Published in final edited form as:

Eur J Neurosci. 2009 August ; 30(3): 431–438. doi:10.1111/j.1460-9568.2009.06830.x.

The Chimpanzee Brain Shows Human-Like Perisylvian Asymmetries in White Matter

Claudio Cantalupo^{1,2,*}, Joanne Oliver¹, Jarrod Smith¹, Talia Nir², Jared P. Taglialatela², and William D. Hopkins^{2,3}

¹ Department of Psychology, Clemson University, Clemson, SC 29634

² Division of Psychobiology, Yerkes Primate Research Center, Atlanta, GA 30329

³ Department of Psychology, Agnes Scott College, Decatur, GA 30030

Abstract

Modern neuroimaging technologies allow scientists to uncover inter-species differences and similarities in hemispheric asymmetries that may shed light onto the origin of brain asymmetry and its functional correlates. We analyzed asymmetries in white to grey matter ratios of the lateral aspect of the lobes of the brains of chimpanzees. We found marked leftward asymmetries for all lobar regions. This asymmetry was particularly pronounced in the frontal region and was found to be related to handedness for communicative manual gestures as well as for tool use. These results point to a continuity in asymmetry patterns between the human and chimpanzee brain, and support the notion that the anatomical substrates for lateralization of communicative functions and complex manipulative activities may have been present in the common hominid ancestor.

Keywords

hemispheric asymmetry; white matter; gray matter; tool use; handedness; chimpanzee

Since the pioneering work of nineteenth century scholars like Broca and Wernicke, a remarkable number of studies have been conducted showing the presence of brain asymmetries and their functional and behavioral correlates in humans (Davidson, 1995; McManus, 2002; Toga & Thompson, 2003; Goulven & Tzourio-mazoyer, 2004). Many research efforts in this area have strived to assess the relation among asymmetries at the cellular, anatomical and behavioral levels of analysis (Galaburda, 1995; Amunts *et al.*, 1999; Cooper, 2006; Sherwood *et al.*, 2007; Gannon *et al.*, 2008). For example, the anatomical asymmetry of the so-called language areas of the neocortex (i.e., Broca's and Wernicke's areas) has been shown to be related to asymmetries in measures of functional activation in these areas during language tasks (Binder *et al.*, 1997; Frost *et al.*, 1999; Vikingstad *et al.*, 2000). Similarly, asymmetries in the brain's structural and functional organization have been shown to be related to asymmetrical behavioral traits such as handedness, auditory

*Corresponding author and reprint requests: Claudio Cantalupo, Ph.D., Department of Psychology, 418 Brackett Hall, Clemson University, Clemson, SC 29634, Phone: (864) 656-4978, Fax: (864) 656-0358, ccantal@clemson.edu.

perception and motor preferences (Ahonniska *et al.*, 1993; Knecht *et al.*, 2000a; Knecht *et al.*, 2000b; Josse *et al.*, 2003; Hatta, 2006).

Thus, hemispheric asymmetry has been established as one of the prominent aspects of the organization of the human brain. Nonetheless, a great deal is still unknown concerning the evolution of hemispheric asymmetry, particularly with respect to neuroanatomical asymmetries. In the last 20 years, there has been a plethora of research on behavioral asymmetries in nonhuman animals, including primates, with handedness being the principle measure (Bradshaw & Rogers, 1993; Ward & Hopkins, 1993; Bradshaw, 1997; Rogers & Andrew, 2002; Hopkins, 2007). Evidence of population-level handedness has been reported in a number of primate taxa, including great apes, Old and New World monkeys as well as prosimians (MacNeilage *et al.*, 1987; Hook-Costigan & Rogers, 1997; Papademetriou *et al.*, 2005; Hopkins, 2006).

The current study addresses the issue of hemispheric specialization in primates from the standpoint of neuroanatomy. Far less research has investigated neuroanatomical asymmetries and our understanding of the evolutionary origin of brain asymmetry and its functional implications in primates is limited because of (a) the relatively low number of studies on non-human primates, particularly the great apes and (b) limitations in the technologies and procedures employed in data collection. In the last decade, some studies have been published showing evidence of population-level brain asymmetries in monkeys and apes. For example, population-level asymmetries have been reported for a variety of sulci, notably the Sylvian fissure in great apes and monkeys (Yeni-Komshian & Benson, 1976; Falk *et al.*, 1986; Heilbronner & Holloway, 1988; Falk *et al.*, 1990; Hopkins *et al.*, 2000; Liu & Phillips, in press). Evidence of leftward asymmetries have also been reported for the planum temporale in both cadaver (Gannon *et al.*, 1998) and *in vivo* great ape brains (Cantalupo *et al.*, 2003). There is also at least one report of leftward asymmetries in the inferior frontal gyrus of great apes (Cantalupo & Hopkins, 2001).

