Published in final edited form as:

Neuroimage. 2008 August 15; 42(2): 491–497. doi:10.1016/j.neuroimage.2008.05.014.

Gray Matter Asymmetries in Chimpanzees as Revealed by Voxel-Based Morphometry

William D. Hopkins^{1,2}, Jared P. Tagliabata², Adrien Meguerditchian³, Talia Nir², Natalie M. Schenker⁴, and Chet C. Sherwood⁴

¹Department of Psychology, Agnes Scott College, Decatur, Georgia 30030

²Division of Psychobiology, Yerkes National Primate Research Center, 954 Gatewood Road, Atlanta, Georgia 30329

³Department of Psychology, Research Center in Psychology of Cognition, Language & Emotion, University of Provence, 29, Av. Robert Schuman, 13621 Aix-en-Provence, France.

⁴Department of Anthropology, The George Washington University, Washington, DC 20052

Abstract

Determination of whether nonhuman primates exhibit neuroanatomical asymmetries would inform our understanding of the evolution of traits in humans that show functional hemispheric dominance, including language and handedness. Here we report the first evidence of population-level asymmetries in the chimpanzee neocortex using voxel-based morphology (VBM). MRI scans of the brain were collected in a sample of 31 chimpanzees including 9 males and 22 females, and the resulting images were segmented into gray matter, white matter and CSF. Gray matter images were then co-registered to a template and these normally oriented volumes were flipped on the left-right axis to create mirror volumes. In total, significant asymmetries were found in 13 regions including several that have been described previously in great apes using traditional region-of-interest approaches. The results from this VBM analysis support previous reports of hemispheric lateralization in chimpanzees and reinforce the view that asymmetries in the central nervous system are not uniquely human.

Dating back to the time of Dax, Broca and Wernicke, it has been well documented that the human brain is asymmetrically organized, particularly for regions associated with handedness and language functions. For example, the planum temporale (PT) and frontal operculum (FO), regions corresponding to the classically-defined language centers of the human cerebral cortex, tend to be larger in the left compared to right hemisphere, particularly among right-handed individuals (Beaton, 1997; Foundas et al., 1998; Shapleske et al., 1999). Historically, the presence of behavioral and neuroanatomical asymmetries has been considered unique to hominin evolution (Corballis, 1992; Ettlinger, 1988; Warren, 1980); however, recent studies in nonhuman animals, and particularly nonhuman primates, have challenged this view (Hopkins, 2007; Rogers and Andrew, 2002). For instance, post-mortem and *in vivo* imaging studies have revealed population-level leftward asymmetries in the PT and FO of great ape brains (Cantalupo and Hopkins, 2001; Cantalupo et al., 2003; Gannon et al., 1998), suggesting

Correspondence and reprint requests should be addressed to Dr. William D. Hopkins, Division of Psychobiology, Yerkes National Primate Research Center, Emory University, Atlanta, Georgia 30322. E-mail: whopkin@emory.edu or whopkins@agnesscott.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

that neuroanatomical asymmetries are not uniquely human but rather reflect a shared trait that was present in the last common ancestor of humans and great apes. These previous studies of great ape neuroanatomical asymmetries have been assessed using traditional region-of-interest (ROI) approaches that utilize sulci and other anatomical landmarks to define specific areas of the brain, such as the PT and FO (Cantalupo and Hopkins, 2001; Gannon et al., 1998; Hopkins et al., 1998). Consequently, some authors have suggested that observer bias might explain the reported patterns of neuroanatomical asymmetries in nonhuman primates (Crow, 2004). It has also been suggested that sulcal variability for some cortical regions in great apes, notably FO, is too inconsistent across subjects for reliable definition and quantification based solely on anatomical landmarks (Sherwood et al., 2003). To specifically address these limitations of ROI-based approaches, we used voxel-based morphology (VBM) to assess neuroanatomical asymmetries in chimpanzees.

