

Toshiyuki Sawaguchi

Department of Neurophysiology,  
Primate Research Institute, Kyoto  
University, Inuyama, Japan

# The Size of the Neocortex in Relation to Ecology and Social Structure in Monkeys and Apes

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## Key Words

Neocortex  
Allometry  
Diet  
Social structure  
Polygyny  
Monogyny  
Monkeys  
Apes  
Brain size

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## Abstract

In an attempt to reveal factors associated with neocortical development in monkeys and apes (anthropoids), relationships between the relative size of the neocortex and differences in ecology and social structure were examined for 24 genera of 11 subfamilies. Relative sizes of the neocortex (RSNs) in a given group were assessed as the difference between actual neocortical volume and the volume expected from an allometric relationship between neocortical volume and the volume of the rest of the brain. We found that RSNs are related to diet and social structure: frugivorous anthropoids had higher values of RSNs than folivorous anthropoids, and polygynous anthropoids had significantly higher values of RSNs than monogynous anthropoids. Furthermore, RSNs were positively correlated with the size of the troop. These results suggest that development of the neocortex is associated with both diet and social structure in anthropoids.

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## Introduction

The neocortex has developed considerably during primate evolution, and monkeys and apes (anthropoids) have particularly well-developed neocortices [1-9]. However, little is known about factors that may have influenced the phylogenetic development of the neocortex in anthropoids. One possible factor is diet, as: (1) it has been repeatedly demon-

strated that brain size relative to body size is related to diet in primates generally [10-12]; (2) increase in brain size is usually associated with increase in cortical size among mammals [13, 14], and (3) there are neocortical areas, such as parietal and premotor cortical areas, that are involved in visuospatial functions and sensorimotor coordinations that may be critical for foraging behaviours. Indeed, Gibson [15] demonstrated that 'neocortical pro-

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Toshiyuki Sawaguchi, PhD  
Department of Neurophysiology  
Primate Research Institute  
Kyoto University  
Inuyama, Aichi 484 (Japan)

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gression indices' (ratios between actual neocortical size and the size predicted for a basal insectivore of similar body size) are associated with differences in diet among anthropoids.

It should be noted, however, that previous studies of relationships between brain size and ecology have examined predominantly the size of the brain or neocortex relative to body size [10–12, 15]. It is possible that the relationship between diet and the size of the brain or neocortex relative to body size simply reflects the fact that different diets are associated with different sizes in digestive organs and/or skeletal muscles. Although Clutton-Brock and Harvey [10] used body length to control this problem and got results similar to those with body weight, it is still possible that body length may be correlated with the size of digestive organs. First of all, these studies cannot examine the relative allocation of brain materials to different brain functions, although they would be useful to throw light on the relative allocation of body resources to the brain. By contrast to these studies, Armstrong et al. [16] calculated sizes of specific brain components (anterior thalamic nuclei) relative to *brain size* and examined relationships between these sizes and ecological factors in anthropoids. Similar measures for the neocortex, namely sizes of the neocortex relative to the size of the rest of brain, would be useful for revealing ecological factors associated with the extent of neocortical development in anthropoids, but no one has examined such measures.

In 1980, Clutton-Brock and Harvey [10] reported that the size of the brain relative to body size tended to be related to social structure in primates. More recently, Armstrong et al. [16] demonstrated that the size of a thalamic nucleus relative to brain size was related to social structure in anthropoids. The neocortex of anthropoids contains areas, such

as prefrontal and temporal cortices, which are closely associated with social interactions [17–22]. It is hence possible that social structures are specifically related to the degree of neocortical development, but there have been few systematic studies that examine relationships between neocortical size and social structure.

The aim of the present study was to reveal ecological and social factors that are associated with the relative development of the neocortex in anthropoids. We focused on anthropoids, because (1) anthropoids have highly developed neocortices, (2) several analytical approaches have demonstrated that neocortical areas differ in structure and function between prosimians and anthropoids [1, 2, 4, 5, 7, 8, 23, 24] and (3) it is difficult to control for taxonomic effects if prosimians and anthropoids are analysed together.

We calculated three measures (RSN-1, RSN-2 and RSN-3) based on allometric equations relating neocortical size to the size of the rest of the brain. The relative size of the neocortex (RSN-1) is the difference between the actual neocortical volume and the volume expected from the allometric equation determined for all anthropoid species. It has been shown, however, that allometric relationships between body size, brain size and the size of brain parts in primates differ among taxa [10, 24–26]. Therefore, it may be necessary to control for the effects of phylogenetic affinity, also referred to as taxonomic effects [10, 12, 27–30]. Allometric relationships in primates differ considerably between superfamilies [25–27, see also Methods section]. We therefore calculated the second RSN (RSN-2) which was based on the allometric equation for individual superfamilies. In primates, numbers of congeneric species are generally too small to permit analysis at the species level, and congeneric species usually have similar ecologies and social structures. Therefore,

analyses at the generic level, combining congeneric species that share a common ecology or social structure, are favoured, as in a number of other comparative studies [10, 12, 28]: values of RSN-1 and RSN-2 were calculated at the generic level. In addition, it has been suggested that analyses at the level of subfamily are also adequate for controlling the taxonomic effect in the case of primates [11]. Therefore, we calculated the third RSN (RSN-3) at the level of subfamily based on the allometric equation among all subfamilies.

