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Received 19 April 1996 Revision received 25 September 1996 and accepted 29 September 1996

Keywords: frontal lobe, hominoid brain, hominid cognition.

The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains

Scenarios regarding the evolution of cognitive function in hominids depend largely on our understanding of the organization of the frontal lobes in extant humans and apes. The frontal lobe is involved in functions such as creative thinking, planning of future actions, decision making, artistic expression, aspects of emotional behavior, as well as working memory, language and motor control. It is often claimed that the frontal lobe is disproportionately larger in humans than in other species, but conflicting reports exist on this issue. The brain of the apes in particular remains largely unknown. In this report we measure the volume of the frontal lobe as a whole and of its main sectors (including cortex and immediately underlying white matter) in living humans, and in post-mortem brains of the chimpanzee, gorilla, orang-utan, gibbon and the macaque using three-dimensional reconstructions of magnetic resonance (MR) scans of the brain. On the basis of these data we suggest that although the absolute volume of the brain and the frontal lobe is largest in humans, the relative size of the frontal lobe is similar across hominoids, and that humans do not have a larger frontal lobe than expected from a primate brain of the human size. We also report that the relative size of the sectors of the frontal lobe (dorsal, mesial, orbital) is similar across the primate species studied. Our conclusions are preliminary, because the size of our sample, although larger than in previous studies, still remains small. With this caveat we conclude that the overall volume of the frontal lobe in hominids enlarged in absolute size along with the rest of the brain, but did not become relatively larger after the split of the human line from the ancestral African hominoid stock. Aspects other than relative volume of the frontal lobe have to be responsible for the cognitive specializations of the hominids.

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Journal of Human Evolution (1997) 32, 375-388

Introduction

Creative thinking, planning of future actions, decision making, artistic expression, aspects of emotional behavior, as well as working memory, language and motor control, are functions attributed mostly to the frontal lobes. Many of these also constitute a major part of our notion of being human. The frontal lobe is the largest sector of the hemisphere, and often it is claimed that in humans it has developed more than other areas. Are the frontal lobes disproportion-ately larger in our species than in the rest of the hominoids? What is the evidence in support of the long-cherished association between high mental capacities and a uniquely large human frontal lobe?

The frontal lobes may first have been associated with higher mental functions by the Greeks, who sometimes represented gods, demigods, poets and artists with large foreheads in their sculptures and paintings. In the late 18th century, physiognomists devised the first anthropometric measures associating mental characteristics with physical features. "Larger facial angles and more fully developed foreheads" were attributed to whites rather than blacks, and an

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increase in the facial angle was found when apes and humans were compared in the "natural chain of being" (Finger, 1994).

Reports of actual measurements that compare the size of the frontal lobes in humans and apes are scarce. Near the turn of the century Brodmann (1912) measured parts of the human and non-human primate cortex. The surface area of the frontal lobe (lobus frontalis) was estimated for the human, chimpanzee and gibbon, along with a few monkey and prosimian species. Its size was reported to be 36.3% of the total surface of the hemisphere for the human, 30.5% for the chimpanzee and 21.4% for the gibbon. Lebourg (1928) found that the volume of the frontal lobe in the human is 38.3% (surface 36.5%), 39% in the chimpanzee (surface 37%) and 30% in the macaque (surface 30.4%). Tilney (1928) estimated the surface area of the frontal lobe in relationship to the "neopallium" to be: 47% for the human, 33% for the chimpanzee and 32% for the gorilla. Weil (1929) measured the surface of endocranial casts and supported the idea of an enlarged human frontal lobe. In a more recent study, including comparative data on the size of the primate frontal lobe, Blinkov & Glezer (1968) reported the surface area of the "frontal region" (prefrontal cortex) and of the precentral region (areas 4 and 6) in relation to total surface of the hemisphere to be: 32.8% in the human, 22.1% in the chimpanzee, 21.3% in the orang-utan and 21.2% in the gibbon. Most recently, Uylings & van Eden (1990) estimated the volume of the prefrontal cortex in relation to the total volume of the isocortex to be approximately 29% for the human, 29% for the orang-utan, 18% for the macaque and 13% for the marmoset. Also, Zilles et al. (1988) found the degree of foldedness (defined as gyrification index) to be increased in the prefrontal areas in the human brain, when compared with the brains of the three great apes.

