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Observer-Independent Characterization of Sulcal Landmarks and Depth Asymmetry in the Central Sulcus of the Chimpanzee Brain

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Abstract

The central sulcus (CS) divides primary motor and sensory cortex in many mammalian brains. Recent studies have shown that experiential factors can influence the volume and lateralization of the CS in both human and nonhuman primates. In this study, we sought to define specific landmarks and the depth of the CS region corresponding to the motor-hand area of chimpanzees for comparison with humans using a novel, observer independent method applied to sample of 32 MRI scans. Our results showed that the dorsal-ventral location of the motor-hand region is comparable between humans and chimpanzees, though the depth of the CS was significantly greater in humans compared to chimpanzees. We further found that CS area corresponding to the motor-hand area was significantly larger in the hemisphere contralateral to the chimpanzees preferred hand. The methods employed here offer some potential advantages over traditional region-of-interest in the comparative study of cortical organization and gyrification in primates and are discussed.

The central sulcus (CS) is one of the most prominent sulci of the mammalian brain and divides the primary motor and sensory cortex. For both the primary motor and sensory cortices, there are designated regions along the dorsal-ventral plane that correspond to various regions of the body, or the so-called motor and sensory homunculi (Bailey, von Bonin, & McCulloch, 1950; Penfield & Boldrey, 1936). For example, stimulation of primary cortex at different point along the dorsal-ventral plane results in movements of different limbs, fingers and oro-facial musculature indicating that there is a topographic organization of the body within the precentral gyrus.

One of the oldest landmarks noted in the CS of the human brain is the “pli de passage fronto-parietal moyen” (PPFM) initially noted by Broca (1888). The “pli de passage” is a cortically buried depression in the central portion of the CS and more recently described by others as the motor-hand area of the precentral gyrus or KNOB (Alkadhi & Kollias, 2004; Boling, Olivier, Bittar, & Reutens, 1999; Herve, Crivello, Perchey, Mazoyer, & Tzouio-Mazoyer, 2006; White, Lucas, Richards, & Purves, 1994; Yousry et al., 1997). The KNOB is an omega or epsilon shaped external sulcal configuration of the CS which results from the primary motor cortex

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displacing the CS posteriorly in the region that roughly correspond to the location of the hand along the motor cortex (Yousry et al., 1997). Stimulation studies using rTMS and recent fMRI studies have identified the KNOB region as corresponding to the location of hand and finger movements, thus confirming its location along the motor strip (Boroojerdi et al., 1999; Dassonville, Zhu, Ugurbil, Kim, & Ashe, 1997; Pizzella, Tecchio, Romani, & Rossini, 1999; Rumeau et al., 1994; Yousry et al., 1997). Studies in human subjects have recently shown that the KNOB region is larger in the hemisphere contralateral to the subjects preferred hand, suggesting that the KNOB may be an anatomical landmark of handedness (Amunts et al., 1997; Hammond, 2002). Furthermore, studies in human subjects have also shown that variation in the volume and lateralization of the KNOB region is associated with manual motor experiential factors, such as musical aptitudes and years of experience playing certain instruments such as the piano (Caulo et al., 2007; Gaser & Schlaug, 2003; Li et al., in press).

Variation in the volume and asymmetry of the KNOB are not restricted to human brains. Recent studies have described the KNOB in great ape brains (see Figure 1) but not in more distantly related Old or New World monkeys, suggesting that the evolution of increasing motor and prehensile skills in Hominids may have resulted in some cortical reorganization of the CS (W. D. Hopkins & Pilcher, 2001). It has further been reported that individual differences in handedness for coordinated bimanual actions in chimpanzees are associated with variation in lateralization in the motor-hand area with subjects having a larger KNOB in the hemisphere contralateral to their preferred hand (Dadda, Cantalupo, & Hopkins, 2006; W. D. Hopkins & Cantalupo, 2004).

