Planum temporale grey matter asymmetries in chimpanzees (*Pan troglodytes*), vervet (*Chlorocebus aethiops sabaeus*), rhesus (*Macaca mulatta*) and bonnet (*Macaca radiata*) monkeys

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ABSTRACT

Brain asymmetries, particularly asymmetries within regions associated with language, have been suggested as a key difference between humans and our nearest ancestors. These regions include the planum temporale (PT) – the bank of tissue that lies posterior to Heschl's gyrus and encompasses Wernicke's area, an important brain region involved in language and speech in the human brain. In the human brain, both the surface area and the grey matter volume of the PT are larger in the left compared to right hemisphere, particularly among right-handed individuals. Here we compared the grey matter volume and asymmetry of the PT in chimpanzees and three other species of nonhuman primate in two Genera including vervet monkeys (*Chlorocebus aethiops sabaeus*), rhesus macaques (*Macaca mulatta*) and bonnet macaques (*Macaca radiata*). We show that the three monkey species do not show population-level asymmetries in this region whereas the chimpanzees do, suggesting that the evolutionary brain development that gave rise to PT asymmetry occurred after our split with the monkey species, but before our split with the chimpanzees.

The two halves of the human brain are not symmetrical (e.g. Holloway & De La Coste-Lareymondie, 1982; Rasdolsky, 1925; Wada, Clarke, & Hamm, 1975). In many brain areas, humans show a population-level tendency for one side of the brain to be larger than the other. A number of these neuroanatomical asymmetries have been well documented in the brain (Galaburda, 1995; Toga & Thompson, 2003), including regions associated with the comprehension and production of language, notably Broca's and Wernicke's areas (Annett, 2002; Bradshaw & Rogers, 1993; Corballis, 1992, 2002; Davidson, 1995).

Probably no other brain asymmetry has received more attention than the planum temporale (PT). The PT is the flat bank of tissue that lies posterior to Heschl's gyrus in the superior temporal lobe. In one of the first systematic studies of asymmetries in this region, Geschwind and Levitsky (1968) quantified the PT on the left and right hemispheres in a sample of 100 post-mortem brains and found that the left side was larger than the right in 65% of the cases. Since that time, a number of subsequent studies using post-mortem specimens and more recently using structural magnetic resonance imaging (MRI) (Larsen, Odegaard, Grude, & Hoien, 1989; Steinmetz et al., 1989) and voxel-based morphometry (VBM) (Good et al., 2001; Watkins et al., 2001) have confirmed the leftward asymmetry in the PT surface and grey matter volume (Good et al., 2001; Watkins et al., 2001).

The significance of the leftward asymmetry in the PT is that it overlaps with Wernicke's area, a key brain region involved language comprehension and other complex functions (Eckert, Leonard, Possing, & Binder, 2006; Pekkola et al., 2006; Shapleske, Rossell, Woodruff, & David, 1999). Thus, the leftward PT asymmetry is thought to be an anatomical marker of cerebral lateralization for language, although studies correlating measures of functional lateralization in language with the anatomical asymmetries of the PT have failed to reveal consistent findings (Dorsaint-Pierre et al., 2006; Eckert et al., 2006). From a clinical standpoint, the asymmetry in PT is important because studies suggest that reversed or bilateral symmetry in this region are associated with neurodevelopmental disorders and learning disabilities (Heiervang et al., 2000; Hugdahl et al., 2003; Rojas, Bawn, Benkers, Reite, & Rogers, 2002; Rumsey

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et al., 1997) and some psychiatric conditions, notably schizophrenia (Sommer, Aleman, Ramsey, Bouma, & Kahn, 2001).

Observation of the prevalence of leftward asymmetries in the PT of humans have led to a focus on this brain region in a number of comparative studies that have either directly or indirectly assessed lateralization in the posterior temporal lobe in other animals. We emphasize direct and indirect measures of asymmetry in the superior temporal lobe because different approaches have been used in various species since the landmarks used to define the PT are not evident in the brains of all animals. Specifically, the anterior border of the PT is usually considered to be Heschl's gyrus (HG) and this landmark is not consistently visible either from cadaver or MRI scans in many species, with the exception of the great apes. Thus, the lack of consistent anatomical landmarks to measure the region corresponding to the PT in nonhuman animals has precluded systematic investigation of this brain region from a comparative perspective, although many have indirectly measured this region by quantifying the length of the sylvian fissure (Falk, Cheverud, Vannier, & Conroy, 1986; Falk et al., 1990; Gilissen, 1992; Heilbronner & Holloway, 1988; Hopkins, Pilcher, & MacGregor, 2000; Liu & Phillips, 2009; Yeni-Komshian & Benson, 1976).

