



Are planum temporale and sylvian fissure asymmetries directly related? A MRI study in great apes

Claudio Cantalupo^{a,b}, Dawn L. Pilcher^b, William D. Hopkins^{a,b,c,*}

^a Language Research Center, Georgia State University, Atlanta, GA 30303, USA

^b Division of Psychobiology, Yerkes Regional Primate Research Center, Emory University, Atlanta, GA 30322, USA

^c Department of Psychology, Berry College, Mount Berry, GA 30149, USA

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Abstract

In humans and great apes, both the planum temporale (PT—part of Wernicke's area) and the sylvian fissure (SF) in the left cerebral hemisphere have been consistently shown to be larger than the corresponding structures in the right hemisphere. The greater length of the SF in the left hemisphere is commonly thought to be a direct consequence of the larger expansion of the PT in the same hemisphere. However, there is a lack of studies that have attempted to directly assess the tenability of this hypothesis. To address this lack of data, we collected magnetic resonance images (MRI) of the brain in 28 apes. The surface area of the PT and the length of the pre- and post-central SF were measured in each hemisphere using image acquisition and analysis software. In accordance with previous findings, the PT was markedly larger in the left hemisphere than in the right, and there was also a leftward asymmetry of the SF, particularly of its post-central section. However, we found no statistically significant correlation between asymmetry of the PT and of the post-central SF, whereas we did find evidence of a positive association between asymmetry of the post-central SF and of the inferior parietal lobe. These results are congruent with those of a recent study with human subjects [Neuropsychiatry, Neuropsychology and Behavioral Neurology 12 (1999) 1]. Overall, this converging evidence leads us to question the widely accepted notion of a direct relationship between PT and SF asymmetries and to consider possible implications of this finding for the study of the evolutionary origin of PT asymmetry in primates.

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1. Introduction

Since the mid 1970s, an increasing number of studies have consistently shown neuroanatomical asymmetries in non-human primates that closely match well-known patterns of asymmetry in the human brain (Bradshaw & Rogers, 1993; Galaburda, 1984; Hopkins, Pilcher, & Cantalupo, in press; Pilcher, Hammock, & Hopkins, 2001; Witelson, 1977). In particular, one of the most striking similarities between great ape and human brain asymmetries has been reported for the planum temporale (PT, a triangular area situated on the superior temporal gyrus), and Brodmann's area 44 (A44, located in the inferior frontal gyrus). In both humans (Foundas, Leonard, & Heilman, 1995; Geschwind & Levitsky, 1968; Shapleske, Rossell, Woodruff, & David, 1999) and great apes (Cantalupo & Hopkins, 2001; Gannon, Holloway, Broadfield, & Braun, 1998; Hopkins, Marino, Rilling, & MacGregor, 1998), the

PT and A44 are larger in the left hemisphere compared to the right. The left PT in humans coincides with part of Wernicke's area, and A44 with part of Broca's area. Both cortical areas are widely believed to be involved in linguistic functions in humans. This close association between morphological asymmetry and language has been the basis for the long-standing assumption that cortical asymmetries were exclusively human traits, directly associated with language acquisition. However, the finding that great apes show a human-like asymmetry in the PT as well as in A44 indicates that the origin of asymmetry in language-related areas of the human brain can be better understood on the basis of a comparative approach instead of considering it as a uniquely human phenomenon. In this line, the study of neuroanatomical asymmetries in the great apes could also offer important insight into unresolved issues in the human literature. For instance, it is well established that the sylvian fissure (SF) in the human brain is longer in the left hemisphere than in the right, particularly in its post-central extent (Foundas, Faulhaber, Kulynych, Browning, & Weinberger, 1999; Rubens, Mahowald, & Hutton, 1976).

* Corresponding author. Tel.: +1-404-727-8235; fax: +1-404-727-3270.
E-mail address: lrcbh@rmy.emory.edu (W.D. Hopkins).