VBM has been used effectively to measure gray and white matter asymmetries in humans (Good et al., 2001; Luders et al., 2004; Watkins et al., 2001) and offers several advantages over traditional ROI techniques for measuring brain asymmetries. First, VBM allows for an assessment of asymmetries in tissue composition (e.g. gray and white matter) rather than morphology, which provides more specific information on regional variation in gyrification and connectivity within specific brain areas. Second, VBM minimizes problems with observer bias that may be associated with manual tracing or other ROI techniques. Lastly, individual variation in morphological landmarks used to define specific ROIs is minimized with VBM because differences between hemispheres are based on voxel intensity differences as determined by an automated segmentation computer application (thus, an objective measure) rather than defined by subjective criteria, such as an observer's determination of the borders of specific sulci. In short, VBM offers a powerful alternative approach for assessing lateralization of the nervous system in human and nonhuman primates.

Methods

Subjects

Magnetic resonance imaging (MRI) scans were obtained from a sample of 31 captive chimpanzees including 9 males and 22 females. All the chimpanzees were members of a captive colony housed at Yerkes National Primate Research Center (YNPRC) in Atlanta, Georgia. The subjects ranged in age from 6 to 50 years (Mean = 21.61, s.d. = 11.69).

Image Collection and Procedure

Subjects were first immobilized by telazol injection (2–6 mg/kg) and subsequently anesthetized with propofol (10 mg/(kg/h) following standard procedures at the YNPRC. Subjects were then transported to the MRI facility. The subjects remained anesthetized 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 ~ 2 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 50 min as a function of brain size. The chimpanzees were scanned using a 3.0 T scanner (Siemens Trio, Siemens Medical Solutions USA, Inc., Malvern, Pennsylvania, USA). 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).

After completing MRI procedures, the subjects were returned to the YNPRC and temporarily housed alone in a 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 7.0 (Mayo Clinic, Mayo Foundation, Rochester, Minnesota, USA) software for post-image processing.

Image Normalization and Registration

Once the images were acquired, the skulls were removed from the images and the image of each subject's brain was co-registered to a template of a chimpanzee brain (Rilling et al., 2007). The chimpanzee brain template was created using a two-tiered procedure. Initially, the MRI scans of 8 chimpanzees (subjects included in this study) were placed in stereotaxic orientation using AFNI software and then averaged together into a single image. Next, each individual MRI scan was spatially normalized to this template using an affine transformation. Subsequently, all the spatially normalized MRI scans were averaged to create the template.

For the VBM analysis, each individual MRI scan was co-registered to the template described above using three-dimensional voxel registration with a linear transformation (Analyze 7.0, Mayo Clinic). The MRI scans were then segmented into gray, white and CSF tissue using FSL (Analysis Group, FMRIB, Oxford, UK) (Smith et al., 2004). From the segmented images, an average gray matter (GM) template was made from the entire sample of scans by averaging all of the GM volumes together. Subsequently, each individual segmented GM volume was registered to the GM template. Each subject's GM volume was then flipped 180° in the left-right axis to create a mirror-image brain volume (see Figure 1). Each of these flipped volumes was then re-registered to the GM chimpanzee template. For each ape, the mirror image GM volumes were then subtracted from the normally-oriented volumes (Figure 1). An average difference volume was created from all of the individual difference volumes, and this volume was low pass filtered with a 5mm isotropic kernel. Voxel-by-voxel t -tests were calculated and significant clusters were identified as three or more contiguous voxels on three or more consecutive 2mm slices in the axial plane with intensity values ≥ 6.00 (i.e. 9 total voxels; 72 mm³). Significance levels of the observed t -values were set at $t \geq 6.00$ ($p < .0001$) to adjust for multiple comparisons.