The majority of previous studies in nonhuman primates have examined asymmetries in morphology or linear measurement of sulcal length. Recent improvements in *in vivo* imaging technologies have made it possible to assess in much greater detail the nature of structural asymmetries across different brain regions by analyzing the relative contribution of gray and white matter to the expression of such asymmetries (Good *et al.*, 2001; Watkins *et al.*, 2001; Pujol *et al.*, 2002; Buchel *et al.*, 2004; Luders *et al.*, 2004; Schenker *et al.*, 2005). The use of these imaging technologies in humans and great apes provides scientists with a new venue to uncover patterns of inter-species differences and similarities in hemispheric asymmetries that may help us shed light onto the origin of brain asymmetry and its functional correlates in primates.

In this line, we have conducted a high-resolution MRI study with a group of 33 captive chimpanzees. We analyzed asymmetries in overall volume as well as white to gray matter ratios within the lateral aspect of the four major anatomical divisions (i.e., lobes) of the left and right hemispheres, using a procedure similar to that employed in a recent study with human subjects (Pujol *et al.*, 2002). Specifically, Pujol and colleagues (Pujol *et al.*, 2002) analyzed overall volume and relative white matter asymmetries of the 4 perisylvian lobar

regions in a sample of 100 human brains. The results of this study revealed marked asymmetries in relative white matter content, with particularly strong leftward asymmetries for the frontal and temporal regions.

The aim of the present study was to assess (a) whether or not the chimpanzee and human brain share a similar pattern of perisylvian regional asymmetries for relative white matter content and (b) if any of the hypothesized regional asymmetries in relative white matter content may be predictors of asymmetries at the behavioral level, namely, handedness. We were particularly interested in assessing the possible asymmetric white matter concentration because it has been suggested by some that the evolution of brain asymmetries in primates are directly linked to expansion in intrahemispheric connectivity, reflected in the relative proportion of white to gray matter (Ringo *et al.*, 1994; Rilling & Insel, 1999; Schoenemann *et al.*, 2005; Schoenemann, 2006).

Methods

Subjects

Magnetic resonance imaging (MRI) scans were obtained from a sample of 34 captive chimpanzees including 12 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 51 years (Mean = 22.44, s.d. = 11.17).

Image Collection Procedures

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. All procedures were carried out in accordance with the NIH Guidelines regarding the care and use of animals for experimental procedures. 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 located at the YNPRC (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 × 320).

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 7.0 (Mayo Clinic, Mayo Foundation, Rochester, Minnesota, USA) software for post-image processing.

Regions of Interest (ROI) Delineation

For each subject, the raw scans were re-aligned in the coronal, axial and sagittal planes using procedures described elsewhere (Hopkins *et al.*, 2007a). Following the study by Pujol and colleagues (Pujol *et al.* 2002), the delineation of the four lobar regions as viewed in sagittal sections, was based on prominent sulcal landmarks including the Sylvian fissure (SF), the central sulcus (CS) and post-central sulcus (PCS). In particular, the frontal lobar region was delimited ventrally by the SF and posteriorly by the CS with downward vertical prolongation from the sulcus' ventral endpoint to intersect the SF (see Figure 1B). The parietal region was delimited anteriorly by the CS, ventrally by the SF and posteriorly by a straight line parallel to the PCS and originating from the posterior end point of the horizontal ramus of the SF. The temporal region was delimited dorsally by the SF and posteriorly by a straight line originating from the endpoint of the horizontal ramus of the SF and perpendicular to the anterior-posterior line that divided the temporal lobe into two parts (dorsal and ventral) showing similar size. The posterior borders of the temporal and parietal regions represented the anterior borders delimiting the occipital region. Next, to establish the lateral to medial extent of the perisylvian ROI we followed the procedure of previous MRI studies that have targeted perisylvian regions in great ape species (Hopkins *et al.*, 2000; Cantalupo *et al.* 2003). In particular, the perisylvian ROI were identified in consecutive 1mm-thick sagittal slices, from the most lateral slice of each hemisphere showing cortical tissue to the slice immediately preceding the opening of the insula (see Figure 1B). This procedure differs to some extent from that employed by Pujol and colleagues with humans (2002) in that it may establish the most medial border of the ROI at a slightly more lateral sagittal section. Nonetheless, the two procedures clearly share a fundamental similarity in that both are aimed at confining the ROI to brain tissue lateral to the insula. In nother words both procedures clearly target the perisylvian aspect of the four lobar regions under investigation in this study.

