

# Asymmetries of the Parietal Operculum in Chimpanzees (*Pan troglodytes*) in Relation to Handedness for Tool Use

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**A left larger than right planum temporale (PT) is a neuroanatomical asymmetry common to both humans and chimpanzees. A similar asymmetry was observed in the human parietal operculum (PO), and the convergence of PT and PO asymmetries is strongly associated with right-handedness. Here, we assessed whether this combination also exists in common chimpanzees. Magnetic resonance scans were obtained in 83 captive subjects. PT was quantified following procedures previously employed and PO was defined as the maximal linear distance between the end point of the sylvian fissure and the central sulcus. Handedness was assessed using 2 tasks that were designed to simulate termite fishing of wild chimpanzees and to elicit bimanual coordination without tool use. Chimpanzees showed population-level leftward asymmetries for both PT and PO. As in humans, these leftward asymmetries were not correlated. Handedness for tool use but not for nontool use motor actions mediated the expression of asymmetries in PT and PO, with right-handed apes showing more pronounced leftward asymmetries. Consistent PT and PO asymmetry combinations were observed in chimpanzees. The proportions of individuals showing these combinations were comparable in humans and chimpanzees; however, interaction between handedness and patterns of combined PO and PT asymmetries differed between the 2 species.**

**Keywords:** apes, brain asymmetries, handedness, parietal operculum, planum temporale

## Introduction

Functional and anatomical asymmetries are well-documented features of the human brain (Broca 1861; Dax 1863, 1865; Witelson and Kigar 1988). That is to say, the left and right cerebral hemispheres are specialized for different sensory, motor, and cognitive processes (Hecaen and Albert 1978; Nass and Gazzaniga 1987; Bryden 1988; Gazzaniga 1994, 1995; Harrington 1995). Moreover, regions within the 2 hemispheres are not anatomically symmetrical but rather differ, which presumably reflects hemispheric specialization or the differential expansion of right and left brain regions associated with specific perceptual, motor, and cognitive processes (Witelson and Kigar 1988; Galaburda 1995).

Perhaps the most extensively studied asymmetry in the human brain is the planum temporale (PT). Specifically, the PT is an area in the posterior superior temporal gyrus within the sylvian fissure and corresponds to part of “Wernicke’s speech area” in humans. In one of the first systematic studies of this brain region, Geschwind and Levitsky (1968) measured the PT in a sample of 100 postmortem brains. They found that 65% of the sample had a leftward asymmetry and 11% a rightward

asymmetry. Since that time, numerous postmortem and more recent in vivo imaging studies consistently described a left larger than right PT in humans, using length, surface area measurements or volumetric data of the underlying gray matter (Steinmetz 1996; Shapleske et al. 1999; Westbury et al. 1999).

In humans, leftward asymmetry of surface area or gray matter volume of the PT is associated with specific cognitive processes such as reading and math achievements (Larsen et al. 1990; Habib 2000; Billingsley et al. 2002) that remain difficult to define with regard to the complete neural substrates (Heiervang et al. 2000). There are also consistent reports of an association between reversed PT asymmetries and various neurodevelopmental and psychiatric disorders, such as schizophrenia (Crow et al. 1989; Falkai et al. 1992; Fritzsche 2003; Collinson et al. 2004; but see Narr et al. 2001).

Another well-established functional correlate of PT surface area asymmetry in humans is handedness. Several studies have shown that right-handed individuals have a significantly greater degree of leftward PT asymmetry compared with left-handed individuals (see Habib and Galaburda 1986; Steinmetz and Galaburda 1991; Steinmetz et al. 1991; Foundas et al. 1995, 2002; Steinmetz 1996; Shapleske et al. 1999; Knaus et al. 2006). It should be noted, however, that not all studies have found an association between handedness and PT asymmetry (Good et al. 2001; see also Shapleske et al. 1999 for review) and some have suggested that the manner in which the PT is quantified influences the observed relationship between asymmetry and handedness (Westbury et al. 1999; Zetzsche et al. 2001).

Though initially thought to be uniquely human, there is growing evidence of population-level brain asymmetries in nonhuman animals, notably primates (Hopkins and Cantalupo 2004a, 2004b; Hopkins et al. 2007; Balzeau and Gilissen 2010; Hopkins and Nir 2010; Balzeau et al. 2012). Of specific interest to this paper is the evidence of asymmetries in the posterior temporal lobe and parietal regions that correspond to the PT and parietal operculum (PO). With regard to the PT, findings in 3 different laboratories using postmortem brains or in vivo imaging technologies have reported leftward asymmetries in the PT of chimpanzees (Gannon et al. 1998; Hopkins et al. 1998; Gilissen 2001; Hopkins and Nir 2010). The evidence of results parallel to those reported in humans is of significant importance for the study of the evolution of the neural substrates of cognitive functions and more precisely for the study of the evolution of the relationships between neuroanatomical and functional asymmetries.

In contrast, to date, there are no studies on the PO in nonhuman primates. The PO is a brain region located just above

the PT and includes parts of Brodmann's areas 40 and 43 in humans as well as the anterior portion of the supramarginal gyrus of the inferior parietal lobule (Eickhoff et al. 2006). Three main reasons underscore our interest in this brain region. First, it has been suggested that structural differences between right and left PT might reflect anatomical differences in surrounding cortical regions, such as the PO (Binder et al. 1996). Second, the human PO shows a pattern of asymmetry comparable to the human PT (Habib et al. 1995, 1999). More specifically, right-handers show more marked leftward asymmetry for both the PT and the PO than left-handers. PT and PO asymmetries are, however, not correlated to each other at the population level and may therefore be divergent within the same subject. It has been suggested that it is their convergence that is strongly associated with right-handedness in humans (Habib et al. 1995, 1999). Third, because the direction and magnitude of behavioral and brain asymmetries in human and nonhuman primates are still a subject of considerable scientific debate, the comparison of structural asymmetries involving the PT and the PO is ideal as they are based on objective and consistent types of measures across species and identical landmarks and procedures can be used to quantify them in both humans and chimpanzees (Hopkins and Nir 2010).

Thus, the primary aim of this study was to assess whether the combination of PT and PO asymmetries observed in humans by Habib et al. (1995, 1999) also exists in common chimpanzees and, if it occurs, what are their potential relationships with behavioral asymmetries, such as handedness. The evolutionary significance of PO asymmetries, including structural asymmetries in parietal and perisylvian regions, is of considerable interest. As suggested by Tobias (1987), Holloway (1995), and Bruner (2003, 2004), parietal areas seem to have been a major determinant in modern human brain evolution, essentially through visuospatial integrative processes. These views are confirmed by recent functional magnetic resonance imaging (fMRI) studies conducted in parallel in awake humans and monkeys and concentrating on the posterior parietal cortex where, in human, more regions are devoted to aspects of vision than in monkeys (Vanduffel et al. 2002; Orban et al. 2006). Although human and monkey posterior parietal cortices (inferior and superior parietal lobules) are homologous structures (Galetti et al. 1997) and that the functional relevance of these structures for visuomotor tasks is similar in human and monkey (Bremmer et al. 2001; Grefkes and Fink 2005), newly evolved functional areas and reorganization in humans possibly reflect differences in the evolution of the dorsal visual stream and the inferior parietal lobule. These adaptations may provide the capacity for the enhanced visual analysis of moving images that is necessary for the sophisticated control of manipulation and the tool handling capabilities that characterize the human species (Vanduffel et al. 2002; Grefkes and Fink 2005; Orban et al. 2006). Furthermore, left supramarginal areas, which are part of the left PO, are associated with language processing in human. Geschwind (1965) has argued that the ability to learn names of objects depends on the ability to form cross-modal associations and that cross-modal abilities are subserved by a cortical area receiving indirect connections from many sensory areas. Geschwind (1965) identified this area as the angular and supramarginal gyri of the parietotemporal cortex in humans, lesions of which produce aphasia, if in the dominant hemisphere, and simulation of which produces aphasic arrest