Results

Hemispheric Asymmetries as Assessed from VBM

The centroid position and average t -statistic of significant GM clusters are shown in Table 1 (see Figure 2 for reference points of X, Y, and Z). As a reference, we also indicate cytoarchitectural areas corresponding to the location of GM clusters based on the parcellation of chimpanzee neocortex from Bailey et al. (1950), with the analogous areas from Brodmann (1909). Note that centroid positions are referenced on the X,Y, and Z coordinates derived from our matrix for the chimpanzee brain and do not refer to standard coordinate systems used with the human brain, such as the Talairach space. Significant population-level asymmetries were found in 13 clusters including 6 in the left hemisphere and 7 in the right hemisphere (see Figure 3a to 3d). Leftward asymmetries were found for the superior frontal gyrus, superior and inferior rostral gyrus, inferior frontal gyrus, the planum temporale, supramarginal gyrus and the occipital gyri. Rightward asymmetries were found for the medial frontal gyrus, precentral gyrus including the motor-hand area, the superior frontal gyrus, postcentral gyrus, angular gyrus and the temporooccipital transition zone.

Significant GM clusters projected on the surface of a 3D-rendered chimpanzee brain (see Figure 3a) reveal a right frontal, left occipital torque asymmetry. Indeed, significant clusters were found in both the right frontal pole and left posterior occipital lobe (Table 2 and Figure 3a). Specifically, the right hemisphere contains significant clusters in the frontal and anterior temporal regions and a complete lack of GM density asymmetry in the occipital lobe (Figure 3a). In contrast, within the left hemisphere, there is a notable absence of clusters on the surface of the frontal lobe but a significant number in the parietal and occipital cortex. Cerebral torque asymmetries have been described similarly in the human brain using these criteria (Watkins et al., 2001).

Individual Differences in Relation to ROI assessments

We next considered the association between asymmetries as detected by VBM in comparison to results obtained using traditional ROI approaches. We were particularly interested in examining individual differences and the consistency of results from these different methods in the anatomical homologues to the human language centers, notably the PT and the IFG. As noted above, we have previously reported significant leftward asymmetries for both of these regions using traditional ROI approaches (Cantalupo and Hopkins, 2001; Cantalupo et al., 2003). To evaluate the concordance between VBM and ROI for the assessment of asymmetries in the IFG and PT, we performed some additional analyses. Specifically, using the X, Y, and Z centroid coordinates derived from the VBM analysis (see Table 1), we positioned a 5×5 voxel box over each subject's GM difference volume at those centroid coordinates and averaged the voxels within this region. Positive values indicate a left hemisphere bias, a value of 0 no bias, and negative values indicate a right hemisphere bias. The distribution of individual asymmetries using VBM was compared to results based on previous ROI analyses.

The method used to assess PT asymmetries in great apes by Cantalupo et al. (2003) was used in this study (see Figure 4). To measure the surface area of the PT, the MR scans were aligned in the coronal plane and cut into 1 mm slices using multiplanar reformatting software (Analyze 7.0, Mayo Clinic). The anterior border of the PT was defined as the most anterior slice in which Heschl's gyrus (HG) was visible. The posterior border was defined as the most caudal slice including the Sylvian fissure (SF). Once the anterior and posterior borders were delineated, the depth of the SF (i.e., width of the PT) on each slice was measured from the superolateral margin of the superior temporal gyrus. 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). PT width was measured to the closest 0.1 mm using a mouse-driven computer-guided cursor. An estimate of the PT surface areas (in mm^2) was computed as the sum of the cumulative PT depth measures for each slice within a hemisphere multiplied by the slice thickness.

The ROI method used to estimate the IFG was performed in the axial plane. The posterior border of the IFG was the precentral inferior sulcus (PCI) and the anterior border was the fronto-orbital sulcus (see Figure 5). The entire gyrus between these two sulci was traced with the edge of the brain serving as the lateral border while the medial ends of the PCI and fronto-orbital sulci served as the medial borders. The areas were traced on successive 1 mm slices and the area measures were summed across slices to derive a volume of the IFG for the left and right hemispheres. Both PCI and FO had to be present to trace the gyrus lying between these two sulci.

For both the PT and IFG, asymmetry quotients (AQ) were derived following the formula $[(AQ = (L-R) / ((R+L) * .5)]$ with positive values reflecting left hemisphere biases and negative values representing right hemisphere biases. For comparison to the VBM analyses, chimpanzees with positive AQ values were classified as having right hemisphere asymmetry and those with negative AQ values were classified as having a left hemisphere bias.