Interestingly, a longer left SF has been shown to be a characteristic of great apes (Hopkins, Pilcher, & MacGregor, 2000; Yeni-Komshian & Benson, 1976). Given that the portion of superior temporal gyrus occupied by PT demarcates part of the post-central extent of SF, the greater length of the SF in the left hemisphere is commonly seen as a direct consequence of the larger expansion of the PT in the same hemisphere (Galaburda, 1984; Galaburda, 1995). However, there is a clear lack of evidence directly in support of this assumption. To the best of our knowledge, only one study has assessed whether SF and PT surface area asymmetry measures are actually directly correlated in human brains. In this study, Foundas et al. (1999) used magnetic resonance imaging (MRI) techniques to assess PT and pre- and post-central SF asymmetries in a sample of adult humans. Consistent with previous findings, both the post-central SF and PT surface area were found to be overall larger in the left hemisphere. However, no correlation was found between the two measures of asymmetry. Although great apes show population-level leftward asymmetries for both PT and SF measures, to our knowledge no study has as yet directly assessed whether such measures are directly related to one another. Clearly, more studies are needed before definitive conclusions can be drawn regarding the relationship between PT and posterior SF asymmetries. To this end, we measured the surface area of PT and the length of pre- and post-central SF in the brains of 28 great apes using MRI. The aim of this study was three-fold: first, to assess whether in great apes, as in humans, the overall asymmetry of SF is mainly due to its post-central section. Second, to obtain a better estimate of the whole PT surface area than reported in a previous MRI study in great apes by using a modified tracing procedure. Third, to systematically assess whether any relationship exists between PT and SF asymmetry measures. We hypothesized that if SF asymmetry in great apes was a direct consequence of asymmetry in PT, then a strong correlation between the asymmetry measures of the two structures should be evident, in particular between PT and post-central SF.

2. Methods

2.1. Subjects

Magnetic resonance images (MRI) of the brain were collected in a sample of 28 great apes (14 males and 14 females), which included 18 chimpanzees (*Pan troglodytes*), four bonobos (*Pan paniscus*), four orangutans (*Pongo pygmaeus*), and two gorillas (*Gorilla gorilla*). All of the apes were housed at the Yerkes Regional Primate Research Center (YRPRC), with the exception of two gorillas and one orangutan who were housed at Zoo Atlanta. Seven of the MRI scans were performed on cadaver chimpanzee brains, whereas the remaining subjects were alive and healthy at time of data collection. The cadaver specimens were stored

in a solution of water and 10% formaldehyde for intervals ranging from 1 week to 5 years.

2.2. Procedure

Subjects were first immobilized by ketamine injection (10 mg/kg) and subsequently anaesthetized with propofol (40–60 mg/(kg h)) following standard procedures at the YRPRC. Subjects were then transported to the MRI facility at Emory University Hospital. The subjects remained anaesthetized for the duration of the scans as well as the time needed to travel between YRPRC and Emory Hospital (total time ~ 2 h). At the MRI facility, the living apes were placed in the scanner chamber in a supine position with their head fitted inside the human-head coil. The cadaver brains were placed inside the human-knee coil with the dorsal side up. Scan duration ranged between 40 and 80 min as a function of brain size. This project involved using two MRI machines (Phillips, Model 51), each with 1.5 Tesla superconducting magnets. For all subjects, T1-weighted images were collected in the transverse plane using a gradient echo protocol (pulse repetition = 19.0 ms, echo time = 8.5 ms, number of signals averaged = 8, and a 256 × 256 matrix). These scan parameters were developed in previous studies (Holloway, 1980; Hopkins et al., 1998), and provided excellent resolution of the brain areas of interest to this study. After completing MRI procedures, the subjects were returned to the YRPRC and temporarily housed in a single cage for 6–12 h to allow the effects of the anesthesia to wear off, after which they were returned to their home cage. The archived MRI data were stored on optical diskettes and transported to an Easy Vision workstation for post-image processing.