When all RSNs are associated with a certain ecological factor, we can conclude with some confidence that such a factor is associated with the neocortical development of anthropoids. Anthropoids can be grouped on the basis of diet, stratification and social structure [10, 28]. We therefore examined the relationships between RSNs and these ecological and social factors in anthropoids at the generic level (for RSN-1 and RSN-2) as well as at the level of subfamily (RSN-3).

## Methods

Table 1 lists the basic data used. Values for neocortical volume ( $\text{mm}^3$ ), body weight (g) and total brain volume ( $\text{mm}^3$ ) of adults were taken from Stephan et al. [31]. Data for neocortical volume include white matter with neocortex and exclude schizocortex, paleocortex and archicortex. Data were available for a total of 26 species from 24 genera of 11 subfamilies belonging to three superfamilies: Ceboidea, Cercopithecoidea and Hominoidea. The classification of subfamilies was the same as that by Harvey et al. [11], and when a subfamily is the only one in its family, we refer to it by the family name. Values for sizes of troops and home ranges (ha) of these species were obtained from recent reviews of field studies [10, 28, 32]. Sizes of home range and troop for each genus were normalized by logarithmic transformation, as was done by Clutton-Brock and Harvey [10].

Classification of ecological categories and social structures was conducted following Clutton-Brock and Harvey [10, 28], Eisenberg et al. [33], Napier and

Napier [34] and Smuts et al. [32]. Species were divided into two categories by diet: (1) frugivorous species (including the 'frugivorous-omnivorous' species of Eisenberg et al. [33]), with a diet composed predominantly of fruits but also including other kinds of food, such as leaves and insects, and (2) folivorous species, whose primary food is leaves. Species were also divided into two categories for stratification: (1) arboreal species, which primarily use forest habitats and (2) terrestrial species (including the 'semiterrestrial' species of Eisenberg et al. [33]), inhabiting open country, forest edges and/or the forest floor. Finally, with respect to social structure, species were again divided into two categories: (1) monogynous (single-female) species and (2) polygynous (multi-female) species. Monogynous species include monogamous species (such as species of *Aotus* and *Hylobates*) and reportedly polyandrous species (such as species of *Saguinus* and *Callithrix*). Although polygynous species include single-male, multi-male and variable-male polygynous forms, they were pooled because some species show a range of social structure (from single-male polygynous to multi-male polygynous) and because distinction between these three types is not clear-cut.

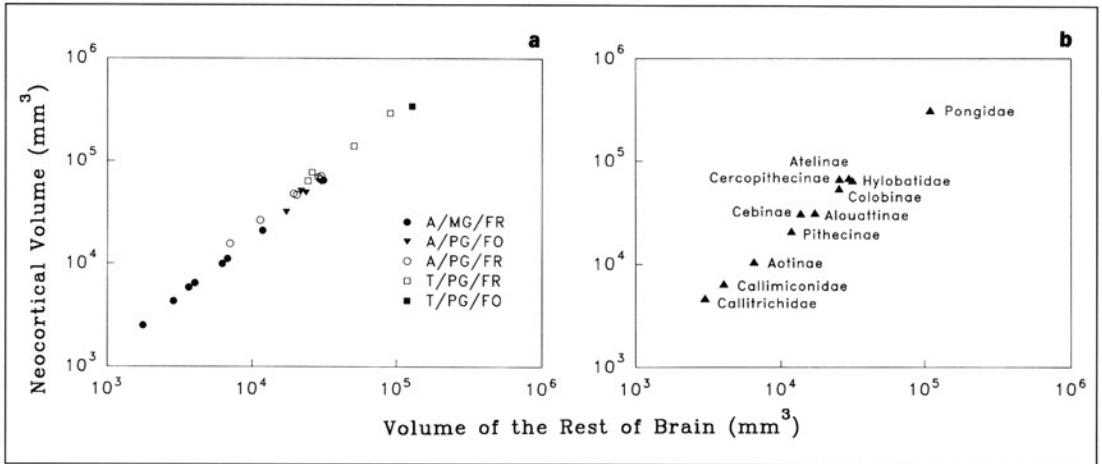
Neocortical volume showed an allometric relationship with volume of the rest of brain as shown in figure 1. Although these two values and body weight were correlated with each other, the multiple-regression analysis revealed that neocortical volume is predominantly dependent on volume of the rest of brain rather than body weight (table 2). RSN-1, RSN-2 and RSN-3 were calculated on the basis of the allometric relationship between neocortical volume and volume of the rest of brain, established by major-axis analysis. Major-axis was used, because, in contrast to regression analysis, it assumes that error is present in both variables in equal amounts. Regression analysis assumes that there is no error in X variables. In fact, however, there is very little difference between results yielded by regression, reduced major axis or major axis when the correlation is high ( $r > 0.97$ ). Table 3 shows coefficients and exponents of the allometric equations for all anthropoids together and for individual superfamilies. RSN-1 (at the generic level) and RSN-3 (at the subfamily level) were taken as the residual values defined from the equations for all anthropoids, and RSN-2 (at the generic level) was done so for individual superfamilies. Values of all RSNs were independent of body weight, as shown in table 4. Differences in values of these RSNs between different ecological and social groups were examined by analysis of variance.

