Gyrification in the Cerebral Cortex of Primates[1,2]

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Abstract. The degree of cortical folding in primates has been analyzed using a gyrification index (GI). Correlation analyses of the GI with body weight, brain weight and neopallial volume show that the human data fit the general trend of the nonhuman anthropoids. Bigger primate brains exhibit a higher degree of fissurization, but a taxonomic difference that is independent of brain weight between prosimians and anthropoids has also been observed. In these regressions, anthropoids differed from prosimians by having a larger increase in gyrification for every unit increase in body or brain weight or neopallial volume. A stepwise regression also shows a prosimian-anthropoid difference. The best predictor for convolutedness in anthropoids is neocortical volume, while in prosimians it is brain weight. The GI in catarrhines is correlated with total sulcal length but not number of sulci. This result suggests paleontological studies of total sulcal length can give direct information on the evolution of cortical folding in primates.

Introduction

Sulcal and gyral features in the cerebral cortex have attracted the attention of many investigators [for a review, see 1]. While it has generally been assumed that the degree of fissurization correlates with brain size [e.g., 2, 3], the roles of connections and laminar design in sulcal formation have also been analyzed. Both extrinsic connections (e.g., thalamic afferents) and intrinsic factors (a greater development of the volume and surface of the outer to inner cortical layers) have been proposed as causes of convolutions [3, 4].

One support of the role of connections in sulcal formation is that many of the cerebral sulci are located at borders defining different cytoarchitectural and functional areas [5–10] or are between cortical fields representing different parts of the body [3, 10].

Additionally, prosimian and anthropoid cerebral folding patterns differ in orientation; most prosimians have a rostrocaudally directed coronal sulcus, whereas anthropoids have a transverse central sulcus [for a review, see 11]. Since the degree of fissurization seems to depend on brain size and functional specialization, a quantitative study of gyrification that controls for brain size within primates could give valuable insight into the evolution of the cortex.

Measuring a convoluted surface is problematic, and different methods have been used [12–15]. In most of these approaches, a ratio is calculated between the total (including sulcal) and superficially exposed surface areas of the brain, without accounting for the effect of having an intersection distance which is greater than one or compensating for the bias caused by having gyri oriented obliquely to the plane of section [16, 17]. Such ratios between total and superficially exposed surfaces do not reliably measure gyrification, because they first determine surface area and the total cortical surface is systematically underestimated. The stereological method of Elias and Schwartz [14] is an improvement, but it did not completely compensate for the bias introduced by the ori-

Table 1. Body weight (S) in grams, brain weight (E) in grams, neopallial volume (NEO) in cubic centimeters, and GIs of the right (GIR) and left (GIL) hemispheres of all species studied: most of the body weight, brain weight and neopallial volume data are from Stephan et al. [20]