ROI Tracings

Prior to ROI delineation and tracing, half of the scans were randomly chosen to be flipped on the left-right axis to prevent possible experimenter bias. The tracings were collected by two raters who were blind to hemisphere side. Using the anatomical landmarks described above, each perisylvian region was traced manually in consecutive sagittal slices of the left and right hemispheres using the ROI module available in Analyze. These tracings were then saved as objects maps and subsequently applied to the white and gray matter volumes.

ROI Measurements

For this step, the skulls were removed and each subject's MRI scans was segmented into gray, white and CSF tissue using FSL (Analysis Group, FMRIB, Oxford, UK). The object maps described above were then applied to the segmented gray and white matter to derive corresponding volume values for each region and hemisphere.

Handedness

The potential effect of handedness on the relative white matter asymmetries was examined for two hand preferences measures including manual communicative gestures and tool use.

Data for these two measures were included in the analysis because we have previously found that hand preferences for both measure have been found to significantly correlate with neuroanatomical asymmetries in the language homologs, measured using traditional ROI analyses (Hopkins & Cantalupo, 2004; Taglialetela et al. 2006). Because the lateral frontal region targeted in this study included primary and premotor areas (see figure 1), including the frontal operculum, we reasoned that hand preference measures for these behaviors might also be associated with variation in relative whitematter asymmetries, particularly within the frontal lobe. Brief descriptions of the two handedness measures are provided below.

Manual Communicative Gestures—At the onset of each trial, an experimenter would approach the subject's home cage and center themselves in front of the subject at a distance of approximately 1.0 to 1.5 meters. If the subject was not already positioned in front of the experimenter at the onset of the trial, the subject would immediately move towards the front of the cage when the experimenter arrived with the food. The experimenter then spoke the chimpanzee's name and offered a piece of food until the subject produced a manual gesture. Only responses in which the chimpanzees unimanually extended the digit(s) through the cage mesh to request the food were considered a response. Other possible manual responses such as cage banging or clapping were not counted as a gesture. Two-handed gestures, although rare, were not scored as were gestures that were produced by the subject prior to the experimenter arriving in front of the subject's home cage. Subjects were tested over a 15-day period, and a minimum of 30 responses were collected from each subject (Hopkins *et al.*, 2005). The number of trials administered on a given day varied with the subject's motivation and availability for testing. Subjects were tested in both the indoor and outdoor sections of their home enclosures, and none of the subjects were separated from their groups or cagemates during testing. Hand use was recorded as right or left for each response.

Tool Use—This task was designed to simulate the motor demands of termite fishing in wild chimpanzees (Lonsdorf & Hopkins, 2005). Testing was conducted using a device consisting of three poly-vinyl-chloride (PVC) pipes (15 cm long, 4 cm in diameter) fixed at 45 degree angles into three holes (4 cm in diameter) placed horizontally 15 cm apart on a rectangular plastic board (50 cm long by 20 cm wide). The end of each tube that was fixed to the rectangular plastic board was open to allow access to the honey at the other end (bottom) of the tube. The bottom end of the tube was comprised of a removable PVC cap. During testing, each PVC tube in the apparatus was first filled with a preferred food that had some adhesive qualities (honey, applesauce, salsa or mustard) to about 1/3 of the whole length of the tube, which made it impossible for the subject to reach the food directly with their fingers. After placing the device on the cage, sticks or bamboo skewers were supplied to the subjects by handing them one directly. The chimpanzees had to insert a small stick (~ .5 cm) into the hole to extract the hidden food. Each time the chimpanzees inserted the stick, a left or right hand response was recorded. A minimum of 100 dipping responses summed between at least two test sessions were obtained from each subject.

Data Analysis

The relative proportion of white matter in each lobar region was calculated by adding the total white matter volume within a region and dividing by the total gray matter volume.

These data were compared between males and females to test the effect of sex on relative white matter concentrations. To assess the presence and degree of lateralization, the relative proportion of white matter was calculated for each lobar region and hemisphere by dividing the white matter volume by the gray matter volume. Subsequently, difference values in the relative white matter were computed between hemispheres by subtracting the right hemisphere values from the left hemisphere for each lobar region. The difference values for each lobar region were then compared between sex and handedness groups.

For the two handedness tasks, binomial z -scores were calculated for each subject based on the total frequency of left and right hand use. Subjects with z -scores greater than 1.95 were classified as right-handed while all other subjects were classified as non-right-handed. For manual gestures, there were 11 non-right-handed and 22 right-handed individuals, respectively. For the tool use task, there were 19 non-right-handed and 13 right-handed individuals. Hand preference data were not available for one chimpanzee on the tool use task.