**Table 1.** Body weight (P), total brain volume (TV), neocortical volume (NV), troop size (TS) and home range size (HRt) for the anthropoid species examined

	P, g	TV, mm <sup>3</sup>	NV, mm <sup>3</sup>	TS	HRt, ha
<b>Ceboidea</b>					
<b>Callitrichidae</b>					
<i>Callithrix jacchus</i>	280	7,241	4,371	5	13
<i>Cebuella pygmaea</i>	140	4,302	2,535	6	0.3
<i>Saguinus oedipus</i>	380	9,537	5,894	6.5	21
<i>Saguinus tamarin</i>	340	9,569	5,883	–	–
<b>Callimiconidae</b>					
<i>Callimico goeldii</i>	480	10,510	6,479	9	45
<b>Aotinae</b>					
<i>Aotus trivirgatus</i>	830	16,195	9,950	3.8	10
<i>Callicebus moloch</i>	900	17,944	11,163	3	4.2
<b>Pitheciinae</b>					
<i>Pithecia monacha</i>	1,500	32,867	21,028	3.6	7
<b>Alouattinae</b>					
<i>Alouatta</i> sp.	6,400	49,009	31,660	10 <sup>1</sup>	26 <sup>1</sup>
<b>Atelinae</b>					
<i>Ateles geoffroyi</i>	800	101,034	70,856	12	60
<i>Lagothrix lagotricha</i>	5,200	95,503	65,873	35	400
<b>Cebinae</b>					
<i>Cebus</i> sp.	3,100	66,939	46,429	21 <sup>1</sup>	100 <sup>1</sup>
<i>Saimiri sciureus</i>	660	22,572	15,541	40	58
<b>Cercopithecoidea</b>					
<b>Cercopithecinae</b>					
<i>Macaca mulatta</i>	7,800	87,960	63,482	40	530
<i>Cercocebus albigena</i>	7,900	97,603	68,733	15	227
<i>Papio anubis</i>	25,000	190,957	140,142	64	596
<i>Cercopithecus mitis</i>	6,300	70,505	49,933	15	21
<i>Cercopithecus ascanius</i>	3,400	63,505	45,166	23	24
<i>Miopithecus talapoin</i>	1,200	37,776	26,427	70	120
<i>Erythrocebus patas</i>	7,800	103,167	77,141	28	4,200
<b>Colobinae</b>					
<i>Pygathrix nemaeus</i>	7,500	72,530	48,763	–	–
<i>Nasalis larvatus</i>	14,000	92,797	62,685	20	130
<i>Colobus badius</i>	7,000	73,818	50,906	41	67
<b>Hominoidea</b>					
<b>Hylobatidae</b>					
<i>Hylobates lar</i>	5,700	97,505	65,800	3.5	44
<b>Pongidae</b>					
<i>Pan troglodytes</i>	46,000	382,103	291,592	53	3,700
<i>Gorilla gorilla</i>	105,000	470,359	341,444	7	2,000

P, TV and NV from Stephan et al. [31]. TS and HRt from various field studies cited by Clutton-Brock and Harvey [10, 28] and Smuts et al. [32].

<sup>1</sup> Mean value for several species belonging to the same genus.



**Fig. 1.** Allometric relationships between neocortical volume and volume of the rest of the brain for anthropoid genera (**a**) and subfamilies (**b**). **a** Genera were grouped based on ecological category: stratification/social structure/diet: A = arboreal; T = terrestrial; MG = monogynous; PG = polygynous; FR = frugivorous; FO = folivorous.

**Table 2.** Correlation matrix of neocortical volume (NV, mm<sup>3</sup>), volume of the rest of brain (RV, mm<sup>3</sup>) and brain weight (P, g) and the results of the multiple-regression analysis

	log <sub>e</sub> RV	log <sub>e</sub> P	log <sub>e</sub> NV
All anthropoids (generic level, 24 genera) <sup>1</sup>			
log <sub>e</sub> RV	1.0		
log <sub>e</sub> P	0.986	1.0	
log <sub>e</sub> NV	0.996	0.977	1.0
All anthropoids (subfamily level, 11 subfamilies) <sup>2</sup>			
log <sub>e</sub> RV	1.0		
log <sub>e</sub> P	0.979	1.0	
log <sub>e</sub> NV	0.997	0.976	1.0

<sup>1</sup> The best-fit multiple-regression line: log<sub>e</sub> NV = 1.178 × log<sub>e</sub> RV – 0.980; standard partial-regression coefficients: 0.996 for RV, 0 for P.

<sup>2</sup> The best-fit multiple-regression line: log<sub>e</sub> NV = 1.177 × log<sub>e</sub> RV – 1.011; standard partial-regression coefficients: 0.997 for RV, 0 for P.