Contrary to the scarcity of the actual measurements, a rich literature exists on the subject of the evolution of the frontal lobe based mainly on the above sources, but as most point out (von Bonin, 1948; Holloway, 1968; Clark & Dewhurst, 1972; Passingham, 1973; Deacon, 1988; Armstrong, 1990; Uylings & van Eden, 1990), the data available on the frontal lobe are few and conflicting, and more studies are necessary.

We decided to start investigating the volume of the frontal lobes (as a whole) in the extant hominoids using three-dimensional (3D) reconstructions of magnetic resonance (MR) brain scans. We also subdivided the frontal lobe into its traditional anatomical subdivisions that are known to be involved to a greater or lesser extent in functions as diverse as language processing (dorsolateral) or social memory (ventromesial). Our measurements included the whole brain represented by the two hemispheres, in order to address relative, as well as absolute, size differences among species. Taking into consideration the results from each individual species examined, we make suggestions about evolutionary changes in this part of the brain in the human/ape line.

Materials and methods

We scanned four living humans, four ape-brain specimens (*Pan troglodytes, Gorilla gorilla, Pongo pygmaeus, Hylobates lai*) and one brain specimen of a macaque (*Macaca mulatta*). All ape specimens were obtained from several zoos after natural deaths of the animals. The rhesus monkey was used as an outgroup comparison for character states within the hominoids. Volumetric studies of brain specimens using MR have the advantage that they are free of shrinkage effects following tissue processing for histology. *In vivo* scans have, in addition to the above, the advantage that they are free of shrinkage related to autolysis time and preservation method. We also scanned one post-mortem human brain to control for possible effects of shrinkage in our comparison between living humans and post-mortem apes. The volumes of

the living human brains and of the post-mortem specimens fall within the range of published values with the exception of the gibbon which is at the high end of variability (von Bonin, 1937; Kennard & Willner, 1941; Stephan *et al.*, 1981; Tobias, 1971sse;r31; Passingham, 1979; Zilles & Rehkämper, 1988; Kennedy *et al.*, 1968).

For each brain, we obtained T_1 -weighted contiguous MR coronal sections throughout the whole brain (1·2–1·6 mm thick, depending on the size of the brain). All were reconstructed in three dimensions (3D) using Brainvox (Damasio & Frank, 1992) and the brain was traced to exclude the following: cerebellum, pons, medulla and the greater part of the midbrain. On each coronal slice where these structures are visible, we connected the two transverse fissures with a straight line. This eliminated all structures below the line (those mentioned above). Then, the two hemispheres were separated.

Volumetric estimates of the hemispheres, the frontal lobes and its sectors were computed for all species using Brainvox. A count of the number of voxels within each traced region was made and the number was multiplied by the volume of a single voxel in millimeters.

Surface area estimates were computed in order to compare our results with those of older studies based exclusively on surface estimates. We focused on the volumetric results of this investigation, because of the inherent difficulties in the accurate estimation of surface area of complex objects in digital form (Russ, 1994). Surface area estimates were computed using a variant of the "marching cubes" algorithm (Lorensen & Cline, 1987). A binary volume mask consisting of all the voxels within the brain was computed from the whole brain surface tracings. This mask was then low-pass filtered (three pixels FWHM) to produce a gray-scale volume. This was done to reduce local digital edge effects in the volume. This smoothed volume was subjected to the marching cubes surface detection algorithm, using a threshold of one-half the difference between the original mask intensity and the background. The areas of the triangles (adjusted by interpixel and interslice spacings) resulting from the marching cubes procedure, within each region of interest, were summed to estimate the regional surface area.

Segmentation procedures

Frontal lobe. Major landmarks, common to all species, were used to separate the frontal lobe from the rest of the hemisphere. On the 3D volume reconstruction, the central sulcus was identified and traced on the lateral and mesial surface of each hemisphere (Figure 1). The most caudal section of the frontal lobe including orbitofrontal cortex was identified on the original coronal sections and was marked. The end of the central sulcus on the mesial surface of the hemisphere was connected, in a straight line, with the most posterior segment of the orbitofrontal cortex. On the mesial surface, above the cingulate sulcus, this line was considered the mesial and posterior limit of the frontal lobe. Anteriorly, the inferior limit is the outer border of the orbital surface, and posteriorly, it is the sylvian fissure and the upper portion of the circular sulcus. These landmarks formed the dorsal, orbital and mesial borders separating the frontal lobe from the rest of the hemisphere in all species.