Results

Shown in Table 1 are the weighted mean volumes for each region, hemisphere and sex in the sample for both gray and white matter (supplementary information can be found at: URL). For the purposes of providing descriptive data on the volumes of white and gray matter in the chimpanzees, in the initial analysis, we compared the volumes of each region and hemisphere using an analysis of co-variance. Region (frontal, parietal, temporal, occipital) and hemisphere (left, right) were the repeated measures while sex (male, female) was the between group factor. Total brain volume served as the covariate. One analysis was on the gray matter and the second analysis was on the white matter

For the gray matter, there was a significant main effect for sex $F(1, 31)=4.868, p < .04$ and a significant three-way interaction between sex, hemisphere and region $F(3, 93)=3.771, p < .02$. Post-hoc analysis of the three way interaction indicated that males and females showed similar leftward asymmetries for the frontal and parietal lobes; however for the temporal lobe, the females showed a significantly greater leftward asymmetry than the males. In contrast, for the occipital lobe, the males showed a significantly greater leftward asymmetry than the females (see Table 1).

For the white matter, the only significant result was a main effect for hemisphere $F(1, 31)=6.566, p < .02$. The overall white volumes of the left hemisphere (Mean = 2245.95) were significantly larger than the right hemisphere (Mean = 1514.94) (see also Table 1). No other significant main effects or interactions were found.

We also examined whether the chimpanzees showed population-level asymmetries in the volumes of the different lobes. Asymmetry quotients (AQ) were derived for each lobar region by subtracting the summed gray and white left hemisphere volumes from the summed gray and white matter volumes for the right hemisphere, dividing by the total volume, and multiplying by .5 [$AQ = (R - L)/(R + L) * .5$]. The AQ values were compared to an estimated mean of zero using a one-sample t -test, which is the value that would be predicted

if the values were normally or bimodally distributed. For the gray matter, significant population-level leftward asymmetries were found for the frontal $t(33) = -4.31, p < .001$, parietal $t(33) = -4.82, p < .001$ and temporal $t(33) = -8.98, p < .001$ regions but not the occipital $t(33) = -1.12, p > .05$. For the white matter, significant population-level leftward asymmetries were found for the frontal $t(33) = -11.42, p < .001$, parietal $t(33) = -8.35, p < .001$, temporal $t(33) = -13.08, p < .001$ and occipital lobe regions $t(33) = -3.26, p < .003$.

Relative White Matter

We next considered the relative proportion of white to gray matter for each region and hemisphere using an analysis of variance. As with the previous analysis, region (frontal, parietal, temporal, occipital) and hemisphere (left, right) were the repeated measures while sex (male, female) was the between group factor. A statistically significant two-way interaction was found between region and hemisphere $F(3, 96) = 11.01, p < .001$. Post-hoc pair-wise comparisons with Bonferroni's correction indicated that significant population-level leftward asymmetries were found for all four regions; however, the leftward asymmetry was significantly higher in the frontal compared the parietal, temporal and occipital regions. Shown in Figure 2 are the mean differences in relative white to gray matter between the right and left hemispheres ($R - L$) for each region.

Behavioral Correlates of Perisylvian Asymmetries—For this analysis, we compared the differences in relative white to gray matter between hemispheres as a function of handedness for manual communicative gestures as well as for tool use in the chimpanzees using a 2×4 repeated measures ANOVA. Region was the repeated measure while handedness (right, non-right) was the between group factor. Separate analyses were done for the hand preference data for manual gestures and tool use. With respect to manual gestures, a significant hand by region interaction was found $F(3, 96) = 4.62, p < .005$. The mean difference in relative white matter between hemispheres right- and non-right-handed chimpanzees are shown in Figure 3A. Non-right-handed chimpanzees had significantly more leftward differences scores than right-handed chimpanzees for the frontal region. No significant differences were found between non-right and right-handed chimpanzees for the occipital, temporal or parietal lobes. For the tool use, the results were nearly identical (see Figure 3B). The analysis of variance revealed a significant two-way interaction between hand preference and region $F(3, 93) = 5.39, p < .006$. Chimpanzees classified as non-right-handed had significantly greater leftward differences scores than right-handed chimpanzees for the frontal region. No significant differences were found between non-right and right-handed chimpanzees for the occipital, temporal or parietal lobes. The finding that non-right-handed apes showed greater leftward asymmetries in relative white-to-grey-matter composition of the frontal region may appear somewhat puzzling. To elucidate this apparent paradox we performed further analyses on possible differences in gray matter between right- and non-right-handed apes for the two tasks. Indeed, when considering the asymmetry quotients for the gray matter alone, right-handed chimpanzees had more robust leftward asymmetries than non-right-handed individuals for both the tool use task (Right-handed Mean AQ = $-.34$ vs Non-right-handed Mean AQ = $-.07$) and manual gestures (Right-handed Mean AQ = $-.20$ vs Non-right-handed Mean AQ = $-.14$). Moreover, the expression of gray matter asymmetries in the frontal lobe is particularly robust when the handedness of

the chimpanzees is considered as a single measure by combining the preferences on the two tasks ($F(2, 30) = 3.66, p < .04$; see Figure 4). For chimpanzees that were right-handed for both manual gestures and tool use ($n = 12$), the mean AQ value was more leftward compared to chimpanzees that were non-right-handed for both tasks ($n = 10$) or were right-handed for one task and non-right-handed for the other ($n = 11$). Thus, it seems that the grey matter asymmetry may have modulated the expression of the asymmetry in white-to-grey-matter composition of the frontal region and its relationship to the handedness of the chimpanzees.