(Penfield and Rasmussen 1950). A recent voxel-based morphometry (VBM) study showed that the gray-matter density of this region, among other parietotemporal regions, is related to reading ability (Carreiras et al. 2009). This is of particular interest because reading is an exclusively human skill that does not develop without intensive tuition and practice and only recently appeared in Neolithic cultures. Hence, although cross-modal abilities exist both in human and in chimpanzee and probably evolved before the split between the 2 lineages (Ludwig et al. 2011), it can be assumed that neuroanatomical asymmetries in human brain parietal regions are at least to some extent associated with the differential hemispheric representation of specifically human processes. The comparison of PO and PT structural asymmetries and their combination as well as an appreciation for their possible behavioral correlates in chimpanzee compared with human may therefore shed light on the evolution of structures that became associated with the specific cognitive functions of the human lineage.

In this framework, a second aim of this study was to test whether handedness significantly influenced variation in asymmetries in the PT and PO, and in particular, the combination of asymmetries in these regions. In humans, Habib et al. (1995) reported that a significantly higher proportion of right-handed individuals (84%) showed leftward asymmetries in both the PT and the PO compared with the subjects who had either mixed or rightward asymmetries for both the PT and the PO regions. Though studies examining the association between handedness and asymmetries in the PO in nonhuman primates are lacking, previous studies in chimpanzees have shown that asymmetries in the PT are associated with hand preferences for certain measures such as tool use and manual gestures but not other tasks, such as simple reaching or bimanual feeding (Hopkins and Cantalupo 2004a; Hopkins et al. 2007; Hopkins and Nir 2010). In this study, we examined whether variation in asymmetries in the PT and PO was associated with hand preferences for tool use in contrast to handedness for nontool use actions. If combined asymmetries in the PT and PO are associated with handedness for complex praxic functions, such as tool use, as has been reported in humans, then we hypothesized that chimpanzees that have leftward asymmetries for both the PT and the PO would be significantly more right-handed than those who were mixed or who showed rightward asymmetries for both brain regions.

## Materials and Methods

### Subjects

Magnetic resonance imaging (MRI) scans were obtained in 83 captive common chimpanzees (*Pan troglodytes*) including 55 females and 28 males ranging from 6 to 50 years of age (mean = 21.07, standard error [SE] 1.43). All of the chimpanzees were members of a captive colony housed at the Yerkes National Primate Research Center (YNPRC) in Atlanta, GA. Most African-born captive chimpanzee population founders in the United States of America are *P. troglodytes verus* (95.0%), and data on subspecies composition of captive US common chimpanzee population are presented in Ely et al. (2005).

### Magnetic Resonance 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 YNPRC standard procedures, and then transported to the MRI facility. Subjects were anesthetized for the duration of the scan and transportation time between the home cage and imaging facility (total time

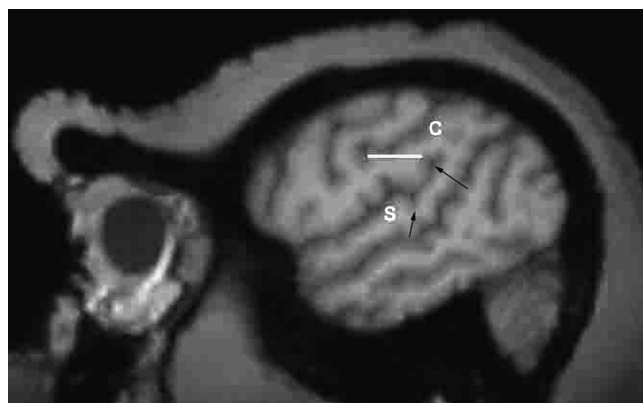
~ 2 h). Subjects were placed in the scanner chamber in a supine position with their head fitted inside the human-head coil. Scan duration ranged between 40 and 80 min as a function of brain size. Approximately half the subjects ( $N = 35$ ) were scanned using a 1.5-T scanner (Phillips, Model 51). The remaining chimpanzees ( $N = 48$ ) were scanned using a 3.0-T scanner (Siemens Trio, Siemens Medical Solutions, USA Inc., Malvern, PA) at the YNPRC.

For all the chimpanzees scanned in vivo using the 1.5-T machine,  $T_1$ -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, matrix size =  $256 \times 256$ , slice thickness = 1.2 mm, voxel size =  $1.2 \times 1.2 \times 1.2$  mm, and slice overlap = 0.6 mm). MRI acquisition information for 1.5-T images is reported in Hopkins and Cantalupo (2004a). For the chimpanzees scanned using the 3.0-T scanner (Siemens Trio),  $T_1$ -weighted images were collected using a 3D gradient echo sequence (pulse repetition = 2300 ms, echo time = 4.4 ms, number of signals averaged = 3, matrix size =  $320 \times 320$ , slice thickness = 0.6 mm, and voxel size =  $0.6 \times 0.6 \times 0.6$  mm). Complete MRI acquisition information for 3.0-T images is provided in Keller et al. (2009). After completing the 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, then returned to their home cage. The archived MRI data were transferred to a PC running ANALYZE 7.0 (Mayo Clinic, Mayo Foundation, Rochester, MN) software for postimage processing.

### Quantification of the PT and PO

#### Planum Temporale

The PT (Fig. 1) was quantified following the procedures previously employed by Cantalupo et al. (2003) and Hopkins et al. (2007). To measure the surface area of PT, the MRI 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 PT was defined by the most frontal slice showing Heschl's gyrus (HG). If there was a second HG, this latter was included in the PT. This procedure is standard when measuring the PT in humans. The posterior border was defined by the most caudal slice showing the sylvian fissure. Once the anterior and posterior borders were delineated, the depth of SF (i.e., width of PT) on each slice was measured from the superior lateral 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). Following a well-established procedure in the human literature, an estimate of the PT surface areas (in square millimeters)



**Figure 1.** In vivo common chimpanzee head MR parasagittal section. The PO is defined as the maximal linear distance (white line) between the end point of the sylvian fissure (S) and the central sulcus (C). If the posterior portion of the sylvian fissure is bifurcated, the posterior end point of distance SC is the tip of the PAR of the sylvian fissure (see Materials and Methods). The PT covers the superior bank of the superior temporal gyrus between the bottom of the Heschl's sulcus (PT anterior border) (tip of the short black arrow) and the posterior end of the horizontal portion of the sylvian fissure (S) (PT posterior border) (tip of the long black arrow).

was computed as the sum of the cumulative PT depth measures for each slice within a hemisphere multiplied by the slice thickness.