Species	S	E	NEO	GIR	GIL	Species	S	E	NEO	GIR	GIL
Prosimians						*Callithrix jacchus*	280	7.6		1.18	1.17
Lepilemur ruficaudatus	915	7.4	3.28	1.13	1.14	*Callithrix jacchus*	280	7.6		1.18	1.20
Varecia variegata	3,000	31.5	15.29	1.31	1.32	*Saguinus mid. tam.*	320	10.7	5.88	1.20	1.19
Lemur catta	1,960	22.0		1.33	1.32	*Saguinus oedipus*	244	9.6	5.89	1.20	1.19
Lemur mongoz	1,600	17.7		1.33	1.33	*Callimico goeldii*	480	11.0	6.48	1.26	1.25
Lemur alb. fulvus	1,385	32.9	12.21	1.46	1.46	*Aotus trivirgatus*	830	17.1	9.95	1.31	1.31
Microcebus murinus	101	2.0	0.74	1.10	1.10	*Saimiri sciureus*	345	19.7	15.54	1.46	1.45
Microcebus murinus	98	1.7	0.74	1.10	1.12	*Saimiri sciureus*	720	24.0	15.54	1.51	1.52
Microcebus murinus	47	2.0	0.74	1.11	1.13	*Cebus albifrons*	3,100	71.0	46.43	1.69	
Cheirogaleus medius	167	3.0	1.22	1.12	1.10	*Ateles paniscus*	8,000	108.0	70.86	1.69	1.67
Cheirogaleus major	400	6.6	2.93	1.15		*Ateles paniscus*	9,000	114.0	70.86	1.93	1.96
Avahi lan. occ.	860	9.7	4.44	1.14	1.15	*Alouatta senic.*	6,400	52.0	31.66	1.47	1.46
Avahi lan. lan.	1,270	11.5	4.81	1.25	1.26	*Lagothrix lagothr.*	4,190	102.3	65.87	1.97	1.97
Propithecus verr.	3,480	26.7	13.17	1.35	1.34	*Pygathrix nem.*	7,500	69.0	48.76	1.65	1.62
Indri indri	6,250	38.3	20.11	1.47	1.44	*Colobus badius*	8,250	75.0	50.91	1.82	1.79
Daubentonia mad.	2,800	45.2	22.13	1.26	1.24	*Cercopithecus spec.*	4,500	67.0		1.77	1.80
Galago senegal.	122	4.8	2.14	1.18	1.16	*Cercocebus alb.*	10,500	116.0	68.73	1.87	1.86
Galago demidovii	82	4.0	1.57	1.21	1.21	*Macaca mulatta*	6,800	78.0	63.48	1.80	1.78
Otolemur crassic.	625	10.4	4.72	1.25	1.26	*Macaca mulatta*	7,900	95.4	63.48	1.83	1.81
Nycticebus couc.	990	10.1		1.22	1.19	*Erythrocebus patas*	7,800	108.0	77.14	1.91	1.91
Nycticebus couc.	800	12.5	6.19	1.30	1.27	*Papio* spp.	16,000	182.0		1.99	1.98
Loris tardigradus	322	6.6	3.52	1.29	1.28	*Papio* spp.	16,000	182.0		2.15	2.15
Perodicticus potto	960	11.9		1.27	1.26	*Miopithecus tal.*	1,200	40.0	26.43	1.74	1.74
Perodicticus potto	1,000	14.0	6.68	1.37	1.38	*Hylobates lar*	5.700	102.0	65.80	1.85	1.86
Tarsius bancanus	115	3.0		1.07	1.08	*Pongo pygmaeus*	54,000	333.0	219.80	2.21	
Tarsius syrichta	87	4.2		1.10	1.10	*Pongo pygmaeus*	54,000	333.0	219.80	2.43	
						Pan troglodytes	46,000	405.0	291.59	2.44	2.47
Anthropoids						*Pan troglodytes*	46,000	405.0	291.59	2.41	2.41
Callithrix jacchus	280	7.6	4.37	1.17	1.17	*Gorilla gorilla*	105,000	500.0	341.44	2.26	
Callithrix jacchus	270	7.0		1.17	1.17						

entation of the plane of sectioning. Consequently, we have developed a semiautomatic measuring technique to calculate an unbiased measure of the degree of cortical fissurization without transformation of the data into surface measures. Because we have measured the gyrification index (GI) from every section, we have also been able to measure the increase in measurement error stemming from increasing the intersection distance. Thus we have determined that 40 equidistant sections through the adult human brain adequately sample the degree of convolutedness without increasing the measurement error [18].

In the present study we have posed the following questions: Does the GI give additional evidence for the causes of cortical folding? Do bigger primate brains have higher degrees of fissurization? What is the influence of body weight, brain weight and neopallial volumes on the degree of cortical folding? Does the degree of convolutedness correlate with one animal's systematic position or orientation of major gyri? Is the GI correlated with surface features, such as the number and length of sulci as seen on endocasts?

Materials and Methods

The measurements come from 42 different primate species, of which 21 are prosimian and 22 are anthropoids. The anthropoids include 10 different New World monkey species and 12 catarrhines (including 4 hominoids). The human GI is the mean value of 61 brains [18]. Altogether, 56 nonhuman individuals have been studied. In nearly all cases both the right and left hemispheres have

been measured and the GI of each hemisphere has been determined (table 1).