Shown in Table 2 are the individual summed VBM and ROI AQ values for each subject as well as the overall distribution of chimpanzees showing a left or right bias as indicated by each analysis. A McNemer test comparing the two distributions in the 31 apes in this study was not statistically significant for the PT but did reach significance for the IFG ($\chi^2 = 2.35$, $n = 31$, $p < .03$), suggesting similar results between the two techniques for PT but somewhat different results for the IFG. We also correlated the summed VBM values for the IFG and PT with their respective ROI AQ values. Though no significant association was found for the IFG ($r = .187$, $p > .05$), a significant positive association was found for the PT ($r = .677$, $p < .02$) indicating that chimpanzees with larger leftward ROI asymmetries had similarly larger leftward VBM

asymmetries. Lastly, one-sample *t*-tests on the AQ scores of VBM data revealed a significant leftward asymmetries for the PT $t(30) = 2.85, p < .01$ and borderline significant effect for the IFG $t(30) = 1.82, p < .08$, largely confirming previous ROI analyses on these brain regions, albeit in a smaller samples of apes.

Discussion

VBM analysis of chimpanzee brain MRI scans revealed significant population-level GM asymmetries in several neocortical regions. Of specific note were several significant findings as they relate to previous reports of population-level asymmetries in great apes using ROI approaches (see Table 2).

First, leftward asymmetries in the posterior parietal and occipital lobes and rightward asymmetries in the frontal regions likely reflect the well known right-frontal, left-occipital petalia asymmetry originally described in the human brain and subsequently shown to be present in great apes (LeMay, 1985; Pilcher et al., 2001). While some authors have suggested that the cerebral torque asymmetry is uniquely human (Barrick et al., 2005) and associated with translocation and subsequent accelerated evolution of the protocadherin 11X/Y gene pair in hominins (Williams et al., 2006), the results presented here are not consistent with this view and point more strongly to homology in cerebral torque asymmetries between chimpanzees and humans.

Second, the leftward GM asymmetry found in the IFG and posterior superior temporal lobe are consistent with previous reports of asymmetries in chimpanzees (Cantalupo and Hopkins, 2001; Cantalupo et al., 2003; Gannon et al., 1998; Hopkins et al., 2000) and VBM findings in humans (Good et al., 2000; Watkins et al., 2001). Moreover, the distribution of leftward and rightward asymmetries as revealed by VBM are comparable to, and do not differ significantly from, those found using ROI approaches (see Table 2). In human brains, similar consistencies between VBM and ROI analyses have been reported, at least with respect to the PT (Luders et al., 2004; Watkins et al., 2001). The consistency between findings using VBM and traditional ROI approaches suggests that the asymmetries in the chimpanzee brain are robust and not attributable to observer bias or other extraneous factors, as has been suggested (Crow, 2004).

The concordance between results based on VBM and ROI methods were more pronounced for the PT compared to the IFG and this warrants some discussion. We believe that one potential explanation for the less pronounced association for the IFG is that the ROI analysis included tissue that is more ventral than the significant cluster identified using VBM. Sherwood et al. (2003) have noted that there is considerable variability in the bifurcation patterns of PCI in brains of chimpanzees and gorillas. The VBM analysis used here seemed very sensitive to detecting this variability. Indeed, based on the VBM analysis, it could be argued that the sulcal variability and complexity in PCI is greater in the left compared to right hemisphere.

Several other interesting asymmetries were identified using VBM that were not anticipated and have not been reported previously in great apes. Specifically, the evidence of population-level asymmetries in the angular and supramarginal gyrus is particularly noteworthy given their implication in certain linguistic disorders such as alexia and agraphia (Damasio & Geschwind, 1984). As far as we know, there are no previous reports of asymmetries in either the angular or supramarginal gyri in nonhuman primates.