2.2.1. Planum temporale measurements

To measure the surface area of PT the MRI scans were aligned in the coronal, sagittal and axial planes and cut into 1 mm coronal slices using multiplanar reformatting software (Easy Vision). Coronal rather than sagittal image sequences were used because these provide the best direct assessment of the full depth of the sylvian fossa, of which the planum is its floor (see (Shapleske et al., 1999) for a review). The anterior border of PT was defined by the most frontal slice showing Heschl's gyrus (HG). The posterior border was defined by the most caudal slice showing SF. Once the anterior and posterior borders were delineated, the depth of SF (i.e. width of PT) on each slice was measured from the superolateral margin of the superior temporal gyrus (in two brains PT could not be measured because HG was missing in one or both the hemispheres). Depth measures were taken up to the lateral ridge of HG in all the slices where HG was present (normally, HG was no longer present in slices proximal to the posterior border of PT, see Fig. 1). This procedure, originally implemented by Larsen, Høien, Lundberg, and Ødegaard (1990) and Larsen, Ødegaard, Grude, and Høien (1989), in studies with human subjects resulted in a more complete

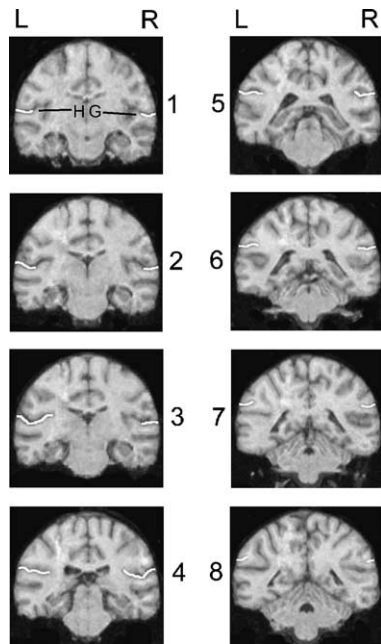


Fig. 1. Sequence of coronal MRI slices through the posterior part of the sylvian fissure of a chimpanzee brain. Slice 1 is the most anterior section and slice 8 is the most posterior section of the brain. The extent of the right and left planum temporale in each slice is marked with a white line. L: left; R: right.

assessment of the full extent of PT area than reported in a previous MRI study in great apes (Hopkins et al., 1998). PT width was measured to the closest 0.1 mm using a mouse-driven computer-guided cursor available in a PC implementation of NIH-Image (Scion Image, Scion Corporation, Frederick, MD). Following a well-established procedure in the human literature (Shapleske et al., 1999; Steinmetz et al., 1990), an estimate of the PT surface areas (in mm²) was computed as the sum of the cumulative PT depth measures for each slice within a hemisphere and multiplied by the slice thickness.

2.2.2. Sylvian fissure measurements

Similar to the procedures used for reformatting MRI scans used in PT measurement, the brain was oriented in the coronal, sagittal, and axial planes, but cut into 1 mm sagittal slices. These sagittal slices provided an excellent overall perspective of the SF. Following a common procedure in the human literature (Foundas et al., 1999; Rubens et al., 1976), we used the central sulcus (CS) as anatomical landmark to divide the SF into anterior (or pre-central) and posterior (or post-central) segments. There were two sagittal planes of interest. These planes were labeled the “Insular”, which was the last sagittal image before the opening of the Insula, and the “Medial” plane, or the image that fell numerically half-way between the Insular plane and the first most lateral sagittal slice showing the SF (for details see (Hopkins et al., 2000)). The SF and CS were identified on these planes using MRI imaging software that allowed simultaneous view of a scan in three mutually orthogonal planes (EasyVision), and a vertical line was drawn from the terminating point of the CS across the horizontal plane of the SF. The point of intersection between this line and the SF was used to delineate the anterior (SF-ANT) and posterior (SF-POST) sections of the SF (see Fig. 2). The necessity to assess the asymmetry of SF-ANT and SF-POST separately originated from studies with humans that have shown that the typical population-level leftward asymmetry is more pronounced in the posterior segments of the SF (see Foundas et al., 1999). Moreover, assessing SF-POST asymmetry was instrumental to testing the long-standing assumption that PT asymmetry is directly related to the asymmetry of SF, particularly of its posterior extent. As for the PT data, a free-hand line tool was used to trace the anterior and posterior length of the SF (in mm).