Most of the brains were processed similarly following a cardiac perfusion with Bouin's fixative or 10% formalin after a short rinse with saline. The brains were embedded in paraffin and serially sectioned (20 μm). The sections were stained with cresyl violet and approximately 40 equidistant sections per brain were taken for the quantitative analysis. This represents approximately every fourth mounted and stained section. A study of the measurement and calculation errors from using a sample instead of all available sections is given in detail in Zilles et al. [18]. The description of the processing of the human brains is found in Zilles [19]. Although the human brains were processed differently from those of the nonhuman primates, the measures of gyrification, being a relative measure (see below), are not affected by this. This has been proved by embedding two human brains in paraffin like the nonhuman primate brains. The GIs of the embedded human brains are well within the variation of the 61 frozen human brains used in this study.

The GI is the ratio between the total lenght of the outer (including sulcal) contour of the prosencephalon and the length of the contour of its superficially exposed surface (fig. 1). This means that the GI is quantitatively describing the amount of folding independent from the absolute size of the brain. This index does not measure the number of convolutions and sulci, but the relative degree of folding. The GI is a more reliable measure than counting sulci, because a great number of shallow sulci can lead to the same surface enlargement as a small number of deep sulci. The GI is also superior to a measure of total sulcal length, since this measure does not take into acount variations in sulcal depth.

In outlining the contours on coronal sections, the olfactory tract was not included in rostral sections where the tract is separated from the orbital surface of the forebrain. On more caudal planes, where the olfactory peduncle merges with the orbital surface, the peduncle was included. Cortical parts within the white matter, being separated from the superficially exposed cortex because of tangential sectioning, were also measured. The outer contour length is defined by the extent of the neo-, paleo-, and archicortex. The cortical boundaries are defined by the end of the callosal sulcus, the beginning of the hippocampal fimbria, the boundary between the uncinate cortex and optical tract and between the fasciolar gyrus and the splenium of the corpus callosum.

The contour lengths were digitized on ink drawings that outlined the histological sections. The digitizer was linked to a Wang 2200MVP computer. A hemisphere's GI is a mean value and was calculated by summing up the complete contour lengths of all sections and dividing these by the sum of the superficially exposed surface contour (outer contour) lengths (fig. 1). In measuring the outer contour length, the opening of a sulcus was closed by a line from the top of a gyrus to the top or crown of the adjoining one. Comparisons between the results achieved by two independent observers have demonstrated an interindividual variation in GI measurements of less than 1% [own unpubl. observations].

The GI values were studied as a function of body weight, brain weight and neopallial volume. In most cases these variables were known for the individual; in a few cases values typical for the species were used [20] (table 1). The neopallial volumes were determined from serially sectioned brains, were corrected for shrinkage and include both cortex and underlying white matter [16]. Correlations between GI and published [1, 14, 21] total sulcal lengths and numbers of sulci were calculated.
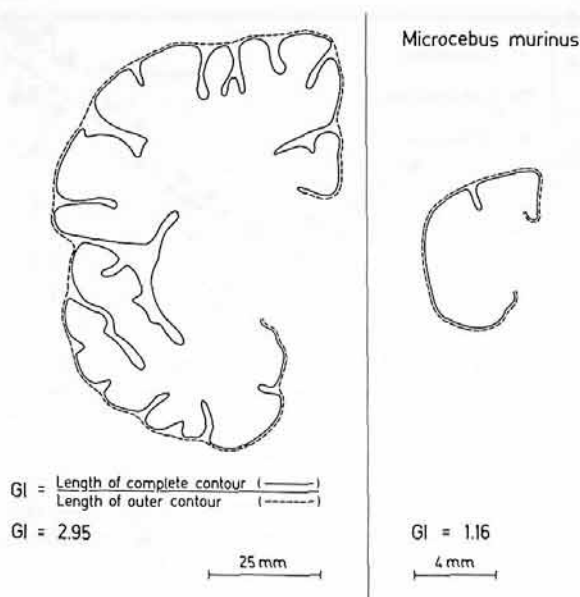

Fig. 1. Determination of the GIs of two single coronal sections, one from a human brain and one from a brain of *M. murinus*. The GI of a section is the ratio between the complete superficial contour (continuous line) and the superficially exposed, outer contour (dashed line) of the cortical part of the prosencephalon.