With respect to the angular gyrus, anatomical and VBM studies in humans have reported leftward asymmetries (e.g., Watkins et al., 2001), a pattern of results opposite to those found in chimpanzees. The function of the angular gyrus in humans has been linked to auditory and written processing of words and speech (Damasio and Geschwind, 1984). With greater selection for cross-modal integration in the semantic-lexical network during human language

evolution, changes in the functional properties of the left and right angular gyri might have been altered in humans compared to chimpanzees. It is of note that a recent positron emission tomography study in chimpanzees revealed bilateral activation of the angular gyrus during passive auditory processing of species-specific sounds, implicating this region in some auditory perception (Tagliabata, Russell, Schaeffer, & Hopkins, 2008).

In sum, we present the first evidence of population-level asymmetries in a nonhuman primate using VBM. Some of the asymmetries reported here have been documented in great apes using traditional ROI approaches, suggesting not only the robustness of neuroanatomical asymmetries in chimpanzees, but also that VBM is a valid approach to the assessment of asymmetries in nonhuman primates. The validation of VBM in our chimpanzee sample further suggests that this methodology can be applied to future comparative studies of brain organization and lateralization in species that vary considerably in gyral and sulcal morphology.

Acknowledgement

This work was supported in part by NIH grants RR-00165, NS-42867, NS-36605, HD-38051, HD-56232 and F32DC007823. We are very grateful to the veterinarian staff for assisting in the care of the animals during scanning.

Literature Cited

- Barrick TR, Mackay CE, Prima S, Maes F, Vandermeulen D, Crow TJ, Roberts N. Automatic analysis of cerebral asymmetry: an exploratory study of the relationship between torque and planum temporale asymmetry. *NeuroImage* 2005;24:678–691. [PubMed: 15652303]
- Beaton AA. The relation of planum temporale asymmetry and morphology of the corpus callosum to handedness, gender and dyslexia: A review of the evidence. *Brain and Language* 1997;60:255–322. [PubMed: 9344480]
- Cantalupo C, Hopkins WD. Asymmetric Broca's area in great apes. *Nature* 2001;414:505. [PubMed: 11734839]
- Cantalupo C, Pilcher D, Hopkins WD. Are planum temporale and sylvian fissure asymmetries directly related? A MRI study in great apes. *Neuropsychologia* 2003;41:1975–1981. [PubMed: 14572530]
- Corballis, MC. *The lopsided brain: Evolution of the generative mind*. New York: Oxford University Press; 1992.
- Crow T. Directional asymmetry is the key to the origin of modern *Homo sapiens* (the Broca-Annett axiom): A reply to Rogers' review of *The Speciation of Modern Homo Sapiens*. *Laterality: Asymmetries of Body, Brain and Cognition* 2004;9:233–242.
- Damasio AR, Geschwind N. The neural basis of language. *Annual Review of Neuroscience* 1984;7:127–147.
- Ettlinger GF. Hand preference, ability and hemispheric specialization. How far are these factors related in the monkey? *Cortex* 1988;24:389–398. [PubMed: 3191723]
- Foundas AL, Eure KF, Luevano LF, Weinberger DR. MRI Asymmetries of Broca's Area: The Pars Triangularis and Pars Opercularis. *Brain and Language* 1998;64:282. [PubMed: 9743543]
- Gannon PJ, Holloway RL, Broadfield DC, Braun AR. Asymmetry of chimpanzee Planum Temporale: Humanlike pattern of Wernicke's language area homolog. *Science* 1998;279:220–222. [PubMed: 9422693]
- Good CD, Johnsrude I, Ashburner J, Henson RNA, Friston KJ, Frackowiak RSJ. Cerebral asymmetry and the effects of sex and handedness on brain structure: A voxel-based morphometric analysis of 465 normal human brains. *NeuroImage* 2001;14:685–700. [PubMed: 11506541]
- Hopkins, WD. *Evolution of hemispheric specialization in primates*. Oxford: Elsevier; 2007.
- Hopkins WD, Marino L, Rilling JK, MacGregor LA. Planum temporale asymmetries in great apes as revealed by magnetic resonance imaging (MRI). *NeuroReport* 1998;9:2913–2918. [PubMed: 9760145]