The lack of direct comparative data on the PT is unfortunate. These data could be essential to outlining the evolutionary development of brain asymmetries and their behavioral correlates in human and nonhuman primates. For example, in nonhuman animals, notably primates, a number of researchers have suggested that orienting asymmetries in response to conspecific vocalizations may be subserved by underlying asymmetries in the temporal lobe of the brain (Ghazanfar, Smith-Rohrberg, & Hauser, 2001; Gil-da-Costa & Hauser, 2006; Hauser & Anderson, 1994). Therefore, it could be hypothesized that species showing population-level orienting asymmetries should likewise show asymmetries in the PT region. Similarly, it might be hypothesized that PT asymmetries are most likely in species that show complex communicative systems and auditory asymmetries. Both vervet monkeys and macaques have been shown to have complex communicative systems including basic semantic processing of different vocalizations (e.g. Cheney & Seyfarth, 1990; Coss, McCowan, & Ramakrishnan, 2007; Ghazanfar et al., 2001; Gil-da-Costa & Hauser, 2006; Gouzoules, Gouzoules, & Marler, 1984; Hauser, 1998) and have also been reported to demonstrate orienting asymmetries in responses to species-specific sounds. Thus, these monkeys should be ideal species for assessing PT asymmetries.

In this study, we attempted to directly measure the region corresponding to the PT in nonhuman primates by developing criteria for quantifying the grey matter volumes of the posterior temporal lobe in monkeys and apes using identical procedures that do not rely on the use of Heschl's gyrus as an anatomical landmark. In previous studies in great apes we observed that the posterior margin of HG in the coronal plane often coincides with or immediately precedes the posterior closure of the inferior limb of the insular sulcus (see Fig. 1). Thus, because HG terminates posteriorly at or about the same point as the closure of the inferior insular sulcus, we adopted a procedure that defined the anterior region of the PT as the closure point of the insular sulcus, which was readily visible in the MRI scans of all the species. Through this approach, we were able to quantitatively compare the relative size and asymmetry of the temporal lobe (PT or Tpt) in various species without reliance on the presence of Heschl's gyrus.

1. Methods

1.1. Subjects

Grey matter volumes of the posterior temporal lobe were obtained from magnetic resonance images (MRI) in four nonhuman primate species including:

chimpanzees (Pan troglodytes, n = 82), vervet monkeys (Chlorocebus aethiops sabaeus, n = 43), rhesus monkeys (Macaca mulatta, n = 21) and bonnet monkeys (Macaca radiata, n = 15; see details in Table 1).

All of the chimpanzees were members of a captive colony housed at Yerkes National Primate Research Center (YNPRC) in Atlanta, Georgia. The vervet monkeys were members of the Vervet Research Colony at UCLA (Fears et al., 2009a, 2009b). The bonnet and rhesus monkeys were housed at the Wake Forest University Primate Center (WFUPC). For all species, the scanning procedures had been approved by university animal care and use committees.

1.2. Imaging collection and procedure

This study was opportunistic in terms of availability of the MRI scans, thus the magnets and scanning protocols were not identical in all species (see Table 2). Though this does present some challenges and limitations for certain comparative analyses, the measures of asymmetry were assessed within each individual and so differences across subjects in scanning protocols should not have influenced the results reported here. The magnet strengths and scanning protocols used with each species are shown in Table 2.

Magnetic resonance images (MRI) were obtained from in vivo scans in all four species. Subjects were first immobilized by ketamine injection as appropriate for the species and subsequently anaesthetized with propofol (chimpanzees), midazolam and ketamine (vervets), or isofluorane (macaques). The animals remained anaesthetized for the duration of the scans as well as the time needed to transport them between their home cage and the imaging facility (total time ~2 h, MRI acquisition time ranging from 36 to 60 min). All scans were examined at the time of acquisition and any image with artifact was excluded in the subsequent image processing.

1.3. Image segmentation and regions-of-interest measurement

Prior to measurement, the raw T-1 MRI scans were aligned in the axial, coronal and sagittal planes along the AC-PC line. The aligned MRI scans were then segmented into grey, white and CSF tissue using FSL (Analysis Group, FMRIB, Oxford, UK) (for more information, see Fears et al., 2009a, 2009b) (see Fig. 1).

1.3.1. Total grey matter brain volumes

The total volume of grey matter in the brain was defined to include the cerebrum, cerebellum and brainstem. The caudal boundary of the brainstem was defined by the most inferior edge of the cerebellum. The volume was computed using an automated volume calculator function in Analyze 7.0 (Mayo Clinic, Mayo Foundation, Rochester, Minnesota, USA).