Right and left GI differences were tested with a Wilcoxon matched-pair test. Differences in the central location between two groups were tested with the Mann-Whitney U test. The correlation between different variables was calculated with linear regressions after logarithmic transformation of the independent variables. An analysis of covariance was used to test the significance of differences in slopes and adjusted means among different taxonomic groups and to study the interaction among these parameters. A stepwise regression identified how much of the GI variation could be explained by the different independent variables. Mean values and the standard errors of the means are given throughout this paper.

Results

The prosimian GIs are between 1.07 and 1.47. The lowest indices are found in *Tarsius bancanus*, *Tarsius syrichta* and *Microcebus murinus*. The highest values are found in *Indri indri* and *Lemur albifrons*. The eight lemurid species show a mean GI of 1.25 (± 0.05), the three indrid species have a mean GI of 1.34 (± 0.06), *Daubentonia* has a value of 1.25, the six lorisids have a mean GI of 1.25 (± 0.02), and two species of Tarsiidae have a mean GI of 1.09 (table 1). The indices of gyrification do not significantly differ between our samples of Lemuridae and Lorisidae, the two largest prosim-
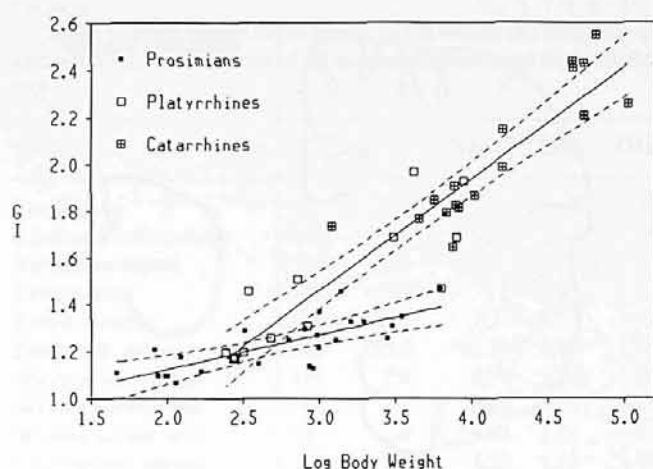
Fig. 2. Correlations between GI and body weight in prosimians, platyrrhines and catarrhines. The body weight is logarithmically transformed.
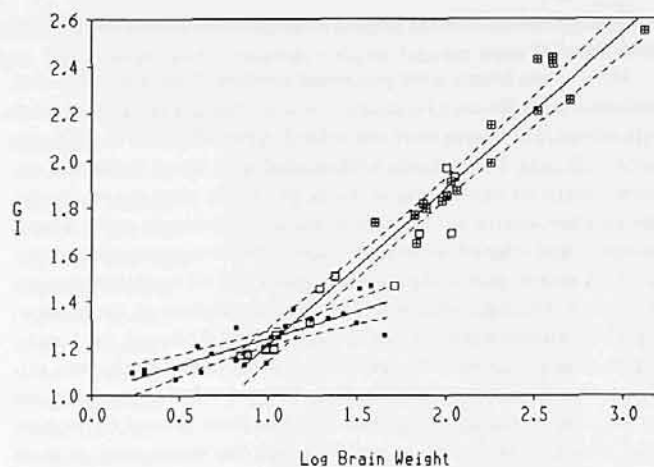

Fig. 3. Correlations between GI and brain weight in prosimians platyrrhines and catarrhines. The brain weight is logarithmically transformed.

ian families. This is the case whether or not sizes of the animals and/or brains are taken into account. When GI is studied as a function of brain or body weights or neocortical volume (see below), *Tarsius* always clusters with the other prosimians.