Discussion

The findings of this study are straightforward. First, the chimpanzee brain shows marked leftward asymmetries in relative white-matter of the lateral aspect of the perisylvian cortical regions. This pattern of asymmetry is remarkably similar to results reported in humans (Pujol et al. 2002) despite the above-mentioned slight differences in ROI delineation. Further, the results of this study converge with and expand the findings of prior studies that have shown overall volumetric leftward asymmetries of perisylvian regions of the chimpanzee brain such as the Sylvian fissure, the planum temporale, and parts of the frontal lobe including the frontal operculum (Cantalupo & Hopkins, 2001; Cantalupo et al., 2003; Gannon et al. 1998; Hopkins et al. 2000; Schenker *et al.*, 2005). In particular, the results of the present study suggest that white-matter composition is likely one crucial factor in determining the expression of volumetric cortical asymmetries at the macroscopic level. This finding supports the notion that an increase in intrahemispheric connectivity could be directly linked to the expression of cortical asymmetries in higher primates such as the great apes and humans, as a consequence of the relatively reduced size of the interhemispheric commissures (the corpus callosum in particular, see Rilling & Insel, 1999).

The results of this study are also consistent with one previous report of white matter asymmetries in chimpanzees that employed a different methodology and approach. Specifically, Hopkins et al. (2007c) quantified gray and white matter areas on 10 equally spaced coronal slices from the anterior to the posterior regions of the chimpanzee brain. Significant population-level leftward asymmetries were found in three central regions of the brain that encompassed the anterior portion of the frontal lobe to the posterior regions of the parietal and temporal lobe. These areas partially correspond to the areas quantified in this study, though quantified only on a single coronal slice.

In addition to merely assessing the presence of lateral asymmetries at the anatomical level, this study shows also clear evidence of a specific connection between anatomy and behavior. In particular, the asymmetry of grey and relative white-matter content of the frontal region were found to be a predictor of the expression of hand preference of the chimpanzees when engaging in communicative manual gestures or when performing a tool-use task. These results further support and expand the findings of previous research that macroscopic morphological asymmetry of the frontal operculum region of the chimpanzee brain seem to be specifically related to handedness for manual gestures and complex motor tasks like tool use (Hopkins & Cantalupo, 2004; Taglialatela *et al.*, 2006; Hopkins *et al.*, 2007b). Incidentally, it should be noted that because the present study was confined to the lateral aspect of each lobe, the portion of the frontal lobe that was targeted included almost

exclusively motor and premotor areas, including the frontal operculum (see Figure 1A and B). The finding of an association between perisylvian asymmetries and handedness in our chimpanzee sample is significant for the study of such association between anatomy and behavior in humans. To date, the relationship between handedness and perisylvian asymmetries in humans is unclear. Traditional morphometry studies have indicated a possible link between the overall asymmetry of posterior regions like the planum temporale and planum parietale (which are part of Wernike's area) and handedness (for a review, see Janke & Steinmetz, 2003). However, recent MRI studies have failed to detect evidence of an association between handedness and grey or white matter asymmetries of perisylvian regions (Good et al., 2001; Watkins et al., 2001; Vernooij et al., 2007). For the most part, this discrepancy in results are likely due to methodological differences between the different studies. Our own findings suggest that in chimpanzees a) the asymmetry of grey matter may modulate the asymmetry of white matter composition of frontal regions (i.e., motor and premotor, and b) the asymmetry of these anterior perisylvian regions rather than posterior ones (i.e., planum temporale and parietale) may be related to the expression of lateralized hand use.

The leftward asymmetry of the perisylvian regions in chimpanzees may be due, in part, to well-known white matter tracts, such as the arcuate fasciculus (AF), connecting the superior temporal lobe, inferior parietal lobe and frontal operculum (Catani & Ffytche, 2005; Catani et al., 2005). Recent diffusion-tensor MRI studies in humans have reported population-level leftward asymmetry for the AF (Buchel et al., 2004; Vernooij et al., 2007). Interestingly, a recent *in vivo* imaging study has shown that the AF can be visualized in the chimpanzee and macaque brain using diffusion tensor imaging, though no laterality data were reported (Rilling et al., 2008). Based on the findings of this study, as well as the previous reports of leftward asymmetries in the IFG and PT in chimpanzees, we would hypothesize that chimpanzees, like humans, would show leftward asymmetries in the AF.