## Results

Values of RSNs, calculated for 24 genera of 11 subfamilies, are shown in table 5. We found that RSN-1 and RSN-2 were related to both diet and social structure. RSN-3 was related to social structure and tended to be related to diet, although in this case sample size was too small to permit sufficient statistical analyses. The results for RSN-1 were identical to those for RSN-2, so the results for RSN-1 are described only briefly here.

### *RSN-2 Values*

RSN-2 was calculated for individual superfamilies, and the superfamilies contained genera with different ecologies and/or social structures. In the case of diet, all three superfamilies (Ceboidea, Cercopithecoidea and Hominoidea) included both folivorous genera and frugivorous genera (table 5). Frugivorous genera showed significantly higher values of RSN-2 than folivorous genera ( $p < 0.001$ ;

**Table 3.** Exponent, coefficient and correlation coefficient for the allometric relationships between neocortical volume (NV, mm<sup>3</sup>) and volume of the rest of brain (RV, mm<sup>3</sup>) for all anthropoids together and for the separate superfamilies ( $\log_e NV = \text{coefficient} + \text{exponent} \times \log_e RV$ )

Group	n	r	Exponent	Coefficient	SD
All anthropoids	24	0.996	1.184	-1.062	0.023
Ceboidea	12	0.997	1.165	-0.895	0.031
Cercopithecoidea	9	0.965	1.135	-0.484	0.117
Hominoidea	3	0.988	1.249	-1.822	0.199
All anthropoids	11 <sup>1</sup>	0.997	1.181	-1.046	0.030

r = Correlation coefficient; n = number of genera.

<sup>1</sup> Number of subfamilies.

table 6). As the superfamily Cercopithecoidea included adequate numbers of both frugivorous (n = 6) and folivorous genera (n = 3), we were able to examine differences in RSN-2 within this superfamily. We found that frugivorous genera showed significantly higher values of RSN-2 than folivorous genera ( $F = 15.853$ , d.f. = 1, 7,  $p \leq 0.01$ ).

As genera with a given diet could differ in social structure and/or stratification, it is necessary to exclude the effects of social structure and/or stratification. Most genera examined were polygynous and/or arboreal. We found that frugivorous/polygynous groups and frugivorous/arboreal/polygynous groups showed significantly higher values of RSN-2 than folivorous/polygynous ( $p \leq 0.001$ ) and folivorous/arboreal/polygynous groups ( $p \leq 0.01$ ), respectively (table 6).

Both polygynous and monogynous genera are found in Ceboidea and Hominoidea (table 5), so the relationship between RSN-2 and social structure could be analysed for these two superfamilies. There were no significant differences between polygynous and monogynous groups (table 6). However, as diet was

**Table 4.** Correlation coefficients and their levels of significance for relationships between RSNs and body weight

	r	t value	d.f.
<b>RSN-1</b>			
All anthropoids	-0.043	0.200	22
Ceboidea	-0.286	0.947	10
Cercopithecoidea	-0.379	1.083	7
Hominoidea	0.223	0.229	1
<b>RSN-2</b>			
All anthropoids	-0.121	0.570	22
Ceboidea	-0.161	0.517	10
Cercopithecoidea	-0.253	0.692	7
Hominoidea	-0.129	0.130	1
<b>RSN-3</b>			
All anthropoids	-0.047	0.142	11
Ceboidea	-0.311	0.732	7

r = Correlation coefficient. No significant differences were found at the 5% level.

**Table 5.** Values of the RSNs for anthropoid genera and sub-families

	Category	RSN-1	RSN-2	RSN-3
<b>Ceboidea</b>				
Callitrichidae				
	<i>Callithrix</i>	A/MG/FR	-0.018	-0.001
	<i>Cebuella</i>	A/MG/FR	0.009	0.019
	<i>Saguinus</i>	A/MG/FR	-0.008	0.012
Callimiconidae				
	<i>Callimico</i>	A/MG/FR	-0.026	-0.005
Aotinae				
	<i>Aotus</i>	A/MG/FR	-0.111	-0.085
	<i>Callicebus</i>	A/MG/FR	-0.093	-0.066
Pitheciinae				
	<i>Pithecia</i>	A/MG/FR	-0.116	-0.082
Alouattinae				
	<i>Alouatta</i>	A/PG/FO	-0.157	-0.118
Atelinae				
	<i>Ateles</i>	A/PG/FR	-0.004	0.042
	<i>Lagothrix</i>	A/PG/FR	-0.055	-0.009
Cebinae				
	<i>Cebus</i>	A/PG/FR	0.028	0.070
	<i>Saimiri</i>	A/PG/FR	0.195	0.223
<b>Cercopithecoidea</b>				
Cercopithecinae				
	<i>Macaca</i>	T/PG/FR	0.136	0.079
	<i>Cercocebus</i>	A/PG/FR	0.178	-0.033
	<i>Papio</i>	T/PG/FR	0.064	0.038
	<i>Cercopithecus</i>	A/PG/FR	0.113	0.045
	<i>Miopithecus</i>	A/PG/FR	0.162	0.071
	<i>Erythrocebus</i>	T/PG/FR	0.256	0.202
Colobinae				
	<i>Pygathrix</i>	A/PG/FO	-0.096	-0.155
	<i>Nasalis</i>	A/PG/FO	-0.124	-0.173
	<i>Colobus</i>	A/PG/FO	-0.010	-0.071
<b>Hominoidea</b>				
Hylobatidae				
	<i>Hylobates</i>	A/MG/FR	-0.136	-0.025
Pongidae				
	<i>Pan</i>	T/PG/FR	0.117	0.154
	<i>Gorilla</i>	T/PG/FO	-0.142	-0.130

Category according to stratification/social structure/diet: A = arboreal; T = terrestrial; MG = monogynous (i.e. single-female; monogamous plus presumed polyandrous); PG = polygynous (i.e. multi-female); FR = frugivorous; FO = folivorous.