2.3. Data analysis

For both the PT and SF measures, an asymmetry quotient (AQ) was derived using the formula $(R - L) / [(R + L) \times 0.5]$.

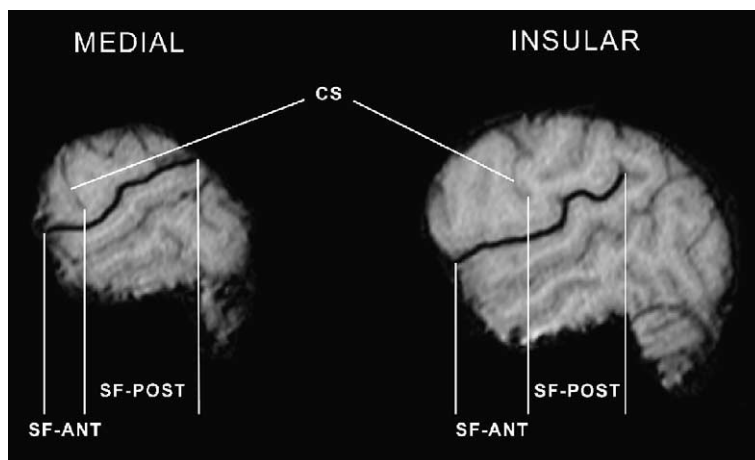


Fig. 2. MRI images from the sagittal plane of a chimpanzee brain demonstrate the scans that were identified as the Medial and Insular regions for measurements of SF-ANT and SF-POST (traced in black). CS: central sulcus.

The sign of the resulting value indicated the direction of asymmetry (positive value = right hemisphere bias; negative value = left hemisphere bias), and the absolute value reflected the magnitude of asymmetry. Following a common procedure in studies with human subjects, apes with AQ scores > 0.025 were categorized as having a rightward hemispheric asymmetry, whereas apes with values < -0.025 were categorized as having a leftward hemispheric asymmetry. Apes whose scores were between -0.025 and 0.025 were classified as having no consistent bias.

3. Results

3.1. PT measurements

A majority of apes exhibited a left hemisphere asymmetry in PT surface area (PT-AREA). In particular, 19 subjects showed a left hemisphere bias, 3 had a right, and 4 exhibited no consistent bias (see Table 1). This distribution departed statistically from equality of proportions ($\chi^2(2) = 18.538$, $P < 0.001$), and the number of individuals with a left hemisphere asymmetry was significantly greater than the number with either a right hemispheric bias ($z = 3.411$, $P = 0.001$) or no hemispheric bias ($z = 3.123$, $P = 0.003$). PT-AREA was larger in the left hemisphere in 12 of 17 chimpanzees, 2 of 3 bonobos, both gorillas, and 3 of 4 orangutans. The data were also analyzed at the continuous level by performing one-sample t -test on the AQ scores. The mean AQ score for the whole sample was -0.150 (± 0.048 S.E.). This value was found to be different from an expected mean of zero ($t(25) = 3.084$, $P = 0.005$), thus confirming the presence of a population-level leftward asymmetry in PT-AREA. To assess for possible differences between AQ scores obtained from cadaver versus live brains, an independent sample t -test was performed. No statistically significant difference was found ($t(24) = -1.291$, ns). Similarly, independent sample t -tests performed on both direction and strength of AQ measures failed to reveal sex differences on PT-AREA asymmetry. Finally, no statistically significant correlation was observed between age of the subjects and PT-AREA asymmetry measures.