1.3.2. PT grey matter volume

For each species, the grey matter (GM) volume of the PT homologue was measured in the coronal plane following the procedures described by Hopkins and Nir (2010) (see Fig. 2). Because Heschl's gyrus is not detectable in the monkey species, the anterior border was defined by the most anterior slice after the insula closed. The posterior border was defined by the most caudal slice showing the Sylvian fissure. The individual segmented GM volumes for the chimpanzees and macaques were imported into ANALYZE at an isotropic resolution of 1 mm while a .5 mm resolution was used with the vervets due to their smaller brain. The GM volumes were placed in the same stereological space as the T-1 MRI scan. The side-by-side display of the T-1 and GM segmented image allowed for the clear delineation of the inferior border of GM of the PT region (see Fig. 2).

For this measurement, raters used a mouse-driven pointer to draw a line from the most lateral portion of the Sylvian fissure (SF) to the most medial point, keeping the line on the most ventral edge of the fissure. The raters then followed the grey matter to its most inferior, medial edge and then followed the grey matter boundary to the lateral edge of the brain. This was repeated on each slice, moving posteriorly until the sylvian fissure fell out of view. If the fissure bifurcated into ascending and descending limbs, the raters followed the descending limb (Ide, Rodriguez, Zaidel, & Aboitiz, 1996; Taglialatela, Dadda, & Hopkins, 2007). Thus, a GM area was generated for each slice and these areas were traced on all images in which the SF was present. The individual GM areas were then summed across all slices and multiplied by the slice thickness to create GM volumes independently for the left and right hemispheres. Prior to data collection, two raters blind to the hemisphere of the chimpanzees and monkeys independently measured the PT in 10 specimens. Inter-rater correlations between the two tracers were positive and significant for both the right ($r = .91$, $p < .01$) and the left hemispheres ($r = .97$, $p < .01$). Similarly, 5 of the 42 vervet monkey specimens (12%) were re-traced as a reliability measure and the correlations were positive and significant (right; $r = .99$, $p < .01$; left $r = .96$, $p < .01$).

1.4. Data analysis

Using procedures previously used to quantify brain asymmetries in human and nonhuman primates (Cantalupo, Pilcher, & Hopkins, 2003; Foundas, Leonard, & Hanna-Pladdy, 2002), an asymmetry quotient (PT_AQ) was derived following the formula [PT_AQ = $(R - L)/((R + L) \times .5)$] where R and L represents the right and left hemisphere GM volume measures. Positive PT_AQ values indicated a rightward
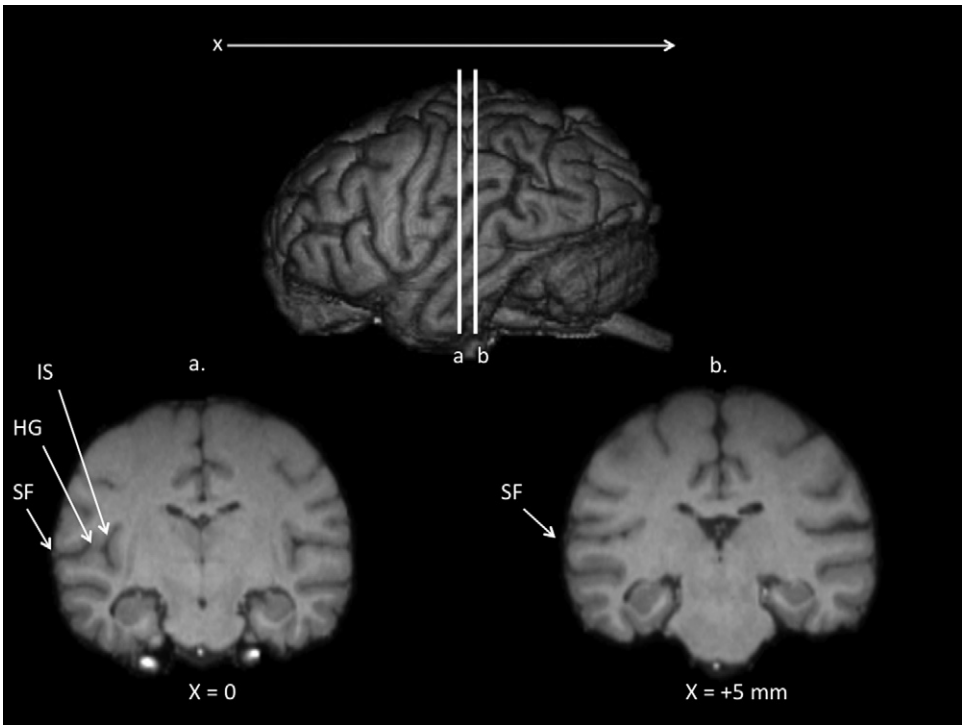
Fig. 1. Upper pane: 3-D reconstruction of a chimpanzee brain. The vertical lines represent coronal cuts through the sylvian fissure (SF) at the posterior point of Heschl's gyrus (HG) (labeled a) and 5 mm posterior to HG (labeled b). (a) Coronal view of a single 1 mm slice of an *in vivo* T1-weighted MRI of a chimpanzee brain with the sylvian fissure (SF), Heschl's gyrus(HG) and the insular sulcus (IS) outlined on the image. (b) Coronal view of a single 1 mm slice of an *in vivo* T1-weighted MRI of a chimpanzee brain 5 mm posterior to HG with the SF outlined on the image. Note that HG and the inferior portion of the IS are no longer visible in the brain. This was the anterior portion of the PT as defined in this study.