#### Parietal Operculum

We followed a procedure modified from Habib et al. (1995, 1999). Using ANALYZE 7.0 (Mayo Clinic), each sagittal image was placed upon a reference diagram showing the level of the bicommissural line taken from the midsagittal image. We measured the linear distance, drawn parallel to the bicommissural plane, between the end point of the sylvian fissure (S) and the opercular part of the central sulcus (C). This measure defines the distance SC (Fig. 1). It is equivalent to the distance SR of Habib et al. (1995), where R is the abbreviation for the sulcus of Rolando (central sulcus). It provides a simple, reliable, and easily reproducible estimate of the anteroposterior extent of the PO and can reliably be used to compare chimpanzees and humans. Another assessment of PO could involve delineating its contours using sulcal-gyral landmarks on a cortical surface 3D rendering or cytoarchitectonic mapping. Unlike humans, however (Eickhoff et al. 2006), PO sulcal patterning and cytoarchitectonic mapping as such remain to be studied in chimpanzees. We measured the distance SC on each sagittal slice where these anterior and posterior borders were recognized. The mean SC distance was then defined as the mean of these measurements for each hemisphere. Because both the posterior ascending ramus (PAR) of the sylvian fissure and the central sulcus may show slightly different oblique directions from the surface to the depth of the hemisphere, we also arbitrarily measured the distance SC on the sagittal section where this distance was maximal (maximal SC distance). Mean and maximal SC distances were correlated (left side:  $r = 0.931$ ; right side:  $r = 0.878$ ). The mean and maximal SC distances do not show any significant differences (pooled male and female chimpanzees, Table 1). We therefore used the maximal SC distance for our analysis, in concordance with the methods employed by Habib et al. (1995, 1999) in human subjects. Furthermore, when the posterior portion of the sylvian fissure was bifurcated, the posterior end point of distance SC was the tip of the anterior branch, that is, the tip of the PAR (limb) of the sylvian fissure (Fig. 2). In humans, distance SC is usually larger in the left compared with the right hemisphere in concordance with the usually more posterior termination of the left sylvian fissure (Witelson and Kigar 1988 for a review).

#### Comparison between Metrics Obtained on 1.5- and 3.0-T MRI Scans

We used 2 different MRI scanners in this study. There is currently no work concerning possible variations in measurements done on specimens scanned at 1.5 and 3 T, and no specimen was scanned twice as regards this methodological issue. The resolution of the device, however, does not appear to have any impact on the metrics, as demonstrated by Maret et al. (2010) for images acquired with cone beam computed tomography and microcomputed tomography. Nonetheless, we were concerned with the possibility that the variation in scanner strength might influence the results. Thus, we initially compared the measures of asymmetry in the PO and PT between the subjects scanned at 1.5 and 3 T (see also Hopkins and Nir 2010).

#### Behavioral Measures of Handedness

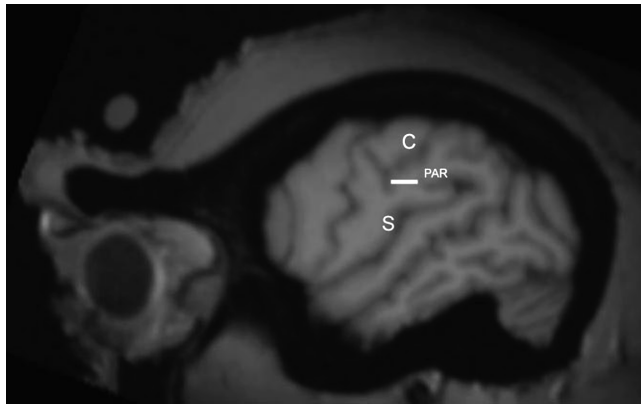
Handedness was assessed on 2 measures. One task (TOOL) was designed to simulate the termite fishing behavior of wild chimpanzees (Lonsdorf

**Table 1**

Descriptive data on average and maximal SC length ( $\pm$ SE) in chimpanzees

	Left	Right	AQ	t-value	P
Mean	20.87 (0.50)	18.78 (0.46)	−0.115 (0.031)	−3.27	0.001
Maximal	23.09 (0.59)	20.63 (0.49)	−0.116 (0.030)	−3.76	0.001

Note: AQ is derived following the formula  $AQ = (R - L) / ((R + L) \times 0.5)$ , where  $R$  and  $L$  indicate right and left SC length. The AQ here indicates leftward asymmetry and does not show any significant difference by using either mean or maximal SC distances (one- or two-tailed  $t$ -test). Male and female subjects are pooled. Left and right SC length values are in millimeters. Numbers in parentheses represent SEs. Correlation between AQs calculated from mean and maximal SC distances,  $r = 0.858$ .



**Figure 2.** In vivo common chimpanzee head MR parasagittal section (other specimen than Fig. 1). The PO is the maximal linear distance (white line) between the end point of the sylvian fissure (S) and the central sulcus (C). Here, the end point of the sylvian fissure is defined as the end point of a long PAR (limb) of the sylvian fissure (PAR) (see Material and Methods). In this example, the sylvian fissure pattern is “inverted” following the terminology of Ide et al. (1996).

and Hopkins 2005; Hopkins et al. 2009). Termite fishing involves the use of fine sensorimotor and visuospatial skills in which the chimpanzees insert small twigs into holes located on a termite mound, wait for the termites to attack, and attach to the stick, whereupon they retract the stick and consume the termites (Goodall 1986). For comparison to the tool use data, hand preferences for a task requiring bimanual coordination, referred to as the TUBE task, were also obtained in the subjects.

All behavioral testing was conducted in the outside portion of their home cages. Subjects were tested on different days of the week between the hours of 10 AM and 7 PM. The order of test administration was pseudorandomly determined for all subjects. Individuals collecting the hand preference data were blind to the brain asymmetry data available for each chimpanzee. Although bouts of hand use could have been recorded for each behavior, we used frequencies of hand use as the level of analysis in determining individual handedness because previous studies have shown significant positive correlations ( $r > 0.96$ ) for handedness values when based on bouts compared with frequencies (Hopkins et al. 2001).

#### *Simulated Termite Fishing (TOOL Task)*

Testing was conducted using a device consisting of 3 polyvinyl chloride (PVC) pipes (15 cm long, 4 cm in diameter) glued at 45° angles into 3 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 glued 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 or applesauce) 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 (~0.5 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 2 tests sessions were obtained from each subject. Data on the TOOL task were available for a subset of 73 chimpanzee subjects.

#### *Coordinated Bimanual Actions (TUBE Task)*

The TUBE task entails the use of PVC tubes (24–31 cm long, 2.5 cm wide) with peanut butter smeared on the inside edge, approximately 2–4 cm in depth (see Hopkins 1995). The tubes were given to the subjects in their home cage by pushing them through the cage mesh. The digit and hand used to remove the peanut butter was recorded as either left or right, each time the subjects inserted their finger, removed peanut butter from the tube, and placed their finger in their mouth. Observations continued

until the subjects stop showing interest in the tube (usually when they have eaten all the peanut butter), dropped it for at least 10 s, or pushed the tube back out of their home cage through the cage mesh. Each chimpanzee was tested on at least 2 different occasions, and we obtained a minimum of 50 responses per session for each chimpanzee.