3.2. SF measurements

To confirm that this method consistently revealed a population-level asymmetry similar to previous reports (Hopkins et al., 2000), Pearson's correlation coefficient and one-sample t -tests were performed for the sum of the anterior and posterior SF length. The AQ scores for the Medial and Insular levels were positively correlated ($r = 0.435$, $n = 28$, $P = 0.021$) and both indicated a statistically significant leftward asymmetry in the average AQ score for whole SF length (Medial: $t(27) = 2.283$, $P = 0.031$, Insular: $t(27) = 3.553$, $P = 0.001$). Therefore, in further

Table 1
Individual asymmetry quotients (AQ) for PT surface area and post-central SF length

	Sex	PT-AREA		SF-POST	
		AQ	Bias	AQ	Bias
Chimpanzee					
Austin	M	-0.011	N	-0.178	L
Carmichael	M	-0.032	L	-0.221	L
Chuck	M	-1.186	L	-0.271	L
Donald	M	-0.255	L	-0.143	L
Hoboh	M	-0.329	L	0.080	R
Jimmy Carter	M	-0.327	L	0.071	R
Lazarus	M	-0.065	L	0.145	R
Merv	M	0.043	R	0.005	N
Storer	M	0.019	N	-0.303	L
Ada	F	-0.195	L	-0.007	N
Anna	F	0.016	N	-0.190	L
Cheri	F	-0.072	L	-0.080	L
Jeannie	F	-0.061	L	0.101	R
Kengee	F	-0.215	L	0.017	N
Lana	F			-0.074	L
Lulu	F	-0.115	L	0.073	R
Mary	F	-0.090	L	0.087	R
Panzee	F	0.021	N	-0.048	L
Bonobo					
Bosondjo	M			-0.518	L
Brian	M	0.115	R	-0.031	L
Jill	F	-0.138	L	-0.156	L
Lorel	F	-0.314	L	-0.358	L
Gorilla					
Kekla	F	-0.189	L	-0.064	L
Kinyani	F	-0.044	L	-0.141	L
Orangutan					
Mentubar	M	0.083	R	-0.151	L
Minyak	M	-0.057	L	-0.127	L
Molek	M	-0.261	L	-0.094	L
Hati	F	-0.227	L	-0.229	L

Sex: M: male, F: female. Bias: L: left hemisphere, R: right hemisphere, N: no bias.

investigations we used a collapsed measure of the Medial and Insular measures. To investigate any population-level asymmetries in the SF, one-sample t -tests were performed. Consistent to that previously reported, measures of whole SF length (SF-WHOLE) revealed a marked population-level leftward asymmetry ($t(27) = 3.643$, $P = 0.001$). However, an interesting pattern emerged when the AQs for the pre-central (SF-ANT) and post-central SF (SF-POST) were considered. The SF-ANT measures did not show any consistent asymmetry ($t(27) = 0.304$, ns), whereas, the SF-POST AQ scores were consistently leftward at the population-level ($t(27) = 3.453$, $P = 0.002$). Specifically, there were 19 apes with a leftward bias, 6 with a rightward bias, and 3 with no difference between the hemispheres for the length of posterior SF, a distribution that differs from chance ($\chi^2(2) = 15.5$, $P < 0.001$; see Table 1). Binomial tests revealed that there were significantly more individuals showing a leftward bias than a rightward one ($z = 2.6$, $P = 0.009$) or no bias ($z = 3.411$, $P < 0.001$). As for

the PT data, no difference was found between cadaver and live brain AQ scores (SF-WHOLE: $t(26) = 1.144$, ns; SF-POST: $t(26) = -0.699$, ns). Possible sex and age differences on the AQ scores were assessed using an independent samples t -test and Pearson's correlation coefficient, respectively. These tests revealed no statistically significant sex or age differences for the directional or absolute values of the SF AQ scores.