- Hopkins WD, Pilcher DL, MacGregor L. Sylvian fissure length asymmetries in primates revisited: A comparative MRI study. *Brain, Behavior and Evolution* 2000;56:293–299.
- LeMay, M. Asymmetries of the brains and skulls of nonhuman primates. Glick, SD., editor. New York: Cerebral lateralization in nonhuman species Academic Press; 1985. p. 223–245.
- Luders E, Gaser C, Jancke L, Schlaug G. A voxel-based approach to gray matter asymmetries. *NeuroImage* 2004;22:656–664. [PubMed: 15193594]
- Pilcher D, Hammock L, Hopkins WD. Cerebral volume asymmetries in nonhuman primates as revealed by magnetic resonance imaging. *Laterality* 2001;6:165–180. [PubMed: 15513168]
- Rilling JK, Barks SK, Parr LA, Preuss TM, Faber TL, Pagnoni G, Bremner JD, Votaw JR. A comparison of resting-state brain activity in humans and chimpanzees. *Proceedings of the National Academy of Sciences* 2007;104:17146–17151.
- Rogers, LJ.; Andrew, JR. Comparative vertebrate lateralization. Cambridge: Cambridge University Press; 2002.
- Shapleske J, Rossell SL, Woodruff PW, David AS. The planum temporale: a systematic, quantitative review of its structural, functional and clinical significance. *Brain Research Reviews* 1999;29:26–49. [PubMed: 9974150]
- Sherwood CS, Broadfield DC, Holloway RL, Gannon PJ, Hof PR. Variability of Broca's area homologue in great apes: Implication for language evolution. *The Anatomical Record* 2003;217A:276–285. [PubMed: 12629670]
- Smith SM, Jenkinson M, Woolrich MW, Beckmann CF, Behrens TEJ, Johansen-Berg H, Bannister PR, De Luca M, Drobnik I, Flitney DE, Niazy R, Saunders J, Vickers J, Zhang Y, De Stefano N, Brady JM, Matthews PM. Advances in functional and structural MR image analysis and implementation of FSL. *NeuroImage* 2004;23(S1):208–219.
- Warren JM. Handedness and laterality in humans and other animals. *Physiological Psychology* 1980;8:351–359.
- Watkins KE, Paus T, Lerch JP, Zijdenbos A, Collins DL, Neelin P, Taylor J, Worsley KJ, Evans AC. Structural asymmetries in the human brain: a voxel-based statistical analysis of 142 MRI scans. *Cerebral Cortex* 2001;11:868–877. [PubMed: 11532891]
- Williams NA, Close JP, Giouzeli M, Crow TJ. Accelerated evolution of *Protocadherin 11X/Y*: A candidate gene-pair for cerebral asymmetry and language. *American Journal of Medical Genetics Part B (Neuropsychiatric Genetics)* 2006;141B623.633

Figure 1. Schematic of the basic image manipulation of MRI scans. In the center is an axial view of a chimpanzee brain. From the left to right in the bottom panel are a segmented gray matter image, the mirror-image of the normally oriented image and the resulting image when the mirror is subtracted from the normally oriented scan.

Figure 2.
A 3-D rendering of a chimpanzee brain with anatomically defined x (lateral-medial), y (anterior-posterior) and z axis (ventral-dorsal) coordinates used to define significant voxels in the VBM analysis.

Figure 3.

Four sagittal views of the left and right hemisphere of a chimpanzee brain. From a to d, images begin with surface projection and move medially in 5 mm intervals (indicated by the green lines on the superior view of the brain). Color bar indicates variation in the t-values for different regions. Note, all the clusters shown are not necessarily significant if they did not reach the minimal criteria for inclusion as a cluster.

Figure 4.

A 3-D rendering of a chimpanzee brain showing the PT projected on the surface region (cyan). Four coronal views of the left and right hemisphere of a chimpanzee brain depicting the tracing of the depth of the sylvian fissure. From 1 to 8, images begin with anterior section demarking Heschl's gyrus (HG) and move posteriorly.