#### *Data Analysis*

For both the PT and the PO, asymmetry quotients (AQs) were derived following the formula  $[AQ = (R - L)/((R + L) \times 0.5)]$ , where  $R$  and  $L$  indicated the surface area (for the PT) and length (for the PO) measures of the right and left hemispheres, respectively. Negative AQ values indicated left hemisphere asymmetries, while positive AQ values indicated right hemisphere asymmetries. We also classified subjects as asymmetrical in favor of the left or right side based on the sign of their AQ value. Subjects with AQ scores  $\geq 0.025$  or  $\leq -0.025$  were classified as asymmetrical in favor of the right or left side. All others were classified as nonasymmetrical. For the 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 nonright-handed. We also computed handedness indices (HIs) for each task and chimpanzee following the formula:  $[HI = (R - L)/(R + L)]$ , where  $R$  and  $L$  represented the number of right- and left-handed responses for each subject. All analyses adopted an alpha of  $P < 0.05$  as the level of significance. Post hoc tests, when necessary, were conducted using Tukey's honestly significant difference with  $P < 0.05$ .

To summarize, one-sample  $t$ -tests, Pearson product moment correlation coefficients and chi-square goodness-of-fit tests were conducted on the AQ classification scores for the PT and PO. Analysis of variance (ANOVA) and chi-square tests were conducted to evaluate the effect of sex and age on PT and PO asymmetries. ANOVA, chi-square goodness-of-fit tests, and Student's  $t$ -tests were conducted to evaluate the relationships between PT and PO asymmetries and handedness. The examiner was blind to hemisphere and sex of specimens. Intrarater and interrater reliability were assessed following Knaus et al. (2006) and Hopkins and Nir (2010).

## **Results**

### *Descriptive Statistics*

We found no significant differences for any of the measures of asymmetry between the chimpanzees scanned at 1.5 compared with 3 T. The mean AQ scores for the PT for apes scanned at 1.5 and 3.0 T were  $-0.104$  and  $-0.109$ , respectively,  $t_{81} = 0.126$ , not significant (NS). Similarly, the mean AQ scores for the PO were  $-0.107$  and  $-0.138$  for the apes scanned at 1.5 and 3.0 T,  $t_{81} = 0.491$ , NS. Because there were no significant differences based on the scanner strength, we combined the data from the 2 groups for the remaining analyses.

One-sample  $t$ -tests were conducted on the AQ scores for the PT and PO to assess whether the apes showed population-level asymmetries or not. For both the PT  $t_{80} = -6.05$ ,  $P < 0.001$  and the PO  $t_{82} = -3.76$ ,  $P < 0.001$ , the chimpanzees showed significant leftward asymmetries. The mean surface area for the PT and maximal SC distances for PO in each hemisphere and sex are shown in Table 2. Though leftward asymmetries were found for both the PT and the PO, a Pearson product moment correlation failed to reveal a significant association between the AQ measures,  $r_{80} = 0.195$ ,  $P = 0.075$  (NS, two-tailed) (Fig. 3). There was no within hemisphere correlation between PT and PO (maximal distance SC), either in the left ( $r_{81} = 0.207$ ,  $P = 0.063$ ) or in the right ( $r_{81} = 0.127$ ,  $P = 0.260$ ) hemisphere.

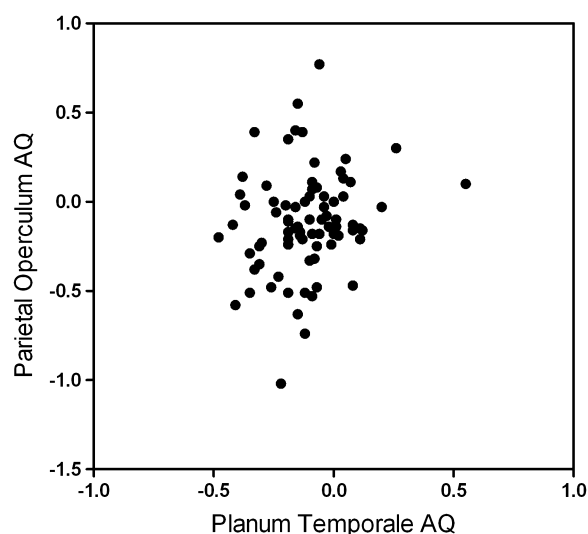
We next considered asymmetries in the PT and PO when based on the classification criteria. These analyses largely confirmed the results from the AQ scores. The distribution of lateralization for the PT and PO is shown in Table 3. Chi-square



**Table 2**Mean AQ measures ( $\pm$ SE) for the PT and the PO in female and male chimpanzees

	PT			PO		
	Left	Right	AQ	Left	Right	AQ
Females	338.09 (9.61)	300.96 (8.69)	−0.121 (0.023)	23.52 (0.68)	20.38 (0.57)	−0.129 (0.039)
Males	338.24 (13.59)	305.73 (12.28)	−0.094 (0.032)	22.66 (0.95)	20.87 (0.80)	−0.093 (0.056)
Total	338.16 (8.32)	303.35 (7.52)	−0.108 (0.020)	23.09 (0.58)	20.63 (0.49)	−0.111 (0.034)

Note: Left and right PT values represent surface areas in square millimeters and left and right PO values correspond to distance SC in milliliters (see Data Analysis). Numbers in parentheses represent SEs.

**Figure 3.** PO AQ versus PT AQ in common chimpanzees. Pearson  $r = 0.195$  (NS,  $P = 0.075$ ) (see Data Analysis).**Table 3**

Distribution of asymmetries in the PT and the PO in female and male chimpanzees

	PT			PO		
	#L	#A	#R	#L	#A	#R
Females	42	4	9	36	4	15
Males	18	4	6	20	1	7
Total	60	8	15	56	5	22

Note: #L = number of subjects with leftward asymmetry, #A = number of subjects with no bias, and #R = number of subjects with rightward asymmetry.  $N$  (total) = 83. Total percentages for PT are #L = 72.3%, #A = 9.6%, and #R = 18%. Total percentages for PO are #L = 67.5%, #A = 6%, and #R = 26.5%.

goodness-of-fit tests indicated that the distribution of lateralized individuals for the PT ( $\chi^2(2, N = 83) = 57.56, P < 0.001$ ) and PO ( $\chi^2(2, N = 83) = 48.75, P < 0.001$ ) differed significantly from what would be expected if asymmetries were randomly distributed. Subsequent chi-square tests indicated that the number of chimpanzees left lateralized for the PT was significantly higher than the number of right ( $\chi^2(1, N = 75) = 27.00, P < 0.001$ ) and nonlateralized ( $\chi^2(1, N = 68) = 39.76, P < 0.001$ ) individuals. Similarly, for the PO, the number of left lateralized chimpanzees was significantly higher than the number of right ( $\chi^2(1, N = 78) = 14.82, P < 0.001$ ) and nonlateralized ( $\chi^2(1, N = 61) = 42.64, P < 0.001$ ) individuals.

### Sex and Age Effect

We initially assessed whether there were sex differences in the direction of asymmetry for the PT and PO using a mixed model

ANOVA. The AQ scores for the PT and PO were the repeated measure while sex was the between group factor. Age served as a covariate. No significant main effects or interactions were found (Table 2). Likewise, for the laterality classification data (Table 3), chi-square tests of independence failed to reveal significant associations between the sex and the distribution of asymmetries.