One aim of the current study was to further examine the organization of the CS morphology in chimpanzees using an observer-independent approach rather than a standard region-of-interest (ROI), user-dependent method. As is the case in human brains (Caulo et al., 2007), there is considerable individual variability in the organization of the CS in chimpanzees and region-of-interest approaches to quantification of the motor-hand area (here in referred to as the PPFM) are challenging due to sulcal variability. The problem of variability in CS sulcal morphology introduces potential challenges with respect to establishing reliability in measurement across different observers. This can be particularly problematic when considering comparative studies in CS morphology between species. Furthermore, the ROI approaches assess CS depth in 2-dimensions rather than the three dimensions which arguably better reflects the true nature of CS variability and organization. Thus, one aim in this study was to characterize sulcal landmarks of the CS in chimpanzees using observer-independent software and procedures previously employed with humans and to compare the results between the two species.

A second aim of this study was to examine whether variation in regions of the CS corresponding to the sulcal landmarks used to quantify the “pli de passage” differ between chimpanzees classified as left- or right-handed. Specifically, in humans, the PPFM is the lowest sulcal point that lies between the maximum superior (SP) and inferior depth (IP) points, along the dorsal-ventral plane of the CS. The region of cortex that encompasses these three anchor points roughly corresponds to the central region of the CS and, at least descriptively, appears to overlaps with the position of the motor-hand area or KNOB region. As noted above, we have previously found that right- and left-handed chimpanzees have significantly larger KNOB volumes in the hemisphere contralateral to their preferred hand, when quantified in two dimensions (Dadda, Cantalupo, & Hopkins, 2006; W. D. Hopkins & Cantalupo, 2004). We hypothesized that if the region of cortex that surrounds the PPFM region encompasses the motor-hand cortex, then significant differences in asymmetry would be found between right- and non-right-handed apes.

Method

Subjects

Magnetic resonance images (MRI) were collected in a sample of 32 captive chimpanzees including 12 males and 20 females. The apes ranged in age from 13 to 44 years of age (Mean = 20.18, s.d. = 10.22). All the chimpanzees were housed at the Yerkes National Primate Research Center (YNPRC) of Emory University.

MRI Image Collection

Scans were obtained at the time the chimpanzees were being surveyed for their annual physical examinations. For all scans, subjects were first immobilized by ketamine (10 mg/kg) or telazol (3–5mg/kg) and subsequently anaesthetized with propofol (40–60 mg/(kg/h)) following standard procedures at the YNPRC. Subjects were then transported to the MRI facility. The subjects remained anaesthetized for the duration of the scans as well as the time needed to transport them between their home cage and the imaging facility (total time ~ 1.5 h). Subjects were placed in the scanner chamber in a supine position with their head fitted inside the human-head coil. Scan duration ranged between 40 and 60 min as a function of brain size.

Twenty-seven chimpanzees were scanned using a 3.0 T scanner (Siemens Trio, Siemens Medical Solutions USA, Inc., Malvern, Pennsylvania, USA) at the YNPRC. T1-weighted images were collected using a three-dimensional gradient echo sequence (pulse repetition=2300 ms, echo time=4.4 ms, number of signals averaged=3, matrix size =320 X 320, with .6 X .6 X.6 resolution). The remaining 24 chimpanzees were scanned using a 1.5T Phillips machine (The Netherlands). 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 x 256 matrix). After completing MRI procedures, the subjects were returned to the YNPRC 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 transferred to a PC running Analyze 8.1 (Mayo Clinic, Mayo Foundation, Rochester, Minnesota, USA) software for post-image processing.

Post-Image Processing

The sequence of post-image processing steps performed from the images are shown in Figures 2a to 2h. The pipeline of processing used to extract central sulcus from the raw T1-weighted image derives from a pipeline initially dedicated to the human brain and freely distributed as a BrainVISA toolbox (<http://brainvisa.info>) (Mangin et al., 2004). The human-dedicated pipeline has been used previously for at least 5000 different subjects. Some tuning of this pipeline has been required to account for specificities of the chimpanzee anatomy. The different processing steps are the following: First, correction of the spatial inhomogeneities of the signal, which prevent direct association between the signal intensity and the nature of the tissue, were performed (see Fig 2.A). The estimation of the spatially smooth bias field (see Fig 2.B) used to restore the signal intensity was performed via minimisation of the signal entropy (Mangin, 2000). After correction, each tissue intensity distribution was stable across the brain (see Fig 2.C). Second, automatic analysis of the signal histogram and mathematical morphology was then used to compute a binary mask of the brain (see Fig 2.D). This approach is built on the fact that the brain is surrounded by dark areas corresponding to skull and cerebro-spinal fluid. Therefore, once the range of intensities corresponding to brain tissue have been defined by histogram analysis, brain segmentation mainly amounts to splitting the connections with external structures like the optical nerves. For the chimpanzee anatomy, some specific tuning had to be applied relative to the human-dedicated processing performed by BrainVISA (Mangin, Coulon, & Frouin, 1998). For some chimpanzees indeed, the largest object in the image after splitting connections turns out to be the muscles. Hence, in order to reliably select