**Table 6.** RSN-2 (means  $\pm$  SD) in different ecological and social groups, calculated from allometric relationships for separate anthropoid superfamilies

RSN-2		F value	Superfamilies
<i>Diet</i>			
FR (n = 19) 0.034 $\pm$ 0.086	FO (n = 5) -0.129 $\pm$ 0.039	F(1, 22) = 16.675***	CEB + CER + HOM
FR/PG (n = 11) 0.080 $\pm$ 0.081	FO/PG (n = 5) -0.129 $\pm$ 0.039	F(1, 14) = 29.342***	CEB + CER + HOM
FR/A/PG (n = 7) 0.058 $\pm$ 0.082	FO/A/PG (n = 4) -0.097 $\pm$ 0.063	F(1, 9) = 17.228**	CEB + CER
<i>Social structure</i>			
PG (n = 8) 0.033 $\pm$ 0.131	MG (n = 8) -0.029 $\pm$ 0.042	F(1, 13) = 1.621 (n.s.)	CEB + HOM
PG/FR (n = 5) 0.096 $\pm$ 0.092	MG/FR (n = 8) -0.029 $\pm$ 0.042	F(1, 11) = 11.319**	CEB + HOM
PG/FR/A (n = 4) 0.081 $\pm$ 0.100	MG/FR/A (n = 7) -0.030 $\pm$ 0.046	F(1, 9) = 6.657*	CEB
<i>Stratification</i>			
T (n = 5) 0.068 $\pm$ 0.127	A (n = 7) -0.049 $\pm$ 0.092	F(1, 10) = 3.430 <sup>+</sup>	CER + HOM
T/FR (n = 4) 0.118 $\pm$ 0.073	A/FR (n = 4) 0.015 $\pm$ 0.051	F(1, 6) = 5.328 <sup>+</sup>	CER + HOM
T/FR/PG (n = 3) 0.105 $\pm$ 0.085	A/FR/PG (n = 3) 0.028 $\pm$ 0.054	F(1, 4) = 1.808 (n.s.)	CER

FR = Frugivorous; FO = folivorous; PG = polygynous; MG = monogynous; T = terrestrial; A = arboreal; CEB = Ceboidea; CER = Cercopithecoidea; HOM = Hominoidea; n = number of genera examined.

\*  $p \leq 0.05$ ; \*\*  $p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ ; n.s. = not significant at the 5% level; <sup>+</sup> = not significant but  $p \leq 0.1$ .

associated with RSN-2, it is necessary to exclude the effects of diet. Frugivorous genera included considerable numbers with the two different types of social structure. We found that polygynous/frugivorous genera showed significantly higher values of RSN than monogynous/frugivorous genera for Ceboidea and Hominoidea combined ( $p \leq 0.01$ ; table 6). A similar relationship was found among arboreal genera: polygynous/frugivorous/arboreal genera showed significantly higher values of RSN-2 than monogynous/frugivorous/arboreal genera ( $p \leq 0.05$ ; table 6). When we considered only Ceboidea, a superfamily including adequate numbers of both

monogynous/frugivorous/arboreal genera ( $n = 7$ ) and polygynous/frugivorous/arboreal genera ( $n = 4$ ), we also found that polygynous/frugivorous/arboreal genera showed significantly higher values of RSN-2 than monogynous/frugivorous/arboreal genera ( $F = 6.657$ , d.f. = 1, 9,  $p \leq 0.05$ ). Furthermore, when we consider only the family Cebidae, which included both monogynous/frugivorous/arboreal genera ( $n = 3$ ) and polygynous/frugivorous/arboreal genera ( $n = 4$ ), we again found that the polygynous/frugivorous/arboreal genera showed significantly higher values of RSN-2 than the monogynous/frugivorous/arboreal genera ( $F = 7.178$ , d.f. = 1, 5,  $p \leq 0.05$ ).



