
Possible Involvement of Sexual Selection in Neocortical Evolution of Monkeys and Apes

Toshiyuki Sawaguchi

Department of Psychology, Hokkaido University, Sapporo, Japan

Key Words

Neocortex · Brain size · Allometry · Sexual dimorphism · Socionomic sex ratio · Sexual selection · Anthropoids

Introduction

Ever since Darwin [1], it has been speculated that sexual competition might play a role in the evolution of intelligence and the brain in monkeys and apes [2], but there has been no quantitative evidence to support this hypothesis. Recently, we demonstrated that the neocortex of monkeys and apes is relatively larger in polygynous (i.e. multifemale) than in monogynous (single female) monkeys and apes [3, 4]. Although this finding implies that sexual competition might be related to neocortical evolution in monkeys and apes, comparative studies using more appropriate indices of the degree of sexual competition are necessary to expand upon this finding. As indices, the degree of sexual dimorphism and the socionomic sex ratio (SSR) may be suitable for this purpose, as has been suggested by other authors [5, 6]. In the present study, we examined the correlations between the relative size of the neocortex and both the degree of sexual dimorphism and the SSR in monkeys and apes. We found that those which showed a higher degree of sexual dimorphism and a higher SSR have relatively larger neocortices, suggesting that intrasexual competition for mating may be involved in neocortical evolution.

Methods

Values for total brain volume and neocortical volume were available for a total of 27 species of monkeys and apes [7]. Body weights of females and males of these species were obtained from Harvey and Clutton-Brock [8]. Since previous studies have demonstrated that the relative sizes of the brain and neocortex are closely associated with diet [3, 8–12], and since most of the sampled species are frugivorous, only data for frugivorous species were considered (19 genera, 21 species). The numbers of adult females and adult males in these species which form a breeding troop were obtained from Smuts et al. [13]. Furthermore, since the number of congeneric species was too small to permit an analysis at the species level, the present analysis was performed at the genus level, as preferred in

Table 1. Monkey and ape genera examined and their RSN, the SDI [log (male body weight)/(female body weight)] and the SSR [log (number of adult females)/(number of adult males)]

Genus	RSN	SDI	SSR
<i>Callithrix</i>	0.083	0.016	0
<i>Cebuella</i>	0.049	0.058	NA
<i>Saguinus</i>	0.011	-0.006	-0.156
<i>Callimico</i>	-0.001	0.089	0.301
<i>Aotus</i>	-0.108	-0.036	0
<i>Callicebus</i>	-0.093	0.010	0
<i>Pithecia</i>	-0.133	0.058	0
<i>Ateles</i>	-0.049	0.022	0.445
<i>Lagothrix</i>	-0.099	0.069	0.018
<i>Cebus</i>	-0.005	0.100	0.376
<i>Saimiri</i>	-0.194	0.116	0.473
<i>Macaca</i>	0.098	0.225	0.404
<i>Cercocebus</i>	-0.025	0.148	0.271
<i>Papio</i>	0.004	0.187	0.273
<i>Cercopithecus</i>	0.081	0.201	0.190
<i>Miopithecus</i>	0.147	0.105	0.318
<i>Erythrocebus</i>	0.216	0.252	0.406
<i>Hylobates</i>	-0.182	0.012	0
<i>Pan</i>	0.039	0.126	0.352

NA=Not available.

previous studies [3, 5, 9, 12, 14]. The variables examined were averaged for congeneric species in each genus as has been done in previous studies [3, 9].

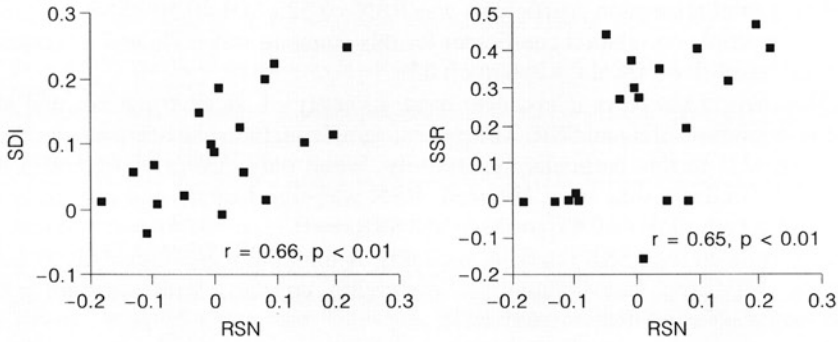
The relative size of the neocortex (RSN) in each genus was calculated from the difference between the exact neocortical volume (NV, mm³) and the neocortical volume expected by an allometric equation between NV and the remaining brain volume (RV, mm³) of the sampled genera. The allometric equation, examined by the major axis analysis, was as follows: $\log NV = 1.209 \times \log RV - 1.244$ (SD=0.03, $r=0.99$, $p<0.001$, t test). RSN was then calculated as: $RSN = \log NV - (1.209 \times \log RV - 1.244)$.

In addition, since our sample represented an adequate number of genera for New World monkeys, intrasuperfamily analysis was performed for this particular superfamily. In this superfamily, the allometric equation between NV and RV was $\log NV = 1.175 \times \log RV - 0.973$ ($r=0.99$, $p<0.001$). Therefore, RSN for this superfamily was calculated as: RSN (for Ceboidea) = $\log NV - (1.175 \times \log RV - 0.973)$.