### Handedness Effects

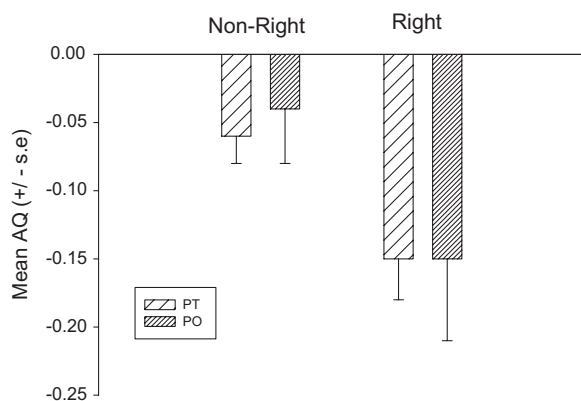
We next considered the effect of handedness on PT and PO asymmetries. For these analyses, a mixed model ANOVA was performed with sex and handedness serving as the between group factors. The AQ values for the PT and PO served as the repeated measures. Separate ANOVAs were performed for the TOOL and TUBE tasks because the 2 sets of data were not independent of each other. For the TOOL task, a significant main effect for handedness was found  $F_{1,69} = 4.31, P < 0.05$ . Right-handed chimpanzees had significantly lower AQ scores than nonright-handed chimpanzees (Fig. 4). For the TUBE task, no significant main effects or interactions were found. Thus, differences in the AQ scores for the PT and PO were associated with handedness for tool use but not for nontool use motor actions.

For the purpose of comparing with Habib et al. (1999), we ran complementary Student's  $t$ -tests on PT and on PO AQ values for right-handed (RH) against nonright-handed (NRH) chimpanzees for TOOL task. There was a significant difference between PT AQ for RH and PT AQ for NRH ( $t = 2.267, P = 0.01$ , one-tailed unpaired  $t$ -test) (Fig. 5) but not between PO AQ for RH and PO AQ for NRH ( $t = 1.394, P = 0.08$ , one-tailed unpaired  $t$ -test) (Fig. 6).

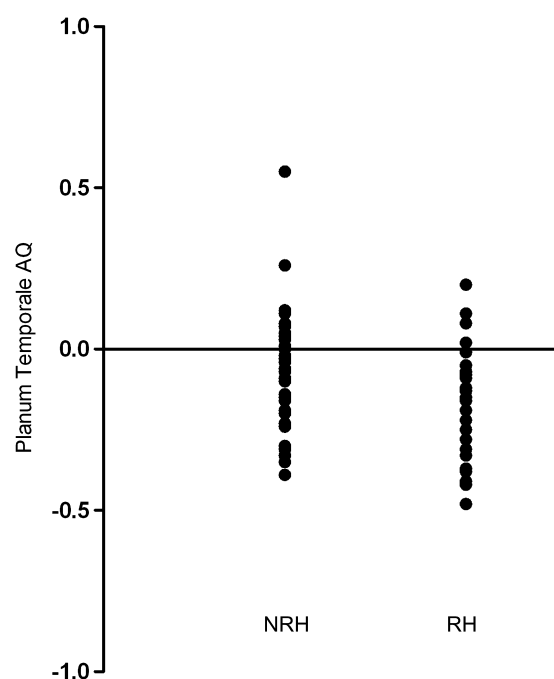
### Combinations of PT and PO Asymmetries and Comparison with Habib et al. Data

In this set of analyses, we examined the association between handedness for the TOOL task and the combined directional asymmetries in the PT and PO (Habib et al. 1995, 1999; Table 4). As was done by Habib et al. (1995, 1999) in human brains, the chimpanzees were classified as asymmetrical in favor of the right (positive AQ values) or left (negative AQ values) side for the PT and for the PO. We then classified the apes as either leftward for both the PO and the PT (LL), leftward for the PT and rightward for PO (LR), rightward for the PT and leftward for PO (RL), or rightward for both the PT and PO (RR).

Chi-square goodness-of-fit tests indicated that the number of LL chimpanzees ( $N = 37$ ) was significantly higher than the number of LR ( $N = 16$ ) ( $\chi^2(1, N = 53) = 8.32, P < 0.01$ ), RL ( $N = 12$ ) ( $\chi^2(1, N = 49) = 12.76, P < 0.01$ ), and RR ( $N = 8$ ) ( $\chi^2(1, N = 45) = 18.69, P < 0.001$ ) subjects. To compare the chimpanzee data with the distribution of combined PT and PO asymmetries in humans, we used the data for the 40 human brains reported by Habib et al. (1995) with the distribution reported here for



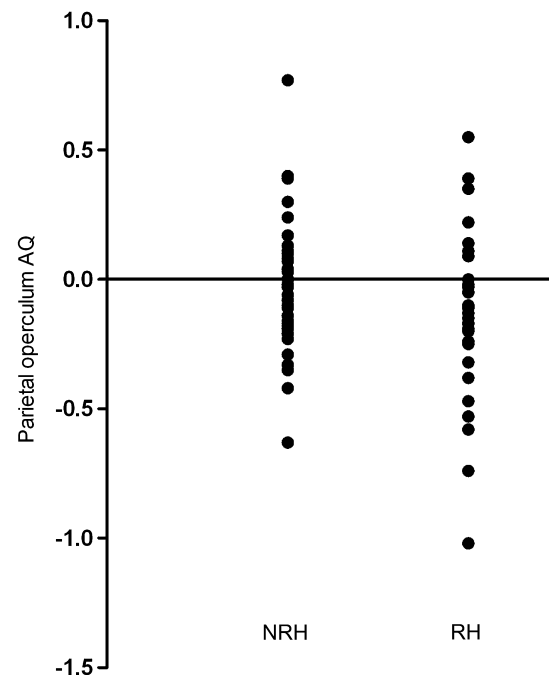
**Figure 4.** Mean AQ scores ( $\pm$  SE) (see Data Analysis) for right-handed and nonright-handed chimpanzees based on their hand preference for the TOOL task.



**Figure 5.** Distribution of right-handed (RH) and nonright-handed (NRH) subjects for tool use according to the degree of PT asymmetry in chimpanzees (see Data Analysis). Negative AQ values indicate left hemisphere asymmetries. Positive AQ values indicate right hemisphere asymmetries.

chimpanzees using a chi-square test of independence. No significant differences were found  $\chi^2(3, N = 123) = 1.54$ , NS. As can be seen, the human and chimpanzee distributions appear comparable. The percentages for chimpanzees are LL = 50.7%, LR = 22%, RL = 16.5%, RR = 11% and the percentages for humans are LL = 47.5%, LR = 15%, RL = 22.5%, RR = 15%.

Chi-square tests of independence failed to reveal an association between sex and the asymmetry classification; however, handedness for the TOOL task was borderline significantly associated with the asymmetry classification distribution ( $\chi^2(3, N = 73) = 6.86$ ,  $P < 0.06$ ) (Table 4). In general, the proportions of right- and nonright-handed chimpanzees were comparable within the LL, LR, and RL groups but among the RR chimpanzees, 0% were right-handed for the TOOL task and 11% were classified as nonright-handed. Again, for comparison to the previous



**Figure 6.** Distribution of right-handed (RH) and nonright-handed (NRH) subjects for tool use according to the degree of PO asymmetry in chimpanzees (see Data Analysis). Negative AQ values indicate left hemisphere asymmetries. Positive AQ values indicate right hemisphere asymmetries.

