is most highly developed in hominids (PENFIELD, 1966; JERISON, 1973; PASSINGHAM, 1973; RADINSKY, 1975), many authors have suggested that the development of social structures among primates, including hominids, may have been associated with the evolution of the neocortex and intelligence (e.g. HOLLOWAY, 1973; CASPARI, 1979; JOLLY, 1985; FOLEY, 1987). However, little quantitative evidence has been offered to support the hypothesis that the development of the neocortex is related to social structures. We therefore examined the relationships between neocortical development and social structures based on data accumulated during recent field studies and neuroanatomical investigations. We infer that differences in degree of neocortical development are closely associated with differences in social structure among primates.

METHODS

Standard values for neocortical volume (in mm^3), brain weight, and body weight are available for a total of 44 species of primates (prosimians, N = 18; anthropoids, N = 26) (STEPHAN et al., 1981). The basic ecology of these species was elucidated in studies cited by CLUTTON-BROCK and HARVEY (1977, 1980), NAPIER and NAPIER (1986), and SMUTS et al.

Table 1. Examined species and their ecology, social structure, relative size of the neocortex (RSN) and troop size.

Congeneric group	Category1)	RSN2)	Troop size	Species
Lemuriformes				
Cheirogaleus	N/S/FR	−0.017	1	*Cheirogaleus major* *Cheirogaleus medius*
Avahi	N/S/FR	0.014	1	*Avahi l. laniger* *Avahi l. occidentalis*
Microcebus	N/S/IN	0.001	1	*Microcebus murinus*
Daubentonia	N/S/IN	−0.019	1	*Daubentonia madagascariensis*
Lepilemur	N/S/FO	−0.017	1	*Lepilemur ruficaudatus*
Varecia	D/S/FR	−0.011	1	*Varecia variegatus*
*Lemur*3)	D/P/FO	0.032	9.5	*Lemur fulvus*
*Propithecus*3)	D/P/FO	0.002	6.5	*Propithecus verrauxi*
*Indri*3)	D/G/FO	0.015	3	*Indri indri*
Ceboidea				
Callithrix	A/G/FR	0.001	5	*Callithrix jacchus*
Cebuella	A/G/FR	0.003	6	*Cebuella pygmaea*
Saguinus	A/G/FR	−0.002	6.5	*Saguinus oedipus* *Saguinus tamarin*
Callimico	A/G/FR	0.003	9	*Callimico goeldii*
Aotus	A/G/FR	−0.011	3.8	*Aotus trivirgatus*
Callicebus	A/G/FR	−0.009	3	*Callicebus moloch*
Pithecia	A/G/FR	−0.012	3.6	*Pithecia monachus*
Alouatta	A/P/FO	−0.015	10	*Alouatta* sp.
Ateles	A/P/FR	0.002	12	*Ateles geoffroyi*
Lagothrix	A/P/FR	0.002	35	*Lagothrix lagotricha*
Saimiri	A/P/FR	0.028	40	*Saimiri sciureus*
Cebus	A/P/FR	0.011	21	*Cebus* sp.
Hominoidea				
Hylobates	A/G/FR	−0.002	3.5	*Hylobates lar*
Pan	T/P/FR	0.014	53	*Pan troglodytes*
Gorilla	T/P/FO	−0.013	7	*Gorilla gorilla*

1) Activity timing/social structure/diet for Lemuriformes; stratification/social system/diet for Ceboidea and Hominoidea. N: Nocturnal; D: diurnal; S: solitary; G: monogynous (i.e. monogamous and polyandrous); P: polygynous (i.e. one-male multi-female and multi-male and multi-female); A: arboreal; T: terrestrial (including "semi-terrestrial"); IN: insectivorous; FR: frugivorous; FO: folivorous; 2) RSN was calculated as follows (NV: neocortical volume, in mm^3; E: brain weight, in g): RSN $= \log NV - (1.074 \times \log E + 2.586)$ for Lemuriformes; RSN $= \log NV - (1.048 \times \log E + 2.716)$ for Ceboidea; RSN $= \log NV - (1.052 \times \log E + 2.708)$ for Hominoidea; 3) categorized as "troop-making" prosimians.

(1987). As regards their social structures, the species were divided into three groups based on previous studies (Clutton-Brock & Harvey, 1977, 1980; Eisenberg et al., 1972; Wilson, 1975; Wrangham, 1987): namely, solitary; monogynous (i.e. monogamous and presumed polyandrous); and polygynous (multi-female) (i.e. one-male multi-female and multi-male multi-female). The species were grouped into congeneric groups in which congeneric species shared common ecological and social parameters, as in previous studies (Clutton-Brock & Harvey, 1977, 1980; Mace et al., 1980) (cf. Table 1).