Figure 5.

A 3-D rendering of a chimpanzee brain showing the IFG projected on the surface region (green). Four axial views of the left and right hemisphere of a chimpanzee brain depicting the tracing of the inferior frontal gyrus (IFG). From 1 to 4, images begin move from ventral to dorsal.

Table 1
Centroid Positions, Mean t-values and volumes of significant clusters.

	<i>t</i>	mm ³	X	Y	Z	Bailey et al.	Brodmann
L > R							
SFG, sfs	12.57	480	46	66	35	FE, FDp	10,46
IRoG, SRoG	15.32	616	42	61	26	FG, FH	11,12
IFGOp, ifs	18.32	680	52	56	31	FCBm	44
PTe, Pop	12.70	352	54	41	31	TB,TC, PFD	41,42,22
SMG	12.73	512	54	34	32	PF	40
OcG, lu	12.80	1016	53	24	34	OA, OB, OC	19,18, 17
R > L							
MFG	11.43	368	30	58	37	FDp, FDI ⁺	46, 9
PrG	14.73	512	24	55	32	FB	6
SFG, sfs	17.12	256	35	52	43	FB	6
PrG, hand region	12.84	416	33	46	43	FA, FB	4, 6
PoG	13.50	672	30	41	40	PB, PC, PD	3b, 1, 2
AnG	13.36	824	26	38	33	PG	39
TOTZ	13.05	672	26	31	31	TA	22

Abbreviations of brain areas. AnG – angular gyrus, IFGOp – inferior frontal gyrus, opercular part, ifs – inferior frontal sulcus, IRoG – inferior rostral gyrus, lu – lunate sulcus, MFG – medial frontal gyrus, OcG – occipital gyri, PoG – postcentral gyrus, Pop – parietal operculum, PrG – precentral gyrus, PTe – planum temporale, SFG – superior frontal gyrus, sfs – superior frontal sulcus, SMG – supramarginal gyrus, SRoG – superior rostral gyrus, TOTZ – temporooccipital transition zone.

Table 2

Distribution of Left and Right Hemisphere Asymmetries for the Inferior Frontal Gyrus (IFG) and Planum Temporale (PT) Using VBM Compared to ROI Approaches.

Subject	VBM	PT	ROI	VBM	IFG	ROI
Females						
Brodie	128.00		.03	147.00		-.36
Callie	1.00		.08	315.00		.05
Cheeta	-274.00		-.11	237.00		.10
Dara	258.00		.31	384.00		-.06
Edwina	181.00		.23	126.00		.03
Elvira	-3.00		.09	74.00		.04
Evelyne	322.00		.33	462.00		.02
Faye	142.00		.13	90.00		.21
Foxy	198.00		.15	63.00		.31
Frannie	326.00		.25	289.00		.17
Heppie	3.00		.07	469.00		.30
Jacqueline	-22.00		.15	425.00		.52
Jewelle	84.00		-.01	666.00		.44
Julie	222.00		.20	372.00		.12
Katrina	180.00		.28	559.00		-.13
Lena	35.00		.10	98.00		-.04
Maxine	181.00		.15	37.00		-.30
Melinda	254.00		.38	549.00		.38
Melissa	62.00		.15	511.00		.02
Sabrina	309.00		.37	210.00		-.31
Sara	-25.00		-.26	406.00		.34
Suwanee	318.00		.12	266.00		.40
Males						
Arthur	175.00		.42	657.00		.03
Iyk	-93.00		-.55	-321.00		.24
Jarred	46.00		-.12	334.00		.04
Jolson	215.00		.16	478.00		.12
Joseph	202.00		.02	510.00		-.12
Justin	85.00		-.19	289.00		-.29
Lucas	123.00		.06	263.00		.06
Patrick	-35.00		-.03	141.00		-.12
Perecles	159.00		.30	121.00		.10
Total L	25		.24	30		.22
Total R	6		.7	1		.9

Positive values indicate left hemisphere biases and negative values indicate right hemisphere biases for the two different analyses.