The nonhuman anthropoid GIs range between 1.17 and 2.47. The lowest index is found in *Callithrix jacchus,* the highest value is in *Pan troglodytes.* The four species of Callitrichidae have a mean GI of 1.21 (± 0.02), the six species of Cebidae 1.62 (± 0.09), the eight species of Cercopithecoidae 1.83 (± 0.05), the *Hylobates lar* 1.86, the two species of Pongidae 2.39, and *Homo sapiens* 2.56 (± 0.02). The indices of the New World monkey families, Callitrichidae and Cebidae, significantly differ ($p < 0.001$), with the cebids having the higher GI. The values of the Cercopithecidae are not significantly larger than those of the Cebidae ($p > 0.05$). Human values are close to those expected for a nonhuman anthropoid whose brain, body weight or neocortical volume is scaled to human dimensions, and so *H. sapiens* is considered with the catarrhines.

We compared the GIs between the right and left hemispheres. For all primates the mean value of the right side is 1.51 (± 0.05), and the value for the left side is 1.48 (± 0.05). The Wilcoxon matched-pair test shows no significant hemispheric difference ($p = 0.077$), within either primates or any smaller taxonomic group.

Primate GIs increase as body weights increase (fig. 2). Following logarithmic transformation of

body weight, the correlation for all primates is statistically significant ($r = 0.902$, $p < 0.001$). An analysis of covariance shows the prosimian slope is 0.147 ($r = 0.778$) while the anthropoid slope is 0.477 ($r = 0.942$). The difference between the slopes is statistically significant ($p < 0.001$), showing that the scaling between gyrification and body weight is lower in prosimians than anthropoids. This indicates that the cortex of prosimians undergoes less folding than that of anthropoids as the animals increase in size. No scaling differences were found within smaller taxonomic divisions of the primates (e.g., differences between New and Old World monkeys or between lorises and lemurs).

Because brain weights correlate with body weights, and because gyrification is thought to be responding to brain size, the correlation between GI and brain size was studied as well (fig. 3). As primate brains increase in size, GI does as well ($r = 0.948$, $p < 0.001$). Prosimians and anthropoids, however, significantly differ in their slopes (prosimian slope = 0.230; anthropoid slope = 0.662; $p < 0.001$), indicating that for every unit increase in brain size, anthropoids acquire a higher degree of cortical folding than do prosimians.

If we restrict our analysis to neopallial volume (fig. 4), we find that as neopallial volume increases in size, gyrification is also augmented ($r = 0.940$, $p < 0.001$). The prosimian slope is 0.200 and that of anthropoids is 0.652. Again, the different slopes between prosimians and anthropoids ($p < 0.001$) suggest
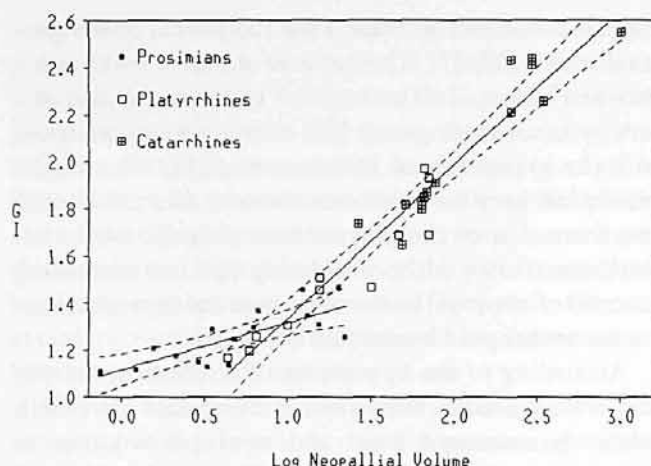
Fig. 4. Correlations between GI and neopallial volume in prosimians, platyrrhines and catarrhines. The neopallial volume is logarithmically transformed.

Fig. 5. Correlations between neopallial volume and brain weight in prosimians and anthropoids. Both variables are logarithmically transformed.

that anthropoids acquire a more convoluted brain per increase in unit neopallial volume than do prosimians.