The landmarks drawn in different colors on the 3D reconstruction of the brain were automatically transferred to the 2D serial sections, allowing for the tracing of the segment of the frontal lobe seen in each section as a separate region of interest (ROI). All sections in which the frontal lobe occurred were traced in this manner.

Subdivisions of the frontal lobe: dorsal, mesial and orbital sectors. The frontal lobes were subdivided into three sectors: dorsal, mesial, orbital. The choice of landmarks separating these three sectors was guided by the principle that they had to be present across species. This was not an easy



Figure 1. Lateral view of the left hemisphere of the human (upper left), chimpanzee (middle left) and gibbon (lower left) based on three dimensional reconstructions of magnetic resonance scans of the brain. On the right, selected coronal sections through the frontal lobe of the same brains showing segmentation of the different sectors. Major landmarks (sulci and gyri) can be identified simultaneously on the 3D and 2D images allowing for their accurate identification on multiple cutting levels. Shaded area in front of the central sulcus (CS) represents the frontal lobe. FMS, frontomarginal sulcus; PRS, principal sulcus; LOS, lateral orbital sulcus; OFS, orbitorfrontal sulcus.

task, because sulci alone are not enough to establish homologies between species, as has been pointed out by many comparative neuroanatomists in the past (Bailey *et al.*, 1950; Welker, 1990), and individual variation in the sulcal pattern in both human and non-human primates adds to the difficulty. Unlike the prominent landmarks used for the identification of the limits of the frontal lobes, the choice of landmarks to subdivide the frontal lobe involved a combination of information about the homologies of sulcal pattern across species and the underlying cytoarchitecture of the cortex. Based on these two types of information, we decided that the frontomarginal sulcus (principal sulcus in the gibbon), the lateral orbital sulcus (orbitofrontal sulcus in the apes) and the circular sulcus would be the most appropriate landmarks to separate the dorsal from the orbital sectors of the frontal lobe. Conolly (1950) considers the orbitofrontal sulcus in the apes homologous to the anterior limiting sulcus of the insula, a homology which we respect in the more caudal sections. In the more rostral sections, we used the lateral orbital sulcus in humans as the limit between orbital and dorsal sectors. This secondary sulcus may or may not be a branch of the inferior frontal sulcus (Duvernoy, 1991). In the apes we used the orbitofrontal sulcus.

	Hemisphere	Frontal lobe	
Macaque	62,737	17,654	
Gibbon	91,385	28,438	
Orang-utan	268,553	94,705	
Gorilla	348,336	112,912	
Chimpanzee	305,521	109,800	
Human	1,125,492	413,103	

Table 1 Volume of the hemisphere and the frontal lobe

Values are given in cubic millimeters and include both hemispheres.

The frontomarginal sulcus is present in the human brain, as well as in the brain of all great apes. Conolly (1950) calls this sulcus "rectus" in the chimpanzee, but Bailey *et al.* (1950) and recently one of us (Semendeferi, 1994) after analyzing the cytoarchitecture of the surrounding cortex have used the term frontomarginal for the great apes and humans to underline the homology.

In the serial coronal sections the frontomarginal sulcus was followed until the lateral orbital sulcus appeared. This latter sulcus was then followed until the appearance of the circular sulcus. The mesial cortex was defined as extending from the tip of the gyrus rectus to the upper end of the mesial surface (including the mesial part of the superior frontal gyrus) following the edge of the interhemispheric fissure (Figure 1).

In the macaque, in the absence of the frontomarginal and orbitofrontal sulci, we used the frontal tip of the principal sulcus and the ventral tip of the arcuate sulcus and connected them in a straight line. In this fashion, we respected the well-established cytoarchitectonic borders in this species between areas 46 (dorsal sector) and 12 (orbital sector). All other landmarks used were the same as in the hominoids.