The fact that the chimpanzees show a leftward white matter asymmetry in the perisylvian regions leads to the question of what mechanisms or factors underlie the development of this pattern of neural organization. Pujol et al. (2006) have recently reported that young children show similar leftward asymmetries in the white matter of the perisylvian regions. The suggestion is that the development of white matter asymmetries is, in essence, innate and reflect a normal maturational gradient of the human brain. It is tempting to suggest that a similar mechanism underlies the asymmetries seen in the chimpanzee; however the evidence that white matter asymmetries were related, albeit indirectly, to the handedness of the chimpanzees suggests that different motor experiences may alter or influence this pattern of development. As noted above, the effect of handedness on the expression of perisylvian white matter asymmetries in humans is still unclear. More studies are needed to further address the questions of what factors influence perisylvian asymmetries in human and nonhuman primates.

In summary, the remarkable degree of similarity between the perisylvian white-matter asymmetries reported here for chimpanzees and by a recent study with humans (Pujol et al., 2002; 2006) suggests that the chimpanzee and human brain may share a basic pattern of macroscopic cortical asymmetry that was present in a common ancestor. Overall, the data

from human and chimpanzee studies further support the notion that macroscopic asymmetries of cortical regions of the brain are not peculiar to the human species, and that the study of the origin of hemispheric asymmetry should be cast in evolutionary rather than strictly anthropocentric terms (Crow, 2004; Vallortigara & Rogers, 2005).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

This work was supported in part by NIH grants RR-00165, NS-42867, NS-36605, HD-38051 and HD-56232. American Psychological Association and National Institute of Health guidelines for the ethical treatment of animals were adhered to during all aspect of this research.

References

- Ahonniska J, Cantell M, Tolvanen A, Lyytinen H. Speech Perception and Brain Laterality: The Effect of Ear Advantage on Auditory Event-Related Potentials. *Brain and Language*. 1993; 45:127–146. [PubMed: 8358593]
- Amunts K, Schleicher A, Burgel U, Mohlberg H, Uylings HB, Zilles K. Broca's region revisited: Cytoarchitecture and intersubject variability. *The Journal of Comparative Neurology*. 1999; 412:319–341. [PubMed: 10441759]
- Binder JR, Frost JA, Hammeke TA, Cox RW, Rao SM, Prieto T. Human brain language areas identified by functional magnetic resonance imaging. *The Journal of Neuroscience*. 1997; 17:353–362. [PubMed: 8987760]
- Bradshaw, JL. Human evolution: A neuropsychological perspective. Psychology Press.; Hove, U.K.: 1997.
- Bradshaw, JL.; Rogers, LJ. The evolution of lateral asymmetries, language, tool use, and intellect. Academic Press, Inc.; San Diego: 1993.
- Buchel C, Raedler T, Sommer M, Sach M, Weiller C, Koch MA. White matter asymmetry in the human brain: A diffusion tensor MRI study. *Cerebral Cortex*. 2004; 14
- 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]
- Catani M, ffytche DH. The rises and falls of disconnection syndromes. *Brain*. 2005; 1–16. [PubMed: 15596793]
- Catani M, Jones DK, Ffytche DH. Perisylvian language networks of the human brain. *Annals of Neurology*. 2005; 57:8–16. [PubMed: 15597383]
- Cooper DL. Broca's Arrow: Evolution, Prediction and Language in the Brain. *The Anatomical Record (Part B: New Anatomy)*. 2006; 289B:9–24.
- Davidson, RJ. Cerebral Asymmetry, Emotion and Affective Style. In: Davidson, RJ.; Hugdahl, K., editors. *Brain Asymmetry*. MIT Press; Cambridge, MA: 1995. p. 361-387.
- Falk D, Cheverud J, Vannier MW, Conroy GC. Advanced computer-graphics technology reveals cortical asymmetry in endocasts of rhesus-monkeys. *Folia Primatologica*. 1986; 46:98–103.
- Falk D, Hildebolt C, Cheverud J, Vannier M, Helmkamp RC, Konigsberg L. Cortical asymmetries in the frontal lobe of rhesus monkeys (*Macaca mulatta*). *Brain Research*. 1990; 512:40–45. [PubMed: 2337807]
- Frost JA, Binder JR, Springer JA, Hammeke TA, Bellgowan PSF, Rao SM, Cox RW. Language processing is strongly left lateralized in both sexes. Evidence from functional MRI. *Brain*. 1999; 122:199–208. [PubMed: 10071049]