**Table 4**

PT and PO asymmetry combinations

	PT L > R PO L > R #LL	PT L > R PO R > L #LR	PT R > L PO L > R #RL	PT R > L PO R > L #RR
Chimpanzees ( $N = 73$ )				
Right-handed	18	8	5	0
Nonright-handed	19	8	7	8
Total	37	16	12	8
Humans ( $N = 40$ )				
Right-handed	16	3	3	2
Nonright-handed	3	3	6	4
Total	19	6	9	6

Note: Occurrences of PT and PO asymmetry combinations in right-handed and nonright-handed chimpanzees and humans. #LL = number of subjects with left PT > right PT and left PO > right PO. #LR = number of subjects with left PT > right PT and left PO < right PO. #RL = number of subjects with left PT < right PT and left PO > right PO. #RR = number of subjects with left PT < right PT and left PO < right PO. Human data are from Habib et al. (1995). Total percentages for chimpanzees are LL = 50.7%, LR = 22%, RL = 16.5%, and RR = 11%. Total percentages for humans are LL = 47.5%, LR = 15%, RL = 22.5%, and RR = 15%.

findings reported by Habib et al. (1995, 1999), we provided the number of right- and nonright-handed individuals within the 4 different PO and PT classification groups. As can be seen, there is a higher proportion of right-handed individuals in the LL and RR groups in the human sample compared with the chimpanzees (Table 4).

As an alternative to the chi-square test described above, we examined the association between handedness and the combination of PT and PO brain asymmetries using a mixed model ANOVA in chimpanzee. For this analysis, the HI score for the TOOL and TUBE tasks served as the dependent measures, while sex and brain asymmetry grouping (LL, LR, RL, and RR) (cf. Table 4) served as between group factors. A significant two-

way interaction between handedness task and brain asymmetry group was found ( $F_{3,65} = 3.51$ ,  $P < 0.03$ ). The mean HI values for the TOOL and TUBE tasks for each brain asymmetry grouping are shown in Figure 7. Post hoc tests indicated that no significant differences in HI scores were found for the TUBE task between the brain asymmetry groups; however, for the TOOL task, the mean HI scores were significantly lower (reflecting greater left-handedness) in the RR compared with all other brain asymmetry groups.

## Discussion

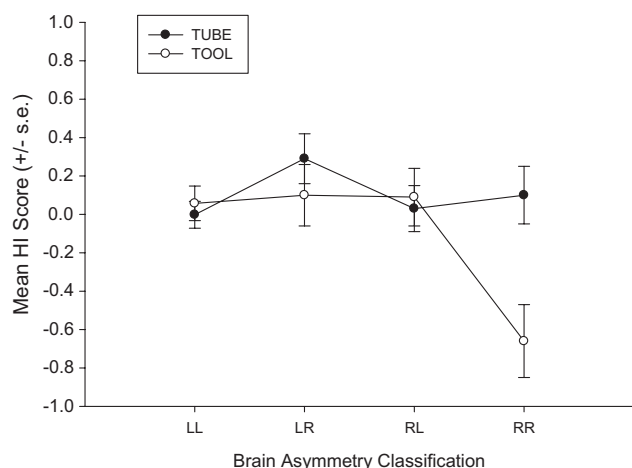
One main finding of this study is that chimpanzees show population-level leftward asymmetries for both the PT and the PO. Although evidence of leftward asymmetries in the PT of chimpanzees have been reported in previous studies (Gannon et al. 1998; Hopkins et al. 1998; Gilissen 2001; Hopkins and Nir 2010), these are the first evidence of leftward asymmetries in the PO in this species and, indeed, any nonhuman primate. It is interesting that comparable significant leftward asymmetries exist in both the inferior (PT) and the superior (PO) banks of the sylvian fissure although there was no significant association between these measures (Fig. 3). This was also reported for humans by Habib et al. (1995) with  $r_{40} = 0.142$ , NS. Similarly, no within hemisphere correlation between PT and PO was observed in humans, either in the left ( $r = 0.22$ , NS) or in the right ( $r = 0.262$ , NS) hemisphere (Habib et al. 1995). This suggests that these asymmetries are somewhat independent of each other in both humans and chimpanzees.

The lack of correlation also appears to characterize other neighboring structural asymmetries, for instance, sylvian fissure segment asymmetries in great apes (Cantalupo et al. 2003). In this case, the asymmetry of the portion of the sylvian fissure delimited by the anterior and posterior margins of PT shows no correlation with asymmetry of the postcentral portion of the sylvian fissure delimited by the terminating point of the central sulcus and the anterior margin of PT although both these measures show significant population-level leftward asymmetry (Cantalupo et al. 2003). Another example involves the region just posterior to the PO, that is, the posterior wall of the PAR of

the sylvian fissure that, when present, defines the planum parietale (PP) in humans (Jäncke et al. 1994; Foundas et al. 2002) and chimpanzees (Gilissen 2001; Gannon et al. 2005; Tagliatela et al. 2007). The direction of PP asymmetry is opposite to that of the adjacent PT in the 2 species and these 2 parameters would be expected to show a significant negative correlation. However, the asymmetries of PT and PP surface areas are only weakly correlated in humans (Jäncke et al. 1994). Foundas et al. (2002) observed that the combination of a larger left PT with a larger right PP only occurs slightly beyond the likelihood of chance. This is here especially relevant because the parameter used by Foundas et al. (2002) for both the PT and the PP was the average length calculated from measurements made on sagittal sections. In chimpanzees, Gilissen (2001) observed a human-like pattern of  $L > R$  PT and  $R > L$  PP surface areas in 10 postmortem specimens, and no significant correlations were found between PT and PP asymmetries (Pearson  $r = 0.12$ ,  $P = 0.7$ ) or between left PT and right PP surface areas (Pearson  $r = 0.33$ ,  $P = 0.34$ ) (reanalysis of the data of Gilissen 2001). Likewise, using a sample of 23 postmortem common chimpanzee brains, Gannon et al. (2005) found a significant pattern with an  $R > L$  PAR of the sylvian fissure, a leftward asymmetric PT margin, and no correlation between the right PAR length and the length of the left lateral margin of the PT. With a larger sample of 78 common chimpanzees, Tagliatela et al. (2007) found a significant rightward asymmetry for the PP in females but not in males. Beyond the effects of sex and handedness that differs between species, overall it seems that structural markers of parietal cortex asymmetry appear to be independent both in humans and in chimpanzees.

A second finding is that handedness for tool use but not for other nontool use motor actions appeared to mediate the expression of asymmetries in both the PT and the PO, with right-handed apes showing a more pronounced leftward asymmetry compared with nonright-handed subjects. This is in concordance with Hopkins et al. (2007) who reported an association between combined brain AQs (PT surface area and frontoorbital sulcus length) and handedness for simulated tool use tasks and with Hopkins and Nir (2010) who confirmed the significantly left larger than right PT surface area in chimpanzee and did not observe any association between PT asymmetries and handedness for the TUBE task.