In the brain specimens, a clear separation between gray and white matter was not consistently visible. Therefore the ROIs just described were outlined by connecting via a straight line the depth of the sulci, thus including the white matter core of each gyrus (Figure 1). The remaining tissue (white matter and subcortical structures) was considered yet another sector.

Results

Hemispheres and frontal lobes

The values of the absolute volume of the hemispheres and of the frontal lobes can be described as forming three plateaus (Table 1; Figure 2). The first plateau includes the small-bodied primates (macaque and gibbon) whose hemispheres have a volume below 100,000 mm³ and frontal lobe volume less than 30,000 mm³. The second plateau includes all large-bodied hominoids (orang-utans, gorillas, chimpanzees) except humans with hemispheric volumes of between 200,000 and 400,000 mm³ and frontal lobe volumes between 90,000 and 120,000 mm³. The last plateau includes only humans with a hemispheric volume of more than 1,000,000 mm³ and a frontal lobe volume of more than 400,000 mm³. The size of the hemispheres in our sample of the living human brains ranges from 1,042,058–1,173,480 mm³ and for the frontal lobes from 369,743–457,068 mm³. In the one human post-mortem specimen, the volume of the hemispheres is 1,077,482 mm³ and that of the frontal lobes 357,871 mm³.



	Frontal lobe/ hemisphere		Sectors Dorsal		s of the frontal lobe/fronta Mesial		al lobe* Orbital	
	Volume	Surface	Volume	Surface	Volume	Surface	Volume	Surface
Macaque	28.1	30.8	60.1	52.0	25.1	24.7	14.8	25.0
Gibbon	31.1	31.8	53.7	60.8	29.1	22.3	17.2	20.7
Orang-utan	35.3	27.5	58.2	59.2	31.1	28.7	10.7	13.6
Gorilla	32.4	29.7	54.0	55.1	29.3	28.6	16.7	18.3
Chimpanzee	35.9	38.1	57.9	54.8	26.2	30.6	16.0	18.8
Human	36.7	35.9	58.4	63.5	26.4	17.8	15.2	21.7

Table 2 Volume and surface (in %) across species

*Values represent the percentage of the frontal lobe (cortex and immediately underlying white matter) occupied by the different sectors.

The relative values of the frontal lobe (calculated as a ratio of the rest of the hemispheric volume) form a smooth ascending ramp as follows: $28\cdot1\%$ (macaque), $31\cdot1\%$ (gibbon), $35\cdot3\%$ (orang-utan), $32\cdot4\%$ (gorilla), $35\cdot9\%$ (chimpanzee), and $36\cdot7\%$ for the human (range $35\cdot5-38\cdot9\%$) (Figure 2). When we look at cortical surface, the percentile values for the frontal lobe are: $30\cdot8\%$ (macaque), $31\cdot8\%$ (gibbon), $27\cdot5\%$ (orang-utan), $29\cdot7\%$ (gorilla), $38\cdot1\%$ (chimpanzee) and $35\cdot9\%$ (human mean value; the range being $35-37\cdot5\%$) (Table 2). Relative values might be of particular interest when sectors of similarly sized brains across species are compared, and this is the case with the great apes as will be discussed later.

We regressed the frontal lobe volume against the volume of the hemispheres on a log-log plot and estimated a best fit line on the basis of the non-human primate data (Figure 3) using the reduced major axis (RMA) (Aiello, 1992). The least square regression slope (LSR)



Figure 3. Logarithmic plot of the volume of the frontal lobe (a), the dorsal sector (b), the mesial sector (c), and the orbital sector (d) versus the hemisphere including data on the human, chimpanzee, gorilla, orang-utan, gibbon and macaque brains. The best-fit line is estimated on the basis of the non-human primates using the reduced major axis (b=1.1135 for the frontal lobe; b=1.079 for the dorsal; b=1.1432 for the mesial; and b=1.0645 for the orbital sector).