A stepwise regression was used to determine which of the three variables – brain weight, body weight or neocortical volume – best explained the observed variance in gyrification. In anthropoids neopallial volume was the best predictor (r = 0.970), but in prosimians it was brain weight (r = 0.823). The lower values of the prosimian correlations (see above) indicate that differences in gyrification in prosimian brains are less tightly linked with brain or body weight than in anthropoids. This finding was analyzed further by studying neopallial volume as a function of brain weight. Anthropoids and prosimians have parallel regression lines when neopallial volume is correlated with brain weight (fig. 5). An analysis of covariance shows that the adjusted means of the two taxonomic groups significantly differ (anthropoid adjusted mean = 19.48 ± 1.02; prosimian adjusted mean = 14.48 ± 1.04; p < 0.001).

Sulcal length and number of sulci were correlated with the GI because surface cortical features are the only available paleontological evidence. The number of sulci and total sulcal length, as measured by orthogonal projections of endocasts, have been determined for Cercopithecoidae [1] and the number of sulci for New World monkeys [21]. Data from both studies were combined. Following this, no correlation between the number of sulci and GI was found. Within this combined group, however, the logarithm of the
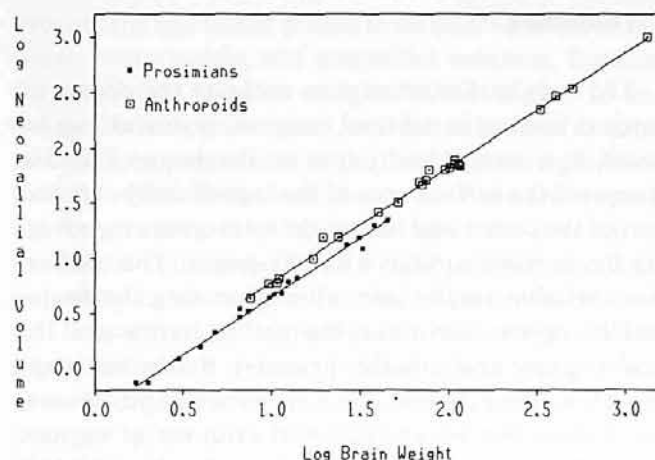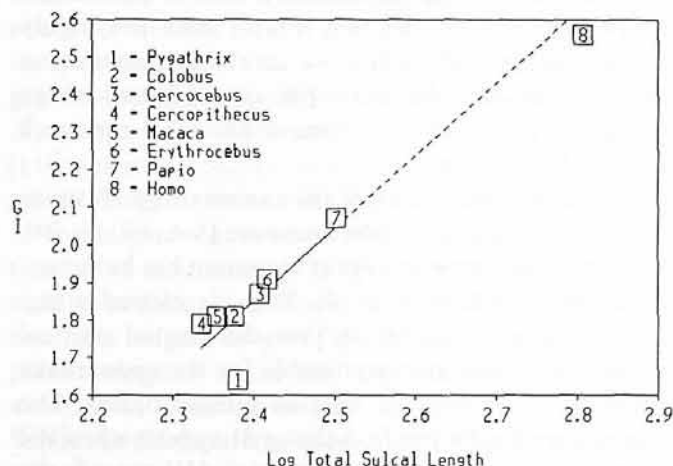

Fig. 6. Correlations between GI and the total lenght of cortical sulci (data from Elias and Schwartz [14] and Falk [1] in six different species of catarrhines. The total sulcal length is logarithmically transformed. Neither *Pygathrix* nor human values were included in the generation of the slope. See Results for further details.

total length of sulci and th GIs are significantly correlated (r = 0.799, p < 0.01). Only *Pygathrix* shows an unexpected low GI (fig. 6). When *Pygathrix* is omitted, the correlation is much higher (r = 0.988), and the nonhuman data predict the human association as determined from our GI data and Elias and Schwartz' [14] total sulcal length values. When the human value is added, the correlation coefficient becomes r = 0.965. Further studies are necessary to show whether *Pygathrix* is as far removed from the other cercopithecids as the above association suggests.