In our study, *t*-tests, however, fail to show a significant association between handedness for tool use and PO asymmetry;  $P = 0.01$  for PT AQ values for right-handed versus PT AQ values for nonright-handed (Fig. 5) but  $P = 0.08$  for PO AQ values for right-handed versus PO AQ values for nonright-handed chimpanzees (Fig. 6). It is, however, interesting that, in humans, the *t*-test results of Habib et al. (1999) give  $P = 0.003$  for PT AQ values for right-handed versus PT AQ values for nonright-handed ( $t = -3.16$ ) but only  $P = 0.04$  for PO AQ values for right-handed versus PO AQ values for nonright-handed ( $t = -2.13$ ). Comparison of the *t*-tests therefore at least shows that a similar trend does exist in chimpanzees and humans, and the difference appears to reside in the degree of asymmetry (Gilissen 2001). This feature already characterized the results of Yeni-Komshian and Benson (1976), in one of the first comparative study of cerebral asymmetry in humans and nonhuman primates using large samples ( $N = 25$  per species). Yeni-Komshian and Benson (1976) observed a significant leftward asymmetry of the sylvian fissure length (SF) in humans



**Figure 7.** Mean HI scores ( $\pm$ SE) (see Data Analysis) for the TOOL and TUBE tasks within each PT and PO asymmetry combination in chimpanzee (cf. Table 4). HI values range from  $-1.0$  to  $1.0$ , with the absolute value representing the strength of the lateral bias; positive values indicate right-hand bias and negative values indicate left-hand bias.

and common chimpanzees but not in macaques. In their study, the mean left and mean right sylvian fissure lengths are, respectively, 83.6 and 73.4 mm in humans, 45.7 and 43.7 mm in chimpanzees, and 33.1 and 32.7 in macaques. Using their figures, we calculated an AQ (dSF) (see Materials and Methods). dSF = -0.13 in humans, -0.04 in chimpanzees, and -0.01 in macaques, but this latest is NS. The weak variation between macaques and chimpanzees, however, crosses the level of significance, and the difference between chimpanzees and humans is an important difference in degree of asymmetry that could well be related to differences in functions (Galaburda 1995). This relationship between function and degree of structural asymmetry is brilliantly illustrated for the human PT by the variations of the asymmetry coefficient among right-handed subjects, where the degree of leftward PT asymmetry increases from right-handers with developmental dyslexia to normal right-handers and is even much more pronounced in right-handed professional musicians with perfect pitch (Schlaug et al. 1995; Steinmetz 1996).

A third finding from this study shows that the distribution of combinations of PT and PO asymmetries is comparable in humans and chimpanzees with a significantly higher proportion of subjects with leftward asymmetry for both the PT and the PO. Proportions of chimpanzees showing these combinations are comparable and do not differ from at least 2 reports in human brains that employed similar methods of measurement in asymmetry for the 2 regions (Habib et al. 1995, 1999). In this context, Hopkins et al. (2008) observed leftward asymmetries for both the PT and the supramarginal gyrus, in concordance with our study, but rightward asymmetries for the angular gyrus. Given that there is no a priori region of interest when using VBM, voxels in the supramarginal gyrus region analyzed by Hopkins et al. (2008) are homologous to voxels included in the posterior portion of the PO measurement as defined in our current study (see Introduction). Reported asymmetries in the angular gyrus in humans (Watkins et al. 2001) are opposite to those reported for chimpanzees. Although this result from VBM remains to be validated with other approaches, such as manual ROI data, it currently appears that the asymmetry in the angular gyrus so far represents the only marked difference between humans and chimpanzees in terms of parietal cortex asymmetry pattern.

In humans, the most frequent convergence of leftward PT and PO asymmetries is strongly associated with right-handedness with the right-handed subjects representing 84% ( $N = 16$ ) of the subjects within the LL category (Table 4; Habib et al. 1995, 1999). In chimpanzees, the proportions of right-handed and nonright-handed subjects for the TOOL task are similar ( $N = 18$  and 19) within the LL category. In contrast, among the RR chimpanzees, the proportion of right-handed versus nonright-handed subjects is very different from what is observed in the other combinations and different from humans (Table 4; Habib et al. 1995, 1999). Although no significant differences in HI scores were found for the TUBE task between brain asymmetry categories, the mean HI scores for the TOOL task were significantly lower in the RR chimpanzees compared with other categories (Fig. 7). In humans, the convergence of leftward PT and PO asymmetries appears to be associated with right-handedness (LL combination) (Table 4; Habib et al. 1995, 1999). Although a comparable proportion of combined PT and PO leftward asymmetries are here reported for chimpanzees, our study suggests that handedness effects are not similar when

comparing the 2 species and that in chimpanzee, the only clear structure-function relationship is the convergence of rightward PT and PO asymmetries that best predicts left-handedness (RR combination) (Table 4).

It should be emphasized that the measures of handedness used by Habib et al. (1995, 1999) are not strictly comparable with the handedness quantifications used in this study because the cognitive demands of a task influence the pattern of hand preference (Gilissen 2001 for a review). Handedness is always considered as a 1D trait in humans and do not take into account possible differences between nontool tasks and tasks that involve manipulating tools, although tool involvement in praxis networks would require specific hand performances that could have an influence on handedness (Heilman 1997; Corey et al. 2001). Given the cognitive landscapes of the 2 species studied here, we did not focus on searching for a strict homology between chimpanzee and human behavioral measures of handedness but rather on the relationship between shared anatomical asymmetries and the specific expression of handedness independently assessed in the 2 species. In chimpanzees, significant relationships between structure and function are revealed when considering specific handedness tasks with different motor demands, such as the TUBE and TOOL tasks (Table 4 and Figs 4 and 7). Chimpanzees show lateralized hand preference when using tools, at least when patterns of tool technology are done on the ground (Lonsdorf and Hopkins 2005; Marchant and McGrew 2007; Sousa et al. 2009). The observed leftward structural asymmetries and their association with handedness for tool use in chimpanzee are interesting because in humans, both left- and right-handed subjects show left-hemisphere dominance for the planning of motor actions (Janssen et al. 2011). It must, however, be kept in mind that although hand manipulation involves similar functional brain regions in nonhuman primates and humans (Peeters et al. 2009), the rostral part of the intraparietal lobule appears to be a new functional human brain area that responds to tool action-specific activation. This functional area does not exist in macaques and probably underlies a specific way of understanding tool actions in humans (Peeters et al. 2009). Chimpanzees have not yet been studied from this functional viewpoint. However, behavior that can be inferred from the earliest evidence for tool technology in *Homo*, the stone toolmaking of the Oldowan culture (*Homo habilis*), dating back at least 2.6 Myr (Semaw et al. 1997; Stout et al. 2010), seems to fall within the range of chimpanzee (Wynn and McGrew 1989; Bradshaw and Rogers 1996) and even capuchin monkey (Westergaard and Suomi 1995; Urbani 2002; Visalberghi et al. 2009) capabilities. A crucial finding here emerges from a recent fMRI study performed with human subjects watching movies of the more simple Oldowan toolmaking method and of the Acheulian method that was used to produce more complex tools (Stout et al. 2011). Acheulian probably originated in Africa as early as 1.76 Myr ago and co-occurred with Oldowan artifacts for a period indicating that groups of hominins distinguished by separate stone-toolmaking behaviors coexisted in Africa at 1.76 Myr ago (Lepre et al. 2011). The study of Stout et al. (2011) reveals that Acheulian compared with Oldowan toolmaking was associated with activation of the left inferior frontal sulcus and left anterior intraparietal sulcus. The center of activation of the latter area as reported by Stout et al. (2011) corresponds to that of Peeters et al. (2009). Hence, the additional-specific sector of the left inferior parietal lobule



devoted to tool use (Peeters et al. 2009) may have occurred during the course of the evolution of the genus *Homo* in Africa after its divergence from other great apes. The functional brain regions underlying tool use and hence handedness for tool use may therefore well differ between chimpanzees and humans, but further studies are needed before any definitive conclusions can be drawn.