(Smith, 1994) was also applied and the slope based on this approach (b=1.1135) was almost identical to RMA (b=1.1150). We also regressed the volume of the frontal lobe versus the volume of the hemispheres minus the volume of the frontal lobe (LRS; b=1.164), due to concerns raised in the literature about the effects of regressing a large segment of the brain against the whole that includes the component under examination (Deacon, 1988; Huxley, 1932). Furthermore, our data were reanalyzed by R. Barton, using the method of independent contrasts (Purvis & Rambaut, 1995), and the resulting slope was similar to the ones obtained with the other analysis (1.135; r=0.988) (Barton, pers. comm.). Regardless of the approach used to estimate the best-fit line, the human values are not found above the line, but rather on it and slightly below. Certainly the small sample of primates results in a not very precise estimate of the slopes; further precision is lost in the extrapolation process. Nevertheless, the proximity of the extrapolation value to the observed human data is remarkable. On the basis of these data, we suggest that the human frontal lobes are not larger than would be expected from a primate of our brain size.

	Dorsal†	Mesial†	Orbital [†]	Central core‡
Macaque	9420	3935	2326	1973
Gibbon	11,903	6454	3817	6264
Orang-utan	43,964	23,512	8059	19,170
Gorilla	50,603	27,497	15.671	19.141
Chimpanzee Human	51,274 193,800	23,199 87,759	14,142 50,405	21,185 81,139

Table 3 Volume of the sectors of the frontal lobe*

*Values are given in cubic millimeters and include both hemispheres.

†Sectors include cortex and immediately underlying white matter.

‡Central core includes white matter and subcortical structures.

Dorsal, mesial and orbital sectors of the frontal lobe

As for the absolute values of the hemisphere and the frontal lobe, the distribution of the absolute volume values of the three sectors can also be described as forming three plateaus with the same general distribution seen for the hemispheres. The macaque and gibbon have the smallest values, followed by the great apes and the human brain, the largest (Table 3). The only noticeable exception is the small size of the orang-utan orbital sector, whose value lies between that of the gibbon and of the other great apes. In all species, the orbital sector is the smallest followed by the mesial and the dorsal sectors. It is clear from the above that small brains have small frontal lobes and small subdivisions of the frontal lobe, and that there is little or no variation from the expected pattern.

The relative values of the three sectors (calculated as a ratio of the volume of the cortex of the frontal lobe and immediately underlying white matter) are quite similar across all species (Figure 4). The dorsal sector ranges between 54% (gibbon and gorilla) to 60% (macaque). The mesial sector values range from 25% (macaque) to 31% (orang-utan). The relative size of the orbital sector ranges from 11% (orang-utan) to 17% (gibbon and gorilla).

The relative size of the cortical surface of the three sectors in relation to the total value for the surface of the frontal lobe is as follows. The dorsal sector values range from a minimum of 52% in the macaque to a maximum of 66·1% in one of the humans. The mesial sector ranges from 14·7% (in one of the human brains) to 30·6% in the chimpanzee. The orbital sector ranges from 13·6% (orang-utan) to 25% (macaque) and the human values fall within the above range (17·7–24·4%).

When the volumes of the dorsal, mesial and orbital sectors of the frontal lobe are regressed against the volume of the hemisphere and a best-fit line is determined on the basis of the non-human primate data, the human values are, in all three cases, as large as expected from a primate of the human brain size. As discussed in the case of the frontal lobe as a whole, a best-fit line is estimated using RMA(Figure 3) for the dorsal (b=1.079), mesial (b=1.1432) and orbital (1.0645) sectors. An LSR was also applied here and the slopes based on this approach (dorsal, b=1.0739; mesial, b=1.1403; orbital, b=1.0400) did not change the position of the human values on the plot.

Discussion

Comparisons with previous studies

Only a few comparative studies exist on the size of the frontal lobe, many of which come from the first half of the 20th century (Brodmann, 1912; Leboucq, 1928; Tilney, 1928; Weil, 1929),



Figure 4. Graphic representation of the percentage of the frontal lobe cortex and immediately underlying white matter occupied by the different sectors across species.

while others are more recent (Blinkov & Glezer, 1968; Zilles *et al.*, 1988; Uylings & van Eden, 1990). Some were based on measurements of the surface area, the volume of the cortex or the degree of foldedness and suggested that the frontal lobe or the prefrontal cortex is relatively larger in humans than it is in other species (Brodmann, 1912; Tilney, 1928; Weil, 1929; Blinkov & Glezer, 1968; Zilles *et al.*, 1988; Uylings & van Eden, 1990). Others combined estimates of surface area and total volume of the frontal lobe and supported a similar relative size for the frontal lobe in humans and apes (Leboucq, 1928). Unfortunately many of these studies encounter one or several methodological problems such as quantitative techniques that are not reproducible or reliable (older studies), incomplete representation of hominoid species and small sample size (one ape brain or even one hemisphere in most of the above studies).