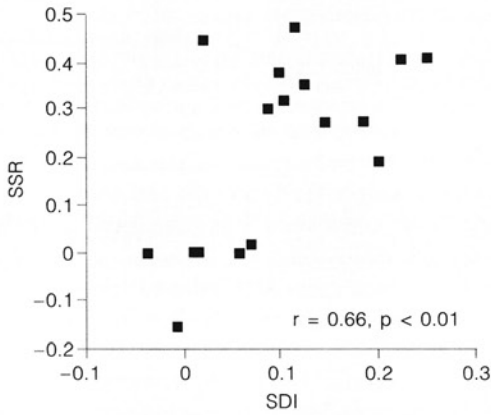
An index of sexual dimorphism (SDI) was defined as the ratio of body weight of adult males to that of adult females for each genus. The SSR was defined as the ratio of the number of adult females to that of adult males, among those adults which formed a breeding group. These SDI and SSR were normalized by logarithmic transformation as had been done in previous studies [3, 9]. Correlation across these values was examined by a regression analysis and multiple regression analysis. Table 1 shows RSN, SDI and SSR of the genera examined.

Results

The correlation between RSN and SDI was examined for 19 genera, and the correlation between RSN and SSR was examined for 18 genera. In figure 1, SDI (a) and SSR (b) are plotted against RSN. RSN was significantly and positively correlated with both SDI ($r=0.66$, $p<0.01$, t test) and SSR ($r=0.65$, $p<0.01$). Furthermore, SDI was



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Fig. 1. Relationships between the RSN and SDI (a) and the SSR (b) in monkey and ape genera. SDI and SSR were plotted against RSN. r = Correlation coefficient examined by a single regression analysis.

Fig. 2. Relationship between the SDI and SSR in monkey and ape genera. SSR was plotted against SDI. r = Correlation coefficient examined by a single regression analysis.

positively correlated with SSR ($r=0.66$, $p<0.01$) (fig. 2), which confirms previous findings by Clutton-Brock et al. [5] and Clutton-Brock and Harvey [14].

To control the effect of the interaction between SDI and SSR on the correlations between RSN and both SDI and SSR, we performed a multiple regression analysis for the 18 genera for which systematic data were available. The partial correlation coefficient was 0.44 for SDI and 0.36 for SSR. The best-fit multiple regression equation with standard partial regression coefficients was $RSN=0.45 \times SDI + 0.35 \times SSR$.

The multiple correlation coefficient was 0.73, and this equation was highly significant ($F=8.52$, d.f.=2, 15, $p<0.005$, Anova).

The genera examined included an adequate number of polygynous genera ($n=11$) for the statistical analysis. Thus the correlations between RSN and both SDI and SSR were examined for these genera. RSN was positively correlated with both SDI ($r=0.58$, $p<0.1$) and SSR ($r=0.54$, $p<0.1$), although neither correlation reached the statistically significant level of 5%. A multiple regression analysis revealed a significant correlation of RSN with SDI and SSR together. The partial correlation coefficient

was 0.62 for SDI and 0.60 for SSR. The best-fit multiple regression equation with standard partial regression coefficients was $RSN = 0.52 \times SDI + 0.50 \times SSR$.

The multiple correlation coefficient for this equation was 0.75, and this equation was significant ($F = 5.04$, $d.f. = 2, 8$, $p < 0.05$).

New World monkeys (Ceboidea) have a variety of social structures and show various degrees of SDI and SSR. The present sample included an adequate number of genera ($n = 11$) in this particular superfamily. When only genera of Ceboidea were examined, similar results were obtained: RSN was significantly and positively correlated with both SDI ($r = 0.63$, $p < 0.05$) and SSR ($r = 0.71$, $p < 0.05$), and SDI was positively correlated with SSR ($r = 0.66$, $p < 0.05$). A multiple regression analysis generated the following best-fit multiple regression equation with standard partial regression coefficient: $RSN = 0.69 \times SSR$.

The multiple correlation coefficient was 0.69, and this equation was significant ($F = 6.99$, $d.f. = 1, 7$, $p < 0.05$). SDI does not appear in this best-fit equation, since SDI was more closely correlated with SSR than with RSN in this case.

Discussion

The present study is the first to demonstrate that the relative size of the neocortex (RSN) of monkeys and apes is positively and significantly correlated with both the degree of sexual dimorphism in body weight (SDI) and the socionomic sex ratio (SSR). Since only frugivorous species were considered, it is considered unlikely that the close association between diet and the relative size of the brain or neocortex [3, 8–12] affected the present findings. Thus, the present data indicate that monkeys and apes which show a higher degree of sexual dimorphism in body weight and a higher SSR have relatively larger neocortices.

RSN is indicative of the amount of neocortical tissue which is independent of the allometric relationship between NV and RV and, hence, is also indicative of the relative extent of neocortical development. Indeed, the size of the neocortex relative to that of the brain is closely associated with learning ability or intelligence in primates [15]. The degree of sexual dimorphism has been demonstrated to be closely associated with the SSR in primates [5, 6, 14]. It has been argued that the degree of intrasexual competition for mating is stronger for a species which shows a higher degree of sexual dimorphism and a higher SSR [5, 6, 14]. Sexual dimorphism itself may evolve through sexual selection arising from intrasexual competition for mating [1, 16, 17], although sexual dimorphism is not always related to sexual selection [6].

Taken together, these findings suggest that intrasexual competition for mating, a form of sexual selection, may have been either directly or indirectly involved in the evolutionary expansion of the neocortex in monkeys and apes. Since several factors must have participated in shaping neocortical evolution, further studies are required to reveal critical factors other than sexual factors that may have been involved in neocortical evolution in monkeys and apes.

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