**Table 7.** RSN-1 (means  $\pm$  SD) in different ecological and social groups of anthropoids

RSN-1		F value
<i>Diet</i>		
FR (n = 19) 0.029 $\pm$ 0.111	FO (n = 5) -0.106 $\pm$ 0.058	F(1, 22) = 6.623 <sup>+</sup>
FR/PG (n = 11) 0.094 $\pm$ 0.093	FO/P (n = 5) -0.106 $\pm$ 0.058	F(1, 14) = 19.158***
FR/A/PG (n = 7) 0.065 $\pm$ 0.093	FO/A/PG (n = 4) -0.097 $\pm$ 0.063	F(1, 9) = 9.515*
<i>Social structure</i>		
PG (n = 16) 0.031 $\pm$ 0.126	MG (n = 8) -0.062 $\pm$ 0.057	F(1, 22) = 3.951 <sup>+</sup>
PG/FR (n = 11) 0.094 $\pm$ 0.093	MG/FR (n = 8) -0.062 $\pm$ 0.057	F(1, 17) = 17.474***
PG/FR/A (n = 7) 0.041 $\pm$ 0.108	MG/FR/A (n = 8) -0.062 $\pm$ 0.057	F(1, 13) = 10.608**
<i>Stratification</i>		
T (n = 5) 0.143 $\pm$ 0.081	A (n = 19) 0.065 $\pm$ 0.093	F(1, 9) = 1.959 (n.s.)
T/FR (n = 4) 0.143 $\pm$ 0.081	A/FR (n = 15) -0.003 $\pm$ 0.098	F(1, 17) = 7.385 (n.s.)
T/FR/PG (n = 4) 0.143 $\pm$ 0.081	A/PG/FR (n = 7) 0.065 $\pm$ 0.093	F(1, 9) = 1.959 (n.s.)

FR = Frugivorous; FO = folivorous; PG = polygynous; MG = monogynous; T = terrestrial; A = arboreal; n = number of genera examined. \*  $p \leq 0.05$ ; \*\*  $p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ ; n.s. = not significant at the 5% level; <sup>+</sup> = not significant but  $p \leq 0.1$ .

With respect to stratification, our sample of Cercopithecoidea and Hominoidea included both terrestrial and arboreal genera (table 5). For these superfamilies, values of RSN-2 did not differ significantly between terrestrial and arboreal genera. This remained the case when genera with the same diet and/or social structure were examined (table 6).

#### *RSN-1 Values*

Values of RSN-1 for different ecological groups are shown in table 7. The results were identical to those found with RSN-2. This is only to be expected as RSN-1 was signifi-

cantly and positively correlated with RSN-2 across anthropoids examined ( $r = 0.899$ ,  $t = 9.644$ ,  $p \leq 0.001$ ). Briefly, frugivorous genera showed significantly higher values of RSN-1 than folivorous genera when genera with the same social structure and/or stratification were examined. Furthermore, polygynous genera showed significantly higher values of RSN-1 than monogynous genera among frugivorous genera. There were no significant differences in values of RSN-1 between terrestrial and arboreal genera.

### RSN-3 Values

Two subfamilies (Cercopithecidae and Pongidae) contained species with different diet or stratification, and the number of subfamilies examined was very small ( $n = 11$ ). It was, therefore, hard to examine relationships between RSN-3 and ecological factors sufficiently. Nevertheless, we found that polygynous/frugivorous subfamilies showed significantly higher values of RSN-3 than monogynous/frugivorous subfamilies ( $p \leq 0.05$ ; table 8). Furthermore, all polygynous/frugivorous subfamilies ( $n = 3$ ) showed positive values of RSN-3, while all polygynous/folivorous subfamilies ( $n = 2$ ) showed negative values, although the sample size was very small and the difference between them did not reach significance level ( $\leq 0.1$ , n.s.; table 8).

### Correlations with Home Range Size and Troop Size

Table 9 shows correlation coefficients and their levels of significance between RSNs and home range size and troop size across all anthropoids and for the three individual superfamilies. There were no significant correlations between any RSN and home range size. With respect to troop size, RSN-1 and RSN-2 were significantly correlated with it across all anthropoids and for Ceboidea. The relationship between troop size and RSN-1 is shown in figure 2a, where troop size is plotted against value of RSN-1 for all anthropoid genera examined. When only frugivorous/arboreal genera of Ceboidea were considered, we also found significant correlations between RSN-1 and troop size ( $r = 0.702$ ,  $t = 2.955$ , d.f. = 9,  $p \leq 0.05$ ) and between RSN-2 and troop size ( $r = 0.792$ ,  $t = 3.898$ , d.f. = 9,  $p \leq 0.01$ ). Furthermore, RSN-3 was significantly correlated with troop size across all subfamilies (table 9, fig. 2b). The correlation coefficient between RSN-3 and troop size was high ( $r = 0.794$ ) among frugivorous/arboreal subfamil-

**Table 8.** RSN-3 (means  $\pm$  SD) in different ecological and social groups of anthropoids

RSN-3		F value
PG/FR ( $n = 3$ ) $0.105 \pm 0.069$	PG/FO ( $n = 2$ ) $-0.078 \pm 0.038$	$F(1, 3) = 7.087^+$
PG/FR ( $n = 3$ ) $0.105 \pm 0.069$	MG/FR ( $n = 5$ ) $-0.033 \pm 0.055$	$F(1, 6) = 7.313^*$

FR = Frugivorous; FO = folivorous; PG = polygynous; M = monogynous; n = number of subfamilies examined. \*  $p \leq 0.05$ ; + = not significant but  $p \leq 0.1$ .

ies of Ceboidea, although it did not reach significance level ( $t = 2.609$ , d.f. = 4,  $p \leq 0.1$ , n.s.).