3.3. Relationship between PT and SF measurements

Pearson's correlation coefficient was used to assess whether there was a relationship between the asymmetries observed in PT-AREA and SF (SF-WHOLE and SF-POST). No statistically significant correlation was found (PT-AREA and SF-WHOLE: $r = -0.067$, $n = 26$, ns; PT-AREA and SF-POST: $r = 0.202$, $n = 26$, ns). To thoroughly assess the possibility that some association existed between PT and posterior SF asymmetries, SF-POST was further divided in two sub-sections (see Fig. 3). The first sub-section (SF-PT) corresponded to the posterior portion of SF-POST, delimited by the anterior and posterior margins of PT. For each subject, an estimate of the length of SF-PT could be obtained in each hemisphere from the number of 1 mm coronal MRI slices in which PT could be observed. The second sub-section (SF-noPT) corresponded to the anterior portion of SF-POST, delimited by the terminating point of the CS and the anterior margin of PT. The length of SF-noPT was computed for each subject by subtracting the length of SF-PT from that of SF-POST. AQ measures were then obtained for each subject for both SF-PT and SF-noPT, and correlation coefficients were computed between these measures and the AQ scores for SF-POST and PT-AREA. As shown in Table 2, a clear pattern emerged. In accordance

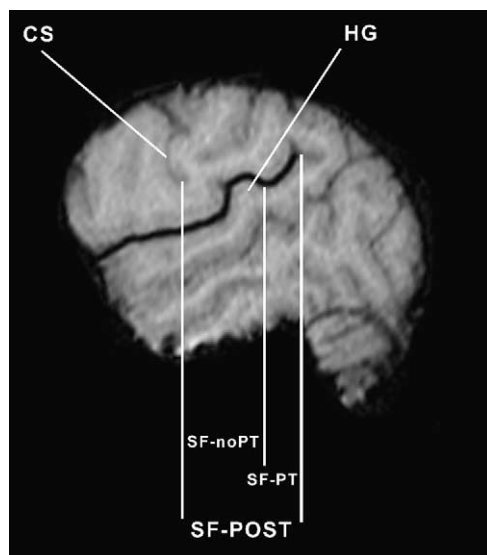


Fig. 3. Subdivision of SF-POST into SF-PT and SF-noPT sections. HG: Heschl's gyrus; CS: central sulcus.

Table 2

Pearson's correlation coefficients between PT and SF asymmetry measures

Coefficients	PT-AREA	SF-PT	SF-noPT
SF-PT			
r	0.706	–	–
P	<0.001	–	–
N	26	–	–
SF-noPT			
r	–0.062	–0.245	–
P	0.736	0.228	–
N	26	26	–
SF-POST			
r	0.202	0.225	0.796
P	0.322	0.270	<0.001
N	26	26	26

with results consistently reported in the human literature (Galaburda, 1984; Galaburda, 1995), SF-PT asymmetry in our great ape sample had a strong positive correlation with PT-AREA asymmetry. Interestingly, however, SF-PT measures showed no correlation with SF-POST or SF-noPT asymmetries. On the other hand, SF-POST and SF-noPT asymmetries did show a strong positive association.

4. Discussion

The present study offers clear evidence in support of the notion that non-human primates, the great apes in particular, show asymmetries in perisylvian regions of the brain that originally were thought to be unique to humans (Galaburda, 1984; Witelson, 1977). First of all, the surface area of the PT in great apes, as in humans, is consistently larger in the left than in the right hemisphere (Foundas et al., 1995; Geschwind & Levitsky, 1968; Shapleske et al., 1999). This finding is congruent with and extends those of Gannon et al.'s (1998) in chimpanzee cadaver specimens and Hopkins et al.'s 1998 earlier MRI study on great apes. Second, the SF of the great apes is also overall longer in the left hemisphere. Moreover, we provide the first evidence that such asymmetry in great apes, like in humans (Foundas et al., 1999), is predominantly due to the post-central section of SF. Third, although the great apes in this study show a consistent leftward asymmetry for both PT surface area and post-central SF length, the two asymmetries appear to be independent of one another. Interestingly, this finding is remarkably consistent with that reported by Foundas et al. (1999) in a recent study with human subjects. Overall, this evidence from humans and great apes clearly does not support the widely accepted and largely unquestioned assumption that asymmetry of the post-central SF is a direct consequence of the differential expansion of the PT in the two hemispheres. From a logical standpoint it may be argued that the failure to detect a statistically significant correlation does not allow per se any definitive conclusion

on whether or not a relationship between the two asymmetries exists. Nonetheless, it seems reasonable to expect that, if there was a strong causal connection between PT and SF asymmetries, direct evidence of such connection should clearly emerge from different studies. No such evidence has been reported to date.