Over the years, many researchers have used the above data in their analyses and reviews on the evolution of the frontal lobe or the prefrontal cortex, and depending on the type of analysis they perform, they come to different conclusions. Many strongly support the idea of a similar relative size for the frontal lobes in humans and apes. Bonin (1948) plotted Brodmann's figures on the surface of the frontal lobes (human, chimpanzee, cynomorphae, cebus, lemur and hapale) and concluded that "they illustrate a very simple case of relative growth". Holloway (1968) emphasized that "the measurements which are most direct, that directly measure cortical area or volume rather than endocasts, give little basis for accepting relative increase". Clarke & Dewhurst (1972) concluded that "this association between the frontal lobe and highest intellectual capacity must finally be abandoned". In contrast, Deacon (1988) who compared different parts of the brain with each other instead of comparing the part with the

			Sectors of the frontal lobe				
	Hemisphere	Frontal	Central core†	Dorsal‡	Mesial‡	Orbital‡	
Subj. 1	1,159,055	421,848	94,353	189,117	87,612	50,766	
Subj. 2	1,173,480	457,068	74,372	225,587	94,988	62,121	
Subj. 3	1,042,058	369,743	73,263	171,792	81,353	43,335	
Subj. 4	1,127,374	403,752	82,568	188,705	87,081	45,398	

Table 4 Volume of brain structures in four humans*

*Values are given in cubic millimeters and include both hemispheres.

†Central core includes white matter and subcortical structures.

\$Sectors include cortex and immediately underlying white matter.

whole, concluded on the basis of the same data set that the prefrontal cortex is considerably larger in humans.

The comparative data available from the studies that include actual measurements on the structure of the hominoid frontal lobe are incomplete. Most of the attempts to analyze these existing data are of interest, but the results cannot be tested with rigorous statistical methodologies because they are based on a limited sample size with the ape species in particular having a very poor representation. If issues regarding the evolution of the frontal lobe and of human cognition are to be addressed, investigations cannot be based mostly on monkey species or other mammals, but they have to focus on the structure of the brain of the apes, as that compares with the human brain. Finally, the complexity of the frontal lobe has to be taken into consideration and several components such as total volume of the lobe, surface area, prefrontal cortex and white matter have to be analyzed.

We believe that a new database has to be created using modern and reproducible techniques across all hominoids in a consistent manner that will build on previous attempts to quantify aspects of the frontal lobe. Here we report the beginning of such an effort by investigating the total volume of the frontal lobe and of its three major components (dorsal, mesial, orbital), while issues regarding other aspects of its organization like size of the prefrontal cortex or white matter must await further investigation. We apply quantitative techniques which may be used to reproduce our results in other samples, and we include all hominoids and a larger sample of human brains than did previous comparative studies. Although our present sample is still small, we discuss our preliminary volumetric results with relative confidence because the variability noted in the human brains is relatively low (Table 4). We are more cautious regarding the surface measurements, because of the observed variability in surface area measurements (Blinkov & Glezer, 1968).

Relatively large frontal lobes are not a uniquely human feature

When the absolute size of the hemispheres and the frontal lobes of the macaque, gibbon, great apes and humans are compared, dramatic differences in the volume are clearly present. Nevertheless, when the relative volumes are considered, markedly large differences across species diminish and the human values do not stand out.

Human frontal lobe size is not relatively larger than expected on the basis of the non-human primates. The human value is almost identical to that of the chimpanzee (36.7 and 35.9%, respectively). The orang-utan and the gorilla (35.3 and 32.4%) come next, followed by the

gibbon and the macaque values (31·1 and 28·1%, respectively). If instead of considering each ape species separately, we were to compare humans and apes, then the values would be $36\cdot7\%$ (mean of four individuals) *vs.* $34\cdot5\%$ for the three great apes. Our results of cortical surface size (Table 2) on the other hand, just like those on volume, do not suggest a larger human frontal lobe, when compared with the chimpanzee (e.g. chimpanzee $38\cdot1\%$ and human $35\cdot9\%$). However, we obviously need to have larger samples to reach firm conclusions.