- Galaburda, AM. Anatomic basis of cerebral dominance. In: Davidson, RJ.; Hugdahl, K., editors. Brain asymmetry. MIT Press; Cambridge, MA: 1995.
- 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]
- Gannon PJ, Kheck N, Hof PR. Leftward interhemispheric asymmetry of macaque monkey temporal lobe language area homolog is evident at the cytoarchitectural, but not gross anatomic level. *Brain Research*. 2008; 1199:62–73. [PubMed: 18262172]
- 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]
- Goulven J, Tzourio-mazoyer N. Hemispheric specialization for language. *Brain Research Reviews*. 2004; 44:1–12. [PubMed: 14739000]
- Hatta T. Handedness and the brain: A review of brain-imaging techniques. *Magnetic Resonance in Medical Science*. 2006; 6:99–112.
- Heilbronner PL, Holloway RL. Anatomical brain asymmetries in New World and Old World monkeys. Stages of temporal lobe development in primate evolution. *American Journal of Physical Anthropology*. 1988; 76:39–48. [PubMed: 3136655]
- Hook-Costigan MA, Rogers LJ. Hand preferences in New World primates. *International Journal of Comparative Psychology*. 1997; 9:173–207.
- Hopkins WD. Comparative and familial analysis of handedness in great apes. *Psychological Bulletin*. 2006; 132:538–559. [PubMed: 16822166]
- Hopkins, WD. *Evolution of hemispheric specialization in primates*. Elsevier; Oxford: 2007.
- Hopkins WD, Cantalupo C. Handedness in chimpanzees is associated with asymmetries in the primary motor but not with homologous language areas. *Behavioral Neuroscience*. 2004; 118:1176–1183. [PubMed: 15598127]
- Hopkins WD, Dunham L, Cantalupo C, Tagliabata JP. The association between handedness, brain asymmetries, and corpus callosum size in chimpanzees (*Pan troglodytes*). *Cerebral Cortex*. 2007a; 17:1757–1765. [PubMed: 17012376]
- 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.
- Hopkins WD, Russell JL, Cantalupo C. Neuroanatomical correlates of handedness for tool use in chimpanzees (*Pan troglodytes*): Implication for theories on the evolution of language. *Psychological Science*. 2007b; 18:971–977. [PubMed: 17958711]
- Hopkins WD, Russell JL, Freeman H, Buehler N, Reynolds E, Schapiro SJ. The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). *Psychological Science*. 2005; 16:487–493. [PubMed: 15943676]
- Hopkins WD, Tagliabata JP, Dunham LA, Pierre P. Behavioral and neuroanatomical correlates of white matter asymmetries in chimpanzees (*Pan troglodytes*). *European Journal of Neuroscience*. 2007c; 25:2565–2570. [PubMed: 17445252]
- Jancke, L.; Steinmetz, H. Anatomical brain asymmetries and their relevance for functional asymmetries. In: Hugdahl, K.; Davidson, RJ., editors. *The Asymmetrical Brain*. MIT Press; Cambridge, MA: 2003. p. 188–229.
- Josse G, Mazoyer B, Crivello F, Tzourio-Mazoyer N. Left planum temporale: an anatomical marker of left hemispheric specialization for language comprehension. *Cognitive Brain Research*. 2003; 18:1–14. [PubMed: 14659492]
- Knecht S, Deppe M, Dräger B, Bobe L, Lohmann H, Ringelstein EB, Henningsen H. Language lateralization in healthy right-handers. *Brain*. 2000a; 123:74–81. [PubMed: 10611122]
- Knecht S, Dräger B, Deppe M, Bobe L, Lohmann H, Floel A, Ringelstein EB, Henningsen H. Handedness and hemispheric language dominance in healthy humans. *Brain*. 2000b; 123:2512–2518. [PubMed: 11099452]
- Liu ST, Phillips KA. Sylvian fissure asymmetries in capuchin monkeys (*Cebus apella*). *Laterality*. in press.