Notably, a different pattern seems to emerge from the present study in great apes and that by Foundas et al. (1999) in humans. In both studies, asymmetry of the post-central portion of SF did not correlate with PT asymmetry, but it did correlate with other asymmetry measures. In particular, Foundas et al. (1999) found in humans a positive correlation between the length of posterior SF and the length of the anterior portion of the inferior parietal lobule. Similarly, by dividing the posterior SF into anterior (noPT) and posterior (PT) portions, we found that, in great apes, only the asymmetry of the noPT portion was a predictor for the asymmetry of the whole posterior SF. Interestingly, the noPT portion of the posterior SF delineates, with its dorsal side, the anterior section of the ventral border of the inferior parietal lobe. Overall, this pattern of converging evidence from humans and great apes supports the idea that asymmetries of the post-central portion of SF may be directly linked to asymmetries of the parietal lobe (Galaburda, 1984). Interestingly, evidence of greater length and width of parts of the parietal lobe in the left hemisphere have been reported in humans (Foundas et al., 1999; Galaburda, 1984; Kertesz, Black, Polk, & Howell, 1986). Another possible scenario could imply a direct relationship between the asymmetry of SF-POST and asymmetry of Heschel's gyrus (HG), which lies on the temporal lobe just anterior to the PT. In fact, the posterior extent of the noPT section of SF-POST in our study delineates, with its ventral side, the dorsal border of HG (see Fig. 3). So it could be conjectured that leftward SF asymmetry might be linked not exclusively to asymmetries of the parietal lobe, but also to that of HG. Yet, this possibility seems unlikely given reports in the human literature of HG as usually comprising two gyri in the right hemisphere, but only one in the left (for a review see (Shapleske et al., 1999)). However, to the best of our knowledge there is a lack of studies that have directly assessed whether or not SF and HG asymmetries are directly correlated in both humans and great apes. Therefore, more direct comparisons of SF length to both parietal lobe and HG volumes are needed in humans and great apes to thoroughly assess whether posterior SF asymmetries are associated with asymmetry of the parietal lobe and/or of HG.

As already noted elsewhere (Galaburda, 1984; Galaburda, 1995; Gannon et al., 1998; Hopkins et al., in press; Yeni-Komshian & Benson, 1976; Witelson, 1977), the similarity of perisylvian asymmetry patterns between human and non-human primates (the great apes in particular) clearly indicates that an interpretation of the origin of such patterns should be cast in evolutionary terms instead of being confined exclusively to the human species. In this line, the evidence discussed here has important

methodological implications for the study of the evolutionary origin of PT asymmetry. Many studies have shown SF asymmetries in a variety of non-human primates (Hopkins et al., 2000; LeMay, 1976; LeMay, Billing, & Geschwind, 1982; Yeni-Komshian & Benson, 1976) and human fossil endocasts (Holloway, 1980; LeMay, 1976; LeMay, 1984; Tobias, 1987), and such asymmetries have commonly been interpreted as reflecting asymmetry of perisylvian regions, usually the PT. However, the validity of such inferences is clearly questioned by the finding that SF and PT asymmetries seem to be unrelated in both humans and great apes. Instead, the evidence presented here suggests that SF asymmetries could be used as reliable indicators of asymmetry of the inferior temporal lobe. Although more research is needed to thoroughly assess this finding, the current study clearly indicates the necessity to further explore the relationship between hemispheric differences in SF anatomy and asymmetry in adjacent areas.

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