Discussion

The only earlier attempt to measure the degree of cortical folding in a broad range of primates can be found in a rarely cited paper by Brodmann [22]. He measured the surface area of the superficially exposed part of the cortex and that of the total cortex by covering the cortical surface with silk paper. The method gives reliable results only after dissecting the brain, and this destruction makes the method impractical for studying rare and valuable primates. Brodmann's approach is also extremely time consuming and tedious, but it does permit an unbiased estimate of surface areas. We calculated GI values from Brodmann's [22] data and compared them with our results from the same species (*Microcebus, Lemur, Callithrix, Cercopithecus, Papio, Hylobates, Pan, Homo*). Brodmann's GI values are slightly higher than our's in most, but not all, cases (Wilcoxon matched-pair test; p = 0.02). More importantly, the two sets of data are highly correlated (r = 0.98). The closeness of the correlation corroborates the value of the present GI methodology compared to that of the time-consuming approach used by Brodmann.

Different hypotheses of the causes of gyrification have been discussed in the literature [3–6, 15, 23, 24]. We think that the most cogent argument has been proposed by Richman et al. [4]. They developed a mechanical model suggesting that differential cortical growth processes are responsible for the appearance of most of the gyri, at least in human brains. The model specifically predicts that gyri appear when the growth of the outer cortical layers (I–III) exceeds the growth of the inner cortical layers (IV–VI).

An extension of this model would suggest that animals with increased outer compared to their inner cortical layers should have a more convoluted brain. Measurements from area 31, a neocortical region of the posterior cingulate gyrus, have determined the volumetric proportions of cortical layers in a series of primates, which differ according to taxonomy [25, 26]. Prosimians have a lower mean volumetric ratio of layers I–III to layers IV–VI (prosimian ratio = 0.94 ± 0.06 than have platyrrhines 1.26 ± 0.08) or catarrhines (1.35 ± 0.06 [table 1 in 25]. When the comparison is focused on layers II–III and V–VI the disproportion in ratios is even clearer [table 3 in 26]. Furthermore, a second aspect of internal growth processes can be determined by the amount of neuropil (the space between cell bodies). The quantity of neu-

ropil is measured by taking the reciprocal of the grey level index [25, 27]. The ratio of the grey level index between layers II–III and IV–VI in area 31 also differs by taxonomic group [26] in a manner consistent with the hypothesis of Richman et al. [4]. That is, the prosimian grey level index ratio of 0.44 (±0.01) differs from that of the platyrrhines (0.36 ± 0.04) or catarrhines (0.39 + 0.02), indicating that an increasing amount of neuropil in the outer cortical layers characterizes anthropoid brains [table 2 in 25].

According to the hypothesis of Richman et al. [4], one would predict that since anthropoids have both relatively increased total and neuropil volumes in their outer compared with their inner cortical layers, they should also have an increased degree of convolutedness. Such is observed, with the mean GIs of prosimians (1.24 ± 0.03), being lower than those of platyrrhines (1.45 ± 0.08) or catarrhines (2.00 ± 0.09). Although all three parameters, GI, grey level index and volumetric proportions, change between prosimians and anthropoids, the GI has the most pronounced shift. Future studies must determine whether the relatively bigger change in GI is the result of analyzing different species in the two studies or the result of a different scaling between these parameters.

Since the outer cortical layers, especially layers II–III, contain a large number of interneurons, the increase in gyrification observed in anthropoids also indicates an internal differentiation towards more intracortical processing. This agrees with a former study of the visual cortex in primates which showed the outer cortical layers to be quantitatively more elaborate than the inner cortical layers [28]. The difference in the slopes describing GI as a function of brain weight or neocortical volume between prosimians and anthropoids indicates an increased processing by the outer cortical layers in anthropoids, which in turn suggests this taxonomic group has an augmentation of intracortical associations.