### Discussion

The present study has demonstrated that the size of the neocortex relative to the rest of the brain is associated with both diet and social structure in anthropoids. Frugivorous genera showed significantly higher values of RSN-1 and RSN-2 than folivorous genera, and polygynous (multi-female) genera gave significantly higher values of these two RSNs than monogynous (single-female) genera among frugivorous genera. Similarly, frugivorous subfamilies tended to show higher values of RSN-3 than folivorous subfamilies, and polygynous/frugivorous subfamilies showed significantly higher values of RSN-3 than monogynous/frugivorous subfamilies. These findings are similar to those from previous studies that examined the relationship between ecology and the size of the brain relative to body size in primates [10–12].

All RSNs were independent of body weight. Furthermore, as RSN-2 was calculated for individual superfamily, there was

**Table 9.** Correlation coefficients and their levels of significance between the RSN and ecological variables for anthropoids

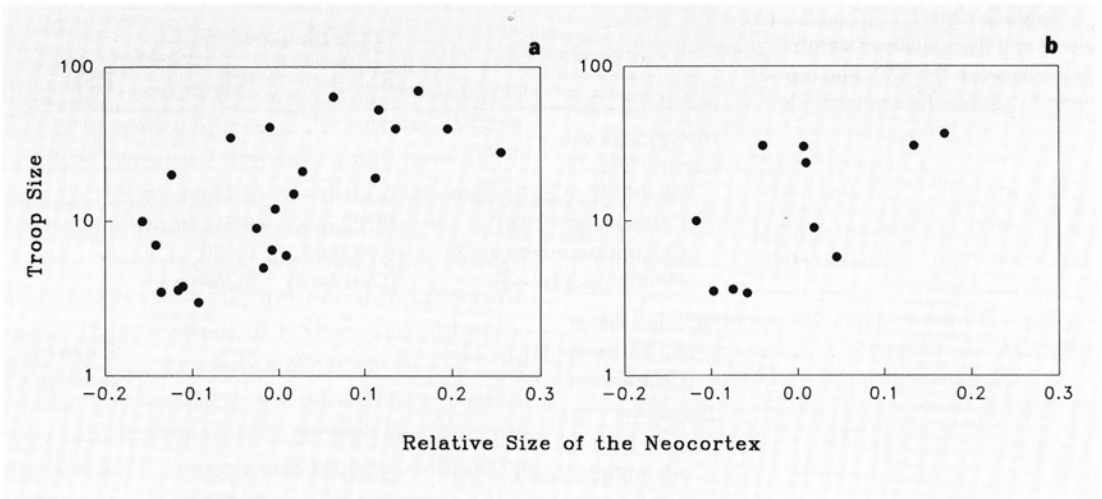
	Correlation coefficient		
	RSN-1	RSN-2	RSN-3
<i>Home range size</i>			
Generic level			
All anthropoids (n = 24)	0.381 <sup>+</sup>	0.319 (n.s.)	
Ceboidea (n = 12)	0.182 (n.s.)	0.311 (n.s.)	
Cercopithecoidea (n = 8)	0.493 (n.s.)	0.659 <sup>+</sup>	
Hominoidea (n = 3)	0.591 (n.s.)	0.364 (n.s.)	
Subfamily level			
All anthropoids (n = 11) <sup>1</sup>			0.486 (n.s.)
Ceboidea (n = 7) <sup>1</sup>			0.480 (n.s.)
<i>Troop size</i>			
Generic level			
All anthropoids (n = 24)	0.690***	0.525*	
Ceboidea (n = 12)	0.611*	0.709**	
Cercopithecoidea (n = 8)	0.315 (n.s.)	0.287 (n.s.)	
Hominoidea (n = 3)	0.964 (n.s.)	0.864 (n.s.)	
Subfamily level			
All anthropoids (n = 11) <sup>1</sup>			0.628*
Ceboidea (n = 7) <sup>1</sup>			0.613 (n.s.)
n = Number of genera examined. * p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001; n.s. = not significant at the 5% level; + = not significant but p ≤ 0.1.			
<sup>1</sup> Number of subfamilies examined.			

minimal phylogenetic bias. This is strengthened by the fact that RSN-3, which was examined at the level of subfamily, gave similar results to those from RSN-1 or RSN-2: analyses at this level have been suggested to be adequate for controlling taxonomic effects in primates [11]. RSNs are indicative of the extent of development of the neocortex relative to the rest of the brain. Passingham [6] demonstrated that size of the neocortex relative to the brain is closely associated with learning ability or intelligence in primates. RSNs may reflect number and/or size of neocortical components (such as intrinsic neurons, and neurons and fibres with corticocortical connections) that are specifically in-

involved in corticocortical information processing and are independent of the rest of the brain. Further studies are necessary, however, to identify the neocortical components reflected by RSNs.