- Lonsdorf EV, Hopkins WD. Wild chimpanzees show population level handedness for tool use. *Proceedings of the National Academy of Sciences*. 2005; 102:12634–12638.
- Luders E, Gaser C, Jancke L, Schlaug G. A voxel-based approach to gray matter asymmetries. *NeuroImage*. 2004; 22:656–664. [PubMed: 15193594]
- MacNeillage PF, Studdert-Kennedy MG, Lindblom B. Primate handedness reconsidered. *Behavioral and Brain Sciences*. 1987; 10:247–303.
- McManus, C. Right hand, left hand: The origins of asymmetry in brains, bodies, atoms, and cultures. Weidenfeld & Nicolson; London: 2002.
- Papademetriou E, Sheu CF, Michel GF. A meta-analysis of primate hand preferences for reaching and other hand-use measures. *Journal of Comparative Psychology*. 2005; 119:33–48. [PubMed: 15740428]
- Pujol J, Lopez-Sala A, Deus J, Cardoner N, Sebastian-Galles N, Conesa G, Capdevila A. The lateral asymmetry of the human brain studied by volumetric magnetic resonance imaging. *NeuroImage*. 2002; 17:670–679. [PubMed: 12377142]
- Pujol J, Soriano-Mas C, Ortiz H, Sebastian-Galles N, Losilla JM, Deus J. Myelination of language-related areas in the developing brain. *Neurology*. 2006; 66:339–343. [PubMed: 16476931]
- Rilling JK, Glasser MF, Preuss TM, Ma X, Zhang X, Zhao T, Hu X, Behrens T. The evolution of the arcuate fasciculus revealed with comparative DTI. *Nature Neuroscience*. 2008; 11:426–428.
- Rilling JK, Insel TR. Differential expansion of neural projection systems in primate brain evolution. *NeuroReport*. 1999; 10:1453–1459. [PubMed: 10380962]
- Ringo J, RD, Demeter S, Simard P. Timing is of essence: A conjecture that hemispheric specialization arises from inter-hemispheric conduction delay. *Cerebral Cortex*. 1994; 4:331–343. [PubMed: 7950307]
- Rogers, LJ.; Andrew, JR. Comparative vertebrate lateralization. Cambridge University Press; Cambridge: 2002.
- Schenker NM, Desgouttes AM, Semendeferi K. Neural connectivity and cortical substrates of cognition in hominoids. *Journal of Human Evolution*. 2005; 49:547–569. [PubMed: 16076478]
- Schoenemann PT. Evolution of size and functional areas of the human brain. *Annual Review of Anthropology*. 2006; 35:379–406.
- Schoenemann PT, Sheehan MJ, Glotzer LD. Prefrontal white matter volume is disproportionately larger in humans than in other primates. *Nature Neuroscience*. 2005; 8:242–252.
- Sherwood CC, Wahl E, Erwin JM, Hof PR, Hopkins WD. Histological asymmetries of primary motor cortex predicts handedness in chimpanzees (*Pan troglodytes*). *Journal of Comparative Neurology*. 2007; 503:525–537. [PubMed: 17534947]
- Taglialetela JP, Cantalupo C, Hopkins WD. Gesture handedness predicts asymmetry in the chimpanzee inferior frontal gyrus. *NeuroReport*. 2006; 17:923–927. [PubMed: 16738489]
- Toga AW, Thompson M. Mapping Brain Asymmetry. *Nature*. 2003; 4:37–48.
- Vernooij MW, Smits M, Wielopolski PA, Houston GC, Krestin GP, van der Lugt A. Fiber density asymmetry of the arcuate fasciculus in relation to functional hemispheric language lateralization in both right- and left-handed healthy subjects: a combined fMRI and DTI study. *Neuroimage*. 2007; 35:1064–1076. [PubMed: 17320414]
- Vikingsstad EM, George KP, Johnson AF, Cao Y. Cortical language lateralization in right handed normal subjects using functional magnetic resonance imaging. *Journal of the Neurological Sciences*. 2000; 175:17–27. [PubMed: 10785252]
- Ward, JP.; Hopkins, WD. Primate laterality: Current behavioral evidence of primate asymmetries. Springer-Verlag; New York: 1993.
- 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]
- Yeni-Komshian G, Benson D. Anatomical study of cerebral asymmetry in the temporal lobe of humans, chimpanzees and monkeys. *Science*. 1976; 192:387–389. [PubMed: 816005]

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Table 1

Mean Gray and White Matter Volumes (weighted by overall brain volume) for Male and Females Chimpanzees for Each Brain Region and Hemisphere

	Gray		White	
	Males	Females	Males	Females
Frontal				
R	2481.73 (206.30)	1969.77 (145.88)	1424.33 (171.55)	1087.18 (121.30)
L	2954.71 (206.26)	2403.49 (145.85)	2242.48 (238.75)	1914.91 (168.82)
Parietal				
R	3886.40 (275.40)	3324.38 (194.74)	1887.97 (144.12)	1807.52 (101.91)
L	4416.07 (268.92)	3832.83 (190.15)	2566.17 (178.25)	2501.16 (126.04)
Occipital				
R	3147.02 (290.03)	2818.06 (205.08)	932.53 (138.57)	831.37 (97.98)
L	3896.53 (358.12)	2760.27 (253.23)	1375.62 (183.24)	1107.45 (129.57)
Temporal				
R	7040.71 (465.12)	6011.72 (328.89)	2201.46 (162.72)	1946.40 (115.06)
L	8082.41 (441.90)	7565.00 (312.47)	3385.12 (184.35)	3074.75 (130.36)

Values in parentheses are standard errors. All volumes are presented in mm³