the brain, we had to introduce an additional constraint relative to the localization of the brain in the center of the head. Once the brain mask had been defined, the mask was split into three parts corresponding to hemispheres and cerebellum (see Fig 2.E) (Mangin, Regis, & Frouin, 1996). In order to improve the robustness of this procedure, the intersection of the anterior and posterior commissures with a mid-sagittal slice are manually specified and used to align the target brain with a template chimp brain.

After a mask has been defined for each hemisphere, a negative mould of the white matter was computed (Mangin, Regis, & Frouin, 1996). The outside boundary of this mould results from a 5mm morphological closing of the masked hemisphere, filling up the folds. The inside boundary is the grey/white interface computed with topology preserving deformations assuring the spherical topology of the mould (see Fig 2.F). The mould is finally skeletonized in order to detect the cortical fold as crest surfaces of the 3D MR image located inside the mould (Mangin et al., 2004). These surfaces stem from a morphological watershed process iteratively eroding the mould from the lightest intensities to the darkest intensities. Topological constraints guarantee that the resulting surfaces have no holes. The end result is a set of topologically elementary surfaces located along the darkest part of the fold corresponding to CSF (see Fig 2.G). These elementary surfaces are split further when a deformation of the deepest part of the fold indicates the presence of a buried gyrus. The clues allowing the detection of buried gyri are embedded in the curvature of the grey/white interface (Mangin et al., 2004). Finally, the folds making up the central sulcus are selected manually by the user using a 3D visualization interface (see Fig 2.H). Usually, the central sulcus is made up of two folds merged at the level of a buried gyrus.

The selected CS is meshed using a triangular mesh, and the resulting surface is parameterized in order to create a normalized x-y coordinate system (Coulon et al., 2006). The parameterization process is constrained by four features: the bottom ridge of the sulcal mesh (i.e., the sulcal fundus), the top ridge (i.e., at the brain envelope), and the end points of the sulcus where these top and bottom ridges joined. From these features, two coordinate fields (x and y) are extrapolated over the entire mesh surface, by solving the heat equation on the surface, with the constraints behaving as constant heat sources (Coulon et al., 2006). This results in a smooth x-y coordinate system, with mesh surface points localized in respect to the features. The coordinate system extended along the length of the CS from the superior (y=1) to the inferior end of the sulcus (y=100), and from the brain envelope (x=1) to the fundus (x=100) of the sulcus (see Figure 3). Depth was measured at 100 sulcal length positions in a superior-to-inferior progression along the parameterized sulcal mesh surface. Position 1 was adjacent to the interhemispheric fissure and position 100 was adjacent to the Sylvian fissure (see Figure 3). At each position y along the length, the depth is computed by measuring a geodesic distance (in millimeters) from x=1 to x=100 at constant y.

Determining the SP, PPFM and IP

Following the previously explained procedure, the individual depth measures for each hemisphere at each of the 100 positions were outputted to a text file. The largest depth value between positions 1 to 50 was determined to be the maximum superior point (SP) of the CS while the largest depth value found between positions 51 to 100 was determined to be the maximum inferior point (IP). Between the SP and IP positions, the lowest depth value was determined to be the PPFM. These depth values and their respective positions along the dorsal-ventral plane of the CS were calculated for each subject and these served as the primary dependent measures. In addition, we computed the size of the PPFM region for each hemisphere following the formula: $[PPFM_size = ((depth(IP) + depth(SP)) / 2.0) - depth(PPFM)]$. Finally, we also computed an asymmetry coefficient for the SP, PPFM and IP depths as well as the PPFM_size following the formula $[AQ = (R - L) / (R + L) * .5]$ where R and L indicated the

respective depth or size values of the CS for the right and left hemispheres. Positive values indicated a rightward asymmetry while negative values indicated a leftward asymmetry.