The fact that we compared living human brains with post-mortem ape brains could raise the theoretical concern that the effects of fixation in our post-mortem ape brains could be responsible for a relatively larger frontal lobe in the apes due to differential shrinkage within the hemisphere. However, this is difficult to reconcile with the fact that the values we obtained in the human specimen are even smaller than those obtained in the living subjects (33% of the total volume as compared with $35 \cdot 5 - 38 \cdot 9\%$).

Our combined preliminary results on the volume and surface of the frontal lobe support previous work that questioned the assumption of disproportionately large frontal lobes in the human brain (Lebouq, 1928; von Bonin, 1948;Holloway, 1968). Such findings are in accord with the idea that many structures of the human brain, and not just the frontal lobes, are as large as would be expected from a primate brain of the human size (Passingham, 1973; Hofman, 1988; Jerison, 1991). Nevertheless, the results of this study do not suggest that humans do or do not have a larger prefrontal cortex. We do not address this point nor the question of cortex alone. More studies such as the ones on volume of the prefrontal cortex (Uylings & van Eden, 1990), on volume and organization of the individual areas of the prefrontal cortex (Semendeferi, 1994) and on gyrification (Zilles *et al.*, 1988), will help answer this question.

There is variation in the size of the frontal lobe among the great apes

In general, our data seem to point out that larger brains have larger frontal lobes (Figure 3). In spite of the small size of the sample, size differences in the frontal lobes do not seem to be related only to differences in overall brain size. Although the absolute size of the hemispheres and the frontal lobes in the great apes form one major plateau, there is variation among them that shows species differences regarding their relative size. Such differences might reflect species-specific adaptations, functional specializations and/or major evolutionary events relating to changes in the organization of the hominoid brain, but a larger sample is necessary.

In the gorilla, the volume of the entire hemisphere is larger than that of the orang-utan or the chimpanzee, but the absolute size of the frontal lobe is similar to that of the other apes (Figure 2). Thus in this species, the frontal lobe is relatively smaller than it is in the other great apes. This small relative size of the gorilla frontal lobe is interesting. A possible explanation could be that our specimen is an outlier and further investigations in a larger sample will have to follow.

On the basis of the large overall size of the gorilla brain (largest among the great apes) one would anticipate that the gorilla frontal lobe would be larger than the chimpanzee or the orang-utan. On the other hand, considering the evolutionary history of the hominoids (orang-utan line having split first from the rest of the great apes—see also next section), one could also have expected the gorilla and orang-utan ratios to be reversed. Our data suggest that the gorilla frontal lobe is specialized, but examination of more specimens is needed before the argument can be taken any further and associations are attempted between this part of the gorilla brain and some of the frontal lobe functional attributes.

Frontal lobes may have become relatively larger during hominoid and not hominid evolution

We suggest that our data may point to the following trend. If the hominoid species studied are ordered with respect to their evolutionary relationships (human, chimpanzee, gorilla, orang-utan, gibbon), a trend of increase can be seen in the size of the frontal lobes. The trend goes beyond changes related to the absolute increase of the brain. It involves an increase in the relative size of the frontal lobes among species with minor differences in their absolute brain size (orang-utan, gorilla and chimpanzee). The frontal lobe in the orang-utan is relatively smaller than in the chimpanzee and the human; in two out of the three hominoids that form the African ape/human group (chimpanzee and human) the relative values are the highest and are almost identical.

If we are to consider the principle of shared and derived character states used in evolutionary reconstructions, then the size of the frontal lobe in extant hominoids that have similar absolute brain sizes might point to a continuous increase in the relative size of the frontal lobes during hominoid evolution. After the split of the common African hominoid stock, no further substantial increase can be detected in the line leading to modern humans because the relative size of the human frontal lobe is almost identical to that of the chimpanzee. Thus, larger frontal lobes can be identified as a hominoid trait and not as a trait related particularly to hominid evolution. This preliminary conclusion, based on a small sample of all hominoids will have to be further investigated.