We have found that the GI is correlated with body weight, brain weight and neopallial volume. This shows that bigger primate brains have higher degrees of fissurization. Separate regressions were calculated for the major taxonomic divisions. Prosimians have a lower slope than anthropoids when GI is studied as a function of body weight, brain weight or neopallial volume, indicating that for every unit increase in neopallial volume (or brain or body weight), prosimian brains undergo fewer changes in gyrification than anthropoid brains. *Tarsius*, a primate genus

sometimes classified with anthropoids as a haplorhine [29–31] has a very low GI. Only *Microcebus*, which has a smaller brain, has an equally low GI. Since *Tarsius* GIs scale like those of prosimians, this suggests that its cortex shares more aspects of gyral formation with prosimians than with anthropoids. Data from the posterior cingulate cortex corroborate this similarity [25] (table 1). Since the prosimian families in the present study do not differ in their GIs, no extant prosimian group appears to be intermediate between anthropoids and prosimians.

Callitrichids have many primitive characteristics, including low GIs which overlap prosimian values (fig. 2–4, table 1). The anthropoid pattern of larger outer-to-inner laminar volumetric proportions observed in the posterior cingulate cortices [25] (table 1) suggests, however, that low GIs in calithrichids reflect their brain size rather than the retention of prosimian-like cortical lamination patterns. Thus a similar degree of convolutedness can arise from different processes. In the case of callitrichids and prosimians, the similar degree of gyrification represents convergent evolution. Sometime during the early evolution of anthropoids, a shift in cortical development led to an increased amount of convolutedness, and this change was correlated with an expansion of the outer cortical layers.

Human brains have the degree of convolutional development expected for a nonhuman anthropoid. That is, if a nonhuman anthropoid brain (or body or neopallial volume) is scaled to human dimensions, the degree of folding approximates that observed in our study. This suggests that human convolutional development follows the same ontogenetic pattern as seen in other anthropoids. Consequently, if neoteny or an alteration in somatic development has caused the enlargement of human brains [32], it did so without changing the basic strategy of anthropoid sulcal development.

In anthropoids, neopallial volume is the strongest factor influencing gyrification, whereas in prosimians brain weight is the best predictor of GI. Anthropoids also differ from prosimians in having a higher proportion of neopallium per brain weight [33, 34]. Keeping in mind the above discussed findings of the anthropoid-prosimian differences in GI and the enlargement of outer to inner cortical layers, these findings suggest that anthropoids have more space for intracortical processsing. This does not exclude an important influence of neopallial volumes on GIs in prosimians but rather points to an altered relation between brain weight and neopallial volumes. Because the neopallial-to-brain weight ratio is higher in anthropoids than prosimians, and indeed comes to comprise a large proportion of the total brain weight, neopallial volume is the best predictor of the anthropoid GI. In prosimians, on the other hand, the amount of neopallial volume per brain weight is lower, and consequently brain weight has the largest influence on GI. The different neopallial-to-brain weight ratios, combined with differing GI associations, suggest that cortical organization and subcortical relations have changed quantitatively between prosimians and anthropoids.

The degree of convolutedness does not correlate with the orientation of major gyri. Although most prosimian brains have a lateral coronal sulcus, *Perodicticus potto* resembles anthropoids in having a transversely oriented, central sulcus [11]. This convergence to the anthropoid pattern, however, does not carry over to the GI (table 1). Furthermore, two of the genera examined in this research *(Propithecus* and *Nycticebus)* are characterized by long Sylvian sulci [11]. Again this feature does not separate these prosimian GIs from those of other prosimians.

Investigators have attempted to approach the question of the evolutionary history of gyrification by analyzing surface sulcal features, in particular the numbers and lengths of gyri [33]. Analysis based on this paleontological appraoch depends upon a similar analysis in extant primates [1, 13, 14, 21, 35, 36]. While the GI should be used if whole brains are available, in paleontological investigations only surface features like sulcal length and numbers can be observed. The correlation between total sulcal length and GI suggest that the former may represent a robust basis for interpreting paleontological data. Although some problems may arise with the degree of predictability for individual cases, the evolutionary history of gyrification may emerge through an analysis of total sulcal length.

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