In the assessment of the degree of neocortical development, to control phylogenetic affinity and the effects of brain size, the relative size of the neocortex (RSN) of a given congeneric group in each superfamily of primates was measured based on the allometric relationships between neocortical volume (NV, in mm^3) and brain weight (E, in g) for each superfamily. The allometric equation between NV and E for a superfamily can, in general, be expressed as follows:

$$NV = k \times E^a,$$

where k and a are constants for the superfamily. Thus,

$$\log NV = a \times \log E + \log k.$$

The allometric equation for each superfamily was obtained by regression analysis (the correlation coefficient between NV and E exceeded 0.98, $p<0.01$, for every superfamily, t-test). Only regression analysis was employed, since there is very little difference between the results yielded by regression, reduced-major axis or major-axis when the correlation is high ($r>0.97$). Based on the allometric equation, RSN was estimated as follows:

$$\text{RSN (for a congeneric group)} = \log NV - (a \times \log E + \log k).$$

In the equation, a and k are the constants for the superfamily to which the congeneric group belongs. RSN was, thus, independent of the effects of brain size and was indicative of the degree of neocortical development within each superfamily. RSN was also independent of body size ($p>0.2$, n.s., for every superfamily, t-test).

In the case of prosimians, we examined the relationship between RSN and the social structure for the infraorder Lemuriformes, since this infraorder includes congeneric groups with different social structures. The second infraorder of prosimians, namely, the Lorisiformes, includes only solitary groups, so that the species belonging to this infraorder were excluded from the analysis. Furthermore, among the prosimian species sampled, only one species was monogynous, only two species were polygynous, and more numerous species were solitary (see Table 1). Therefore, for prosimians, the monogynous congeneric group and polygynous congeneric groups were pooled together into "troop-making" congeneric groups. In the case of anthropoids, two superfamilies, namely the Ceboidea and Hominoidea, were investigated, since these superfamilies included both monogynous and polygynous congeneric groups in the present sample. All of the sampled species of the Cercopithecoidea were polygynous, so that these species were excluded from the analysis. Furthermore, since differences in diet have been shown to be closely related to differences in brain size (CLUTTON-BROCK & HARVEY, 1980; MACE et al., 1980), we examined the relationship between the RSN and social structure only for frugivorous groups of anthropoids, to control the effects of diet. Standard values for the troop sizes were obtained from data recently accumulated in the field (CLUTTON-BROCK & HARVEY, 1977, 1980; GOLDIZEN, 1987; ROBINSON et al., 1987), and they were normalized by logarithmic transformation. Table 1 shows the congeneric groups of the Lemuriformes, Ceboidea, and Hominoidea, which were used in the present study.

RESULTS

The relationships between the relative size of the neocortex (RSN) and the differences in social structure were examined in 9 congeneric groups of prosimians and 14 frugivorous congeneric groups of anthropoids (see Table 1). In the case of prosimians, solitary congeneric groups revealed a significantly smaller RSN than "troop-making" congeneric groups, as shown in Table 2 (analysis of variance, $F = 6.376$, $df = 1, 7$, $p<0.05$). Among the congeneric groups of prosimians, the polygynous congeneric group of *Lemur* revealed the largest RSN (Table 1). RSN was not related to diet or timing of activity in this superfamily (analysis of variance, $p>0.1$, n.s. in every case). Furthermore, in prosimians, there was a significant, positive correlation between RSN and troop size ($r = 0.697$, $df = 7$, $t = 2.574$, $p<0.05$, t-test).

Table 2. Relative size of the neocortex in different social groups in primates.

	Relative size of neocortex				
	Mean	S.D.	*F*-value	*df*	
Prosimians[1]					
"Troop-making"	0.016	0.015 ($N = 3$)	6.376	1, 7	$p<0.05$
Solitary	−0.008	0.013 ($N = 6$)			
Anthropoids[2]					
Polygynous	0.014	0.011 ($N = 5$)	10.147	1, 11	$p<0.01$
Monogynous	−0.004	0.006 ($N = 8$)			

N: Number of congeneric groups examined. 1) Congeneric groups of the Lemuroidea; 2) congeneric groups of frugivorous species in the Ceboidea and Hominoidea.

In the case of the anthropoids studied, polygynous/frugivorous groups demonstrated a significantly larger RSN than monogynous/frugivorous groups of the Ceboidea and Hominoidea (analysis of variance, $F = 10.147$, $df = 1, 11$, $p<0.01$); both superfamilies include both groups, as shown in Table 2. The superfamily of the Ceboidea includes a considerable number of both monogynous/frugivorous groups ($N = 7$) and polygynous/frugivorous groups ($N = 4$). When only this superfamily was examined, it was also found that polygynous/frugivorous groups revealed a significantly larger RSN than monogynous/frugivorous groups ($F = 6.468$, $df = 1, 9$, $p<0.05$). Among the congeneric groups of the Ceboidea, the polygynous/fruigivorous congeneric group of *Saimiri* showed the largest RSN, followed by that of *Cebus*. Furthermore, the family of the Cebidae includes a considerable number of both monogynous/frugivorous groups ($N = 3$) and polygynous/frugivorous congeneric groups ($N = 4$). In this family, the polygynous/frugivorous groups revealed a significantly larger RSN than monogynous/frugivorous groups ($F = 8.308$, $df = 1, 5$, $p<0.05$). In addition, for frugivorous congeneric groups of the Ceboidea, a significant, positive correlation between RSN and troop size was observed ($r = 0.814$, $t = 4.196$, $df = 9$, $p<0.01$, t-test).