Handedness

To assess the chimpanzees' handedness, we used previously published data on a task requiring coordinated bimanual actions referred to as the TUBE task. We selected this measure because previously studies in chimpanzees have linked variation on this task with asymmetries in the motor-hand area (Dadda, Cantalupo, & Hopkins, 2006; W. D. Hopkins & Cantalupo, 2004). Moreover, hand preference for the TUBE task has been shown to be reliable and consistent during test-retest assessments separated by as long as 6 years (W. D. Hopkins et al., 2001). The methods and procedures used to assess handedness on each of these tasks have been previously described and we provide a brief summary below (W. D. Hopkins, 1995). For the TUBE task, peanut butter is smeared on the inside edges of poly-vinyl-chloride (PVC) tubes approximately 15 cm in length and 2.5 cm in diameter. Peanut butter is smeared on both ends of the PVC pipe and is placed far enough down the tube such that the subjects cannot lick the contents completely off with their mouths but rather must use one hand to hold the tube and the other hand to remove the substrate. The hand of the finger used to extract the peanut butter was recorded as either right or left by the experimenter. Each chimpanzee was tested on two occasions so that a minimum of 20 responses were obtained from each subject. Individual hand preferences were classified on the basis of *z*-scores computed based on the frequency of right and left hand use for the TUBE task. Subjects with *z*-scores of 1.96 or higher were classified as right-handed whereas chimpanzees with *z*-scores < 1.96 were classified as non-right-handed.

Results

Descriptive Statistics

CS Morphology—Shown in Figure 4 are the mean CS depths for the chimpanzee sample in the left and right cerebral hemispheres. We have plotted the data from human subjects by Cykowski et al. (2008) for comparison to our data. As can be seen, as with humans, there is variability along the dorsal-ventral plane of the CS with the depth shallow at the most dorsal and ventral points and the greatest depths in the central regions. Moreover, as has been described in humans, there are peaks and troughs along the CS corresponding to the SP, PPFM and IP. We were able to compute the SP, PPFM and IP depths in 28 right hemispheres and 30 left hemispheres. Within the right hemisphere, 89% of the subjects (25 / 28) showed the pattern of CS folding in which the IP depth was greater than the SP depth while this was the case in 90% (27/ 30) of the left hemispheres. These values are similar to those reported in 55 human subjects wherein the PPFM could be identified in 89% of the right and 96% of the left hemispheres, respectively (Cykowski et al., 2008). Table 1 shows the mean positions and depths of the SP, PPFM and IP for all sulci displaying these three features in the chimpanzee sample. Data from human subjects reported by Cykowski et al. (2008) have been provided for comparison to the chimpanzee results. First, as can be seen, the relative positions along the CS of the SP, PPFM and IP are comparable between humans and chimpanzees, and indeed, located in nearly identical locations. Second, the depths of the SP, PPFM and IP are greater in the humans compared to the chimpanzees.

Shown in Figures 5a and 5b are the mean AQ values for the entire sample as well as the right- and non-right-handed chimpanzees for each CS point along the 100 positions. We compared the AQ values between sex and the two handedness groups and none of these results reached statistical significance, after adjusting for multiple comparisons. Nonetheless, as can be seen, there is considerable variability in CS asymmetry along the dorsal-ventral plane and there are a number of points of difference between right- (*n* = 10) and non-right-handed (*n* = 16) individuals (see below).

Handedness—Though we have published data on the TUBE task in sample sizes much larger than those reported here (Hopkins, 1995), here we provide a short description of the data for this sample. Based on the z -scores, there were 14 right-handed and 18 non-right-handed chimpanzees. This difference did not significantly differ from a chance or random distribution of handedness.

Sex and Handedness Effects

Rather than focus on the entire CS, we next considered the potential influence of sex on the specific dimensions of CS morphology. For these analyses, we computed the mean IP, PPFM and SP depths and positions as well as the PPFM_size for each subject by averaging the observed values between the two hemispheres. We then compared the mean values between male and female chimpanzees using an independent sample t -test and no significant differences were found. We also compared the AQ values for the IP depth, PPFM depth, SP depth and PPFM_size in the male and female chimpanzees and found no significant differences. Shown in Table 2 are the mean IP, PPFM and SP depth values for each sex and hemisphere. We next evaluated whether the AQ values for IP, SP and PPFM depth as well as PPFM_size differed significantly for right- ($n = 10$) and non-right-handed ($n = 16$) chimpanzees. The mean AQ values for each measure are shown in Figure 5. The only significant difference was in PPFM_size with right-handed chimpanzees showing a greater leftward asymmetry compared to non-right-handed apes $t(25)=2.12, p < .05$.