Another point of interest is that the relationship of both PT and PO asymmetries with handedness contrasts with previously reported asymmetries of the central sulcus. Asymmetry of the PT is a leftward asymmetry essentially characterized by a degree difference between left- and right-handed subjects in humans (reviewed in Steinmetz 1996) and chimpanzees (Hopkins and Cantalupo 2004a; Hopkins et al. 2007; Hopkins and Nir 2010; this study). The situation is similar for PO asymmetry but completely different for central sulcus asymmetry, which is characterized by AQ scores in opposite directions in left- and right-handed humans (Amunts et al. 1996, 2000) and chimpanzees (Hopkins and Cantalupo 2004a, 2004b). In addition, there is a strong gender effect for central sulcus asymmetry in humans (Amunts et al. 2000) that is not reported in chimpanzees (Hopkins and Cantalupo 2004a). Similarly, we observed no gender difference in the direction of asymmetry for both the PT and the PO and their combinations in chimpanzees. This is in contrast with the PP asymmetries, for which different but significant gender effects were found both in humans (Jäncke et al. 1994) and in chimpanzees (Taglialetela et al. 2007).

Finally, a crucial difference between human and chimpanzee resides in the sulcal patterning of the sylvian fissure. The measurement of PO as defined by Habib et al. (1995) and in this study (distance SC, see Fig. 1) is easy to reproduce in humans and in chimpanzees. It is a consistent type of measurement and the landmarks, we used are identical in both species. Moreover, these landmarks are easy to define and to recognize. The criteria used for quantifying the PO involve the tip of the posterior end of the sylvian fissure. When the posterior portion of the sylvian fissure was bifurcated, the posterior end point of distance SC was defined as the tip of the PAR of the sylvian fissure (see Materials and Methods). The lateral view of a rendered probabilistic map obtained from 12 individual chimpanzee brains (Spocter et al. 2010) shows a bifurcation of the posterior portion of the sylvian fissure into a posterior ascending and a posterior descending ramus. The position of these 2 rami represents a pattern described as “inverted” by Gannon et al. (2005) following a terminology introduced by Ide et al. (1996) for human brains. In this pattern, the posterior descending and ascending rami of the sylvian fissure are both of approximately equal size but the ascending ramus is oriented frontally (Fig. 2). Ide et al. (1996) observed this pattern in 21.25% of the cases in a sample of 40 human brains (20 of each sex) (17 cases of inverted pattern on a total sample of 80 hemispheres). In contrast with humans where the “superior” pattern is the most common (61.25% of the cases, Ide et al. 1996), Gannon et al. (2005) identified the inverted pattern as the most common in a sample of 23 postmortem common chimpanzee brains although the occurrence was not quantified. We frequently observed the bifurcation of the posterior end of the sylvian fissure into a frontally oriented PAR and a posterior descending ramus on the parasagittal sections that we used for measuring distance SC (Figs 1 and 2). In these cases, the frontal orientation of the PAR reduces the distance SC (Fig. 2). In humans, where the inverted pattern is not

present in the majority of the cases, distance SC is larger or smaller depending on the position of the sylvian point (Witelson and Kigar 1988; see Materials and Methods). In a sample of 78 chimpanzee brains, Taglialetela et al. (2007) observed on parasagittal sections that subjects most frequently have the inferior bifurcation pattern (Ide et al. 1996) in the left hemisphere, whereas the “symmetric” pattern (Ide et al. 1996) is most common in the right hemisphere, irrespective of sex. This result underlines the difference between chimpanzees and humans concerning the landmark positions and the anatomical substrate involved in PO definition because the inferior pattern was present in only 6 and the symmetric pattern in only 8 of the 80 human hemispheres observed by Ide et al. (1996).

It is therefore interesting to point out that PO structural asymmetry and its combination with PT asymmetry are similar in humans and chimpanzees although the measurement of distance SC in humans relies, in its vast majority, on a sylvian sulcal pattern that is different from the pattern(s) that characterize chimpanzees (Ide et al. 1996; Gannon et al. 2005; Taglialetela et al. 2007; Spocter et al. 2010; this study). The PO as we defined it here is therefore not strictly similar in humans and chimpanzees at the population level. Further work is necessary to quantify the occurrence of the various sylvian fissure patterns in both hemispheres in male and female chimpanzee brains. For this purpose, 3D reconstructions or surface views of the hemispheres (Ide et al. 1996; Gannon et al. 2005; Spocter et al. 2010) are necessary.

We assumed that the morphological asymmetries that characterize the left and right hemispheres are relevant as putative structural correlates of left or right brain cognitive specializations. The striking similarity of parietal cortex structural asymmetries in chimpanzees and humans (Table 4), however, leads to the conclusion that structural and functional asymmetries are not strictly related, at least at our level of macroscopic analysis. In our study, functions that characterize the human parietotemporal cortex seem to have colonized the brain after the appearance of structural asymmetries or, at least, “asymmetry in brain function follows asymmetry in anatomical form” (Witelson and Kigar 1988). This view is in concordance with embryological studies. Asymmetries of HG, PT, and superior temporal sulcus have been observed in the fetal and in the preterm brain (Witelson and Pallie 1973; Chi et al. 1977; Dubois et al. 2008). Using automatic voxel-based analyses of gray and white matter, Dubois et al. (2010) described in vivo interhemispheric asymmetries in the premature brain of 25 human newborns, from 26 to 36 weeks of gestational age. Their study demonstrated that perisylvian regions are the only regions to be asymmetric from early on and these asymmetries therefore occur prior to language exposure (Dubois et al. 2010). This is also in concordance with Spocter et al. (2010), who observed asymmetry in the number of neurons in area Tpt of 12 common chimpanzee brains. Cortical area Tpt corresponds to the posterior part of Brodmann’s area 22 and comprises a substantial portion of the cortex underlying the PT. It is also a component of Wernicke’s area in human. This asymmetry was positively correlated with asymmetry of neuron numbers in Brodmann’s area 45, a component of human Broca’s frontal language region. Leftward asymmetry of cortical areas involved in language in modern human therefore originated prior to the appearance of language function.

Having said that extant apes, including chimpanzees, and modern humans probably represent relicts and highly

specialized terminal members of what were once diverse radiations (Andrews and Harrison 2005; Wood and Harrison 2011). It can hence be assumed that common anatomical markers of laterality underwent independent evolutionary histories. This emphasizes their differences in terms of functional correlates and more precisely the fact that the interacting effects of sex and handedness may have shaped their evolutionary history in distinct ways.

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## Notes

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