DISCUSSION

The relative size of the neocortex (RSN) appears to be closely associated with social structure in both prosimians and anthropoids. This association is not the consequence of any relationships between the relative size of the neocortex and activity timing or diet. Since all of the species of the Ceboidea examined were arboreal, the effects of the stratification on the RSN were excluded from the results for the Ceboidea. Furthermore, since RSN was measured for each superfamily, any phylogenetic bias arising from differences in allometric relationships between the size of the neocortex and size of the brain among the different taxa did not contribute to the present results (cf. CLUTTON-BROCK & HARVEY, 1980; MACE et al., 1980). The present analysis is, thus, the first to provide quantitative evidence that neocortical development is associated with differences in social structure among primates.

The present data suggest that the neocortex is more fully developed in "troop-making" prosimians and polygynous anthropoids than in solitary prosimians and monogynous anthropoids, respectively. Consistent with this hypothesis, neuroanatomical studies have demonstrated that "troop-making" prosimians of *Lemur* (polygynous) have more developed neocortical areas than solitary prosimians of *Lepilemur* (ZILLES et al., 1982), and monogynous monkeys of *Saguinus* have a more primitive neocortex than the anthropoid monkeys examined (CARLSON et al., 1986). Almost all of the Old World monkeys are polygynous, and it has been shown that the neocortices of Old World monkeys are more fully developed than those of monogynous species of New World monkeys, such as *Callithrix* (JERISON, 1973; PASSINGHAM, 1973; CARLSON et al., 1986). Furthermore, neocortical areas are present in monkeys, namely, the prefrontal and temporal cortices, that are known to be involved in social behaviors such as recognition of faces and vocalization, allogrooming, and maternal behaviors (MYERS, 1972; FRAZEN & MYERS, 1973; MYERS et al., 1973; PERRETT et al., 1982; BAYLIS et al., 1985; HEFFNER & HEFFNER, 1986). These cortices are known to be critical for the maintenance of social bonds and affiliative behavior in polygynous species of anthropoids (for review, see KLING, 1986). The prefrontal cortex is more widely expanded in polygynous monkeys, such as *Macaca*, *Papio*, and *Cebus*, than in monogynous monkeys of *Callithrix* (cf. PASSINGHAM, 1973). Polygynous prosimians of *Lemur* have wider prefrontal cortices than solitary prosimians of *Cheirogaleus*, and the prefrontal cortex of polygynous apes of *Pan* is wider than that of monogynous apes of *Hylobates* (PASSINGHAM, 1973). "Troop-making" prosimians may have more complex social interactions than solitary prosimians, and polygynous monkeys may be involved in complex social interactions, for example affiliative behaviors, rank-order systems, social bonds, and social communication (e.g. CHENEY et al., 1986; DE WAAL, 1987; WRANGHAM, 1987). It has been suggested that monogyny represents a more advanced social structure than the solitary state, and polygyny represents a more advanced society than monogyny (CROOK & GARTLAN, 1966; EISENBERG et al., 1972; WILSON, 1975; EISENBERG, 1981). Furthermore, RSN was positively and significantly correlated with troop size in the Lemuriformes and Ceboidea, and it has been suggested that more advanced social structures of primates are associated with larger sizes of troops (CROOK & GARTLAN, 1966; EISENBERG et al., 1972; WILSON, 1975; RICHARD, 1985). It seems likely, therefore, that the development of social interactions may have been associated with the development of the neocortex, in particular, the prefrontal cortex in primates. This supports the recently proposed hypothesis that social interactions may act as selection pressures on some morphological characters such as of the brain in primates (SAWAGUCHI & KUDO, 1987, submitted for publication), although it should be noted that comparative investigations like the present study cannot reveal causal relationships (cf. ENDLER, 1986).

As has been suggested, hominids have developed their neocortices fully, and have been polygynous (FALK, 1987; FOLEY, 1987; HOLLOWAY, 1974; LOVEJOY, 1981; MARTIN & MAY, 1981). The prefrontal cortex, which is known to be responsible for social interactions, is the most widely expanded in humans among primate species (PASSINGHAM, 1973; FUSTER, 1980; STUSS & BENSON, 1986). We can reasonably assume, therefore, that social factors or interactions associated with polygyny, such as social bonds and social communication, have been associated with the development of the neocortex, in particular the prefrontal cortex, during hominid evolution.

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