Correlation Between CS Morphology Measures

Finally, for each hemisphere, we correlated the IP, PPFM and SP depth measures with the PPFM_size to assess what relationships, if any, were evident among these different dimensions of CS morphology. The results are shown in Table 3. Most consistent were the associations between SP and PPFM depth and PPFM depth and PPFM_size. Greater depth values for SP were associated with larger depth values in PPFM depth. Additionally, chimpanzees with greater PPFM depth values had smaller PPFM_sizes.

Discussion

One aim of the proposed study was to assess the application of an observer-independent approach to the measurement of variability in CS morphology, particularly as it relates to the PPFM in chimpanzees. The results clearly indicate that this approach worked quite effectively with the chimpanzee MRI scans and we were able to reliably detect the PPFM using a specified algorithm in nearly 90% of the hemispheres. These percentages were very similar to values reported from human MRI scans and therefore indicate that the procedures and software manipulations work effectively in chimpanzees.

With respect to the sulcal landmarks used to define the PPFM, when comparing the chimpanzee data reported here with the human data reported by Cykowski et al. (2008), the relative positions of the main landmarks including SP, PPFM and IP along the dorsal-ventral plane of the CS were virtually identical between the species. Thus, the location of the PPFM is comparable between chimpanzees and humans and further reinforces the view that the PPFM corresponds to the location of the hand region of the primary motor cortex. The average depth of the sulcal landmarks SP, PPFM and IP were deeper in humans compared to chimpanzees. This suggests that the gyrification of the human CS is greater in humans than chimpanzees. Previous comparative studies on gyrification in human and nonhuman primate brains and endocasts have shown that human brains are significantly more gyrified in terms of number and complexity of sulci than nonhuman primates (Armstrong, Zilles, & Schleicher, 1993; W. D. Hopkins, Cantalupo, & Tagliatela, 2007; Rilling & Insel, 1999). However, as far as we know, there

are no published data in which human and nonhuman primates have been directly compared on the depths of common sulci and therefore these findings are unique and novel.

The implications of these findings are two fold. First, interpretation of the biological significance of the difference in CS depth is not obvious when considered within the context of brain size differences between humans and chimpanzees. Specifically, because humans have a brain that is roughly three times larger than chimpanzees after adjusting for differences in body weight, it is simple to attribute the greater CS depth to the need for greater cortical folding in human brains; however, to what extent the difference in CS depth between humans and chimpanzees scale to brain size or neocortical surface area or volume is not clear. At face value, the depths of SP, PPFM and IP do not scale to the commonly reported three-fold brain size differences between humans and chimpanzees because the depths of these landmarks are less than a 3:1 ratio (see Table 1). Similarly, the PPFM_size for the humans was 6.80 compared to 3.85 for the chimpanzees, roughly a two-fold difference. Thus other factors or variables must be governing these differences that are not simply allometric in nature. Indeed, comparisons in depths of other sulci between humans and chimpanzees, such as the Sylvian fissure, would be of interest because there could be larger or smaller differences depending on selective expansion of brain regions that play important roles in motor, sensory or cognitive specializations of each species. Second, the application of the post-image analyses of sulcal landmarks and depth, as used in this study, would be of great interest to additional comparative studies of the CS morphology (see Kochunov et al., in press). For example, several authors have noted that the precentral gyrus of the orangutan is quite large relative to other great apes and humans (W. D. Hopkins & Pilcher, 2001; Semendeferi & Damasio, 2000; Semendeferi, Lu, Schenker, & Damasio, 2002) (see also, Figure 1). Though no specific comparative studies have been performed, the application of the algorithms and procedures employed here could provide for a direct comparative analysis of the PPFM in all great apes. Similarities or differences in these landmarks could potentially yield important information on the evolution of the motor cortex in relation to different adaptations for locomotion or posture, which are quite pronounced in orangutans compared to other anthropoid apes.