asymmetry and negative values indicated a leftward asymmetry. We also computed the magnitude or absolute degree of asymmetry (ABS_PT) for each subject by taking the absolute value of the PT_AQ score. The ABS_PT values indicated how far the individual subjects asymmetry deviated from zero, or no bias. Finally, with regard to asymmetry, we also classified each subjects as having a left-, right- or no bias asymmetry based on their PT_AQ value using arbitrary cut-points that have been employed by others measuring asymmetries in human and nonhuman primate brains (Foundas, Leonard, & Heilman, 1995; Knaus, Bollich, Corey, Lemen, & Foundas, 2004; Knaus, Bollich, Corey, Lemen, & Foundas, 2006; Shapleske et al., 1999). Individuals with asymmetries $\leq -.025$ or $\geq .025$ were classified as left- or right-biased. All other individuals were classified as having no bias (NB).

In addition to the measures of asymmetry in the PT, we also computed a ratio of PT grey matter to overall grey matter volume (PT_GM_Ratio). This was computed by dividing the total the sum of the left and right PT_GM volume (left plus right) by the total volume of grey matter in the brain and multiplying by 100. Thus, the

PT_GM_Ratio represented the percentage of PT grey matter relative to the entire volume of grey matter within the brain. All statistical analyses adopted an alpha of $p < .05$ and any post hoc tests were performed using Tukey's Honestly Significant Difference ($p < .05$).

2. Results

2.1. Descriptive analysis

Because two different scanners were used in the chimpanzee sample, we initially assessed whether differences in the PT_AQ or volumes were evident in these two samples. Chimpanzees that

Table 1
Demographic characteristics of the nonhuman primate samples.

Species	Females	Males	Age range	Mean age	SD age
Chimpanzee	54	28	6–51	21.93	11.81
Vervets	39	3	3–23	12.02	6.09
Rhesus	16	5	6–11	9.55	2.28
Bonnet	8	7	1–11	4.12	3.61

Table 2
Scanning parameters and protocols for each species.

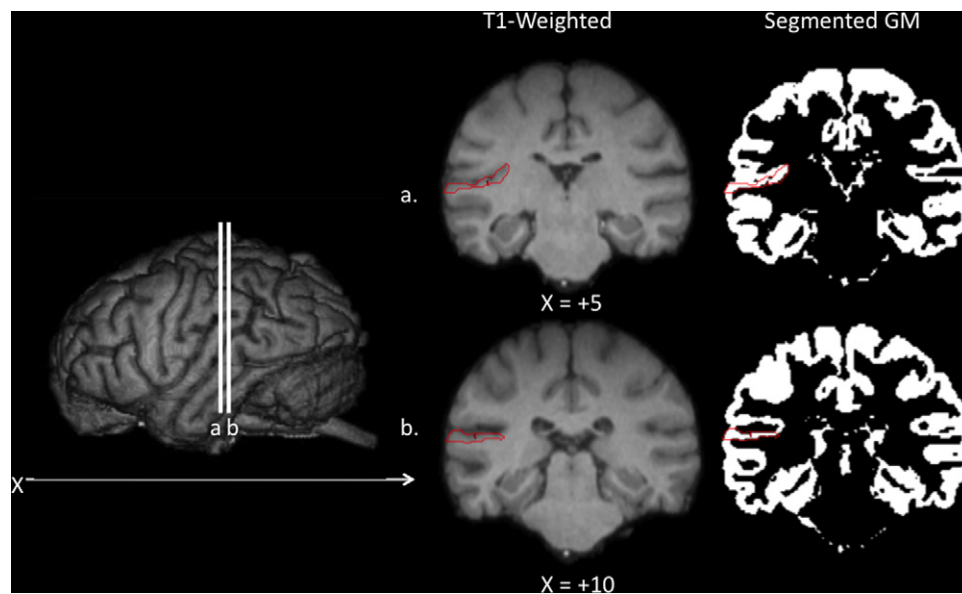|	Chimpanzees (1.5 T)	Chimpanzee (3 T)	Vervets	Macaques
MRI scanner	Phillips, Model 51	3T Siemens Trio, CP Head Coil	1.5T Siemens Symphony, knee coil	1.5 T GE echo-speed Horizon LX MR, knee coil
Sequence	