#### *Possible Factors Associated with Neocortical Development*

*Diet.* Frugivorous anthropoids showed higher values of RSNs than folivorous anthropoids. Previous studies have demonstrated that frugivorous species have relatively larger brain sizes than folivorous species of primates [10–12]. The present findings expand on these studies, indicating that frugivorous anthropoids also have larger neocortices relative



**Fig. 2.** Troop size plotted against RSN for all anthropoid genera (RSN-1, **a**) and subfamilies (RSN-3, **b**).

to the rest of brain than do folivorous anthropoids.

The fact that frugivorous anthropoids have larger RSNs than folivorous anthropoids may be explained by the difference in metabolic turnover between these two groups, as both relative brain size and diet are closely related to basal metabolic rate in vertebrates [35–37]. Alternatively, it is possible that the difference in RSNs between frugivorous and folivorous species is due to difference between them in information processing by the neocortex. Frugivorous species are adapted to exploit foods in clumps which are distributed more widely and unevenly than foods of folivorous species. Hence, frugivorous species may need to store and process more complex spatial information than do folivorous species [1, 10, 12]. There are neocortical areas that play critical roles in the processing and memorizing of spatial information [38–40]. Furthermore, extrastriate visual areas, which process visual and spatial information, are more numerous in anthropoids than in prosimians [1, 2, 5, 9,

23]. Moreover, neocortical size is associated more closely with residual brain size than body size (table 2). It is likely that, whereas brain size relative to body size is related to the allocation of body resources to the brain, neocortical size relative to residual brain size is related to the allocation of brain material to neocortical functions. It is, thus, suggested that development of neocortical areas that are related to certain neocortical functions, namely, processing and memory of spatial information, may be associated with frugivory in anthropoids. Hence, the present findings may support a hypothesis that foraging strategy is a critical factor for the development of brains and associated with cognitive functions of primates [15, 41].

*Social Structure.* Polygynous anthropoids showed significantly higher values of RSNs than monogynous anthropoids among frugivorous anthropoids. A previous study indicated that monogynous primate species tend to have relatively smaller brains than polygy-

nous species [10]. The present finding agrees with this, suggesting that polygynous anthropoids have a more extensively developed neocortex than monogynous anthropoids.

Although some authors have suggested that there may be certain ecological differences, such as the extent of predation pressures, between polygynous and monogynous species, the influence of such differences is unclear [42–45]. However, there are very marked differences in social interactions between polygynous and monogynous species. It can be argued that polygynous species require more complex social interactions than monogynous species. Values of an index of social complexity are much higher for polygynous species than for monogynous species of anthropoids [46]. Furthermore, in polygynous anthropoid species, such as macaques and cercopithecines, there are neocortical areas such as prefrontal and temporal cortical areas that are involved in a variety of social interactions. Examples are the maintenance of social bonds, affiliative behaviours, and recognition of vocalization and faces [17–22, 47–50]. A neuro-anatomical study has demonstrated that some neocortical areas of *Saguinus* (monogynous) are less differentiated than those of Cebidae (such as *Saimiri* and *Cebus*) or Cercopithecoidea (such as *Macaca*) [51]. Moreover, RSNs were positively and significantly correlated with troop size across anthropoids. Taken together these findings suggest that social interactions may have developed in parallel with the development of the neocortex in anthropoids.

Strong, positive selection pressures seem to have favoured the development of the brain throughout primate evolution [13, 52]. There have been several attempts to establish the nature of such selection pressures, and some authors have suggested that selection pressures associated with social interactions may have favoured the development of the

brain in primates and, in particular, in hominids [53–55]. However, evidence to support this hypothesis has been scarce. We have demonstrated that RSNs are associated with social structures. Furthermore, Armstrong et al. [16] demonstrated that size of a certain thalamic nucleus relative to brain size is correlated with social structure in primates. Therefore, it is hypothesized that selection pressures associated with social interactions generally may have favoured evolutionary changes in certain morphological characters of anthropoid brains ('active selection hypothesis' [56]). It should be noted, however, that comparative studies such as the present investigation face problems with respect to the testing of causal relationships [57]. Further studies are required both to examine whether or not social interactions can act as selection pressures involved in evolutionary changes in primate brains and to reveal the nature of those social interactions.

#### *Multiple Factors Involving Neocortical Development*

Both diet and social interactions appear to be associated with the degree of neocortical development in anthropoids. The anthropoid neocortex consists of multiple, parallel circuitries which are involved in multiple, parallel functions. For example, one set of neocortical visual areas is closely associated with visuo-spatial information processing, whereas another set of visual areas is closely associated with the information processing of form and faces [9, 58–61]. Problems arising from foraging may differ from those associated with social interactions, and different neocortical circuitries may be responsible for solving different problems. For example, spatial ability and the neocortical circuitry associated with it may be more critical for foraging behaviours than for social interactions, and the capacity for recognition of faces and the neocortical

circuitry associated with this capacity may be more critical for social interactions than for foraging. It is, therefore, likely that multiple, parallel factors associated with diet and social interactions may have been associated with the development of multiple, parallel neocortical circuitries of anthropoids. This hypothe-

sis, termed here 'multiple-factor hypothesis for primate brain evolution', is supported by the present findings that both diet and social structure are related to the relative size of the neocortex in anthropoids, although further studies are required to confirm and expand it.

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