Unless use of a larger sample changes significantly the present relationships, we would suggest that the frontal lobes have been increasing during hominoid (ape and human) evolution more than the rest of the hemisphere. This increase is associated with overall increases in brain size, but may also be associated with genetic events in favor of a consistently larger frontal lobe during hominoid evolution.

Sectors of the frontal lobe

The relative sizes of the dorsal, mesial or orbital sectors of the frontal lobe also do not stand out in the human brain. As a matter of fact, going against expectation is the fact that the dorsolateral cortex (related to such distinctive human capacities as manipulation of space, numbers and language) is not relatively larger in the human brain, than predicted by the rest of the hominoids. Another interesting case is the orbital sector of the orang-utan which is much smaller in this species (10.7%) than in any of the other hominoids. In another study involving measurements on histological sections of additional orang-utan brain specimens (not scanned prior to sectioning), one of us noted a smaller orbital sector (Semendeferi, 1994). Thus this finding is intriguing, especially if one considers that: (1) recent evidence links the ventromedial frontal sector with social behavior (Damasio, 1994) and (2) the orang-utan is known for its more solitary life.

Regarding the surface area, a similar picture emerges with the distribution of values of the three sectors being similar to that of the volumes (Table 2) with one noticeable exception: the orbital sector of the human brain has larger cortical surface than the mesial sector (which represents a reverse of the relationship noted between those two sectors when volumes were considered).

Conclusions

Questions regarding the evolution of the frontal lobe and of human cognition cannot be addressed adequately unless differences and similarities in the underlying neural circuitry of humans and all extant apes can be identified. Although some data available from older studies on the primate brain have been used by several investigators to address these issues, problems regarding the methodology used in the measurements, the incomplete representation of hominoid species and the small sample included makes the use of new data sets imperative. This report reflects an effort in this direction. Our conclusions are preliminary and we plan to increase our sample and investigate further the organization of the frontal lobes.

In this study we have examined the overall size of the frontal lobe and not every aspect of the frontal lobe organization. Both size and organization of the brain changed during hominid evolution. A more comprehensive analysis involving, among others, the size of the cortex and of the white matter, as well as the organization of individual cortical areas, is necessary before issues regarding specialized human cognition and behavior can be fully addressed.

We believe we can safely conclude that the idea of relatively "larger human frontal lobes" is incorrect. Protruding foreheads present in ancient Greek sculptures might have only been used to symbolize the functions presumed to be associated with the frontal lobes, a symbolism erroneously translated into larger volumes by 18th and 19th century phrenologists. The notion of an association between large frontal lobes and high mental capacities within the "natural ladder" of beings, survived throughout the 20th century and prevails even today, despite the fact that the reports are conflicting and the criticisms are many.

Contrary to the general and popular idea in favor of a uniquely large human frontal lobe, our study reveals that human and chimpanzee frontal lobes show no differences in their relative volume. The values for the chimpanzee frontal lobe fall within the range of the human relative values. The relative values for the orang-utan brain fall close to the lower end of the human range, and unless no variation exists in the size of the gorilla frontal lobe, the range of values in this species should also show some overlap with the range of the human values. What aspects of the complex organization of the frontal lobes differ among hominoids remains to be investigated.

Humans do have a much larger hemisphere and frontal lobe in absolute terms, but not a larger frontal lobe than is expected from a primate of our brain size. Our results suggest that, contrary to the general expectation, a relatively large frontal lobe is not a uniquely human feature, but is shared among all hominoids. In other words, "man has precisely the frontal lobe which he deserves" (Bonin, 1948).

Acknowledgements

We wish to thank Metro Washington Park Zoo, Gladys Porter Zoo, Houston Zoo, Toledo Zoo and Busch Gardens Zoo for providing us with ape specimens, W. Yuh for the scanning of the specimens, C. K. Brown for the statistical analysis, J. Spradling and K. Jones for technical support and E. Armstrong, D. Tranel, K. Rockland, C. Rockland, H. Jerison and L. Aiello for their helpful comments. We also thank R. Barton for his helpful comments and statistical analysis of our data. Supported by NIH NINDS PO1 NS19632.

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