With respect to handedness, we found that right and non-right-handed chimpanzees had significantly larger PPFM_sizes in the hemisphere contralateral to the preferred hand. These results are consistent with previous reports showing an association between handedness and lateralization in the central region of the CS of chimpanzees. The results are also consistent with recent studies in human subjects that have found that asymmetries in the surface area of the CS differs between left- and right-handed individuals and that these results were experience dependent (Kloppel, Mangin, Vongersichten, Frackowiak, & Siebner, in press). The results reported here further indicate that variation in the size of the PPFM is inversely associated with the depth of the PPFM. Thus, subjects with less buried PPFM have a larger volume of CS cortex that lies between the SP and IP points along the CS. This suggests that the relationship between handedness and PPFM_size is manifest as a more shallow CS cortex depth between the SP and IP points. To what extent the development of handedness determines variation in PPFM_size or vice versa remains unclear but should be investigated in future studies.

In summary, the results of this study indicate that the motor-hand area of the precentral gyrus is located in relatively the same position along the dorsal-ventral plane of the CS in humans and chimpanzees. The depth of the three major sulcal landmarks that define the motor-hand area are greater in humans compared to chimpanzees suggesting greater cortical folding and gyrification within the motor-hand area. The methods and procedures employed here potentially provide for a unique approach to the comparative study of cerebral organization that has potential value for understanding different evolutionary factors that have shaped the Hominoid brain. Future studies should increase sample sizes to assess potential relationships with behavioral processes as well as consider additional species that share common sulci.

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Figure 1.
Axial views of the CS and motor-hand region (KNOB) in 4 great ape species.

Figure 2.

Pipeline of image processing extracting central sulcus from a raw T1-weighted image. A: raw data corrupted by spatial inhomogeneities, B: estimated bias field, C: restored image, D: brain mask segmentation, E: hemisphere segmentation, F: white matter mask, G: skeleton of a negative mold of white matter, H: selection of central sulcus.

Figure 3. Parameterization of a CS mesh, with the x and y coordinate fields, the resulting coordinate grid, and the sulcal depth plotted against the y coordinate.

Figure 4. Mean CS depth ($\pm$ s.e.) for the 100 positions for humans and chimpanzees. Data for human subjects are from Cykowski et al. (2008).

Figure 5.
AQ measures (+/- s.e.) of the CS for (a) the entire sample and (b) for right- and Non-Right-handed Chimpanzees.

Figure 6.
Mean AQ values (+/- s.e.) for right- and Non-right-handed chimpanzees for the SP, PPFM, IP and PPFM_size measures.

Table 1
Mean Depths and Location of SP, PPFM and IP in Chimpanzees and Humans

Location	Right Hemisphere			Left Hemisphere		
	SP	PPFM	IP	SP	PPFM	IP
Chimpanzee	38.4	49.2	61.8	40.2	51.1	61.9
s.e.	1.33	1.34	.64	1.33	1.22	.95
Human	37.3	46.3	61.5	34.1	46.4	61.7
s.e.	.91	.74	.78	.96	.80	.79
Depth						
Chimpanzee	13.5	10.5	15.2	13.2	10.5	15.1
s.e.	.48	.49	.21	.29	.35	.21
Human	22.7	17.0	24.9	23.3	16.3	26.3
s.e.	.48	.40	.40	.29	.40	.37

Depth values are in mm. Human data are from Cykowski et al. (2008)

Table 2

Descriptive Statistics for Different Measurement of CS Morphology in Male and Female Chimpanzees

	Males		Females	
	Left	Right	Left	Right
SP Depth	13.44 (.32)	13.47 (.33)	13.98 (.37)	13.05 (.38)
PPFM Depth	10.96 (.45)	10.93 (.63)	10.20 (.39)	10.16 (.45)
IP Depth	15.23 (.38)	15.23 (.27)	14.66 (.33)	14.97 (.23)

Table 3

Intercorrelations between CS Morphology Measures

	SP	PPFM	IP	PPFM_Volume
<i>Left Hemisphere</i>				
SP	----			
PPFM	.557**	----		
IP	.331*	.191	----	
<i>Right Hemisphere</i>				
SP	----			
PPFM	.355+	----		
IP	.133	-.028	----	

+ $p < .10$,
* $p < .05$,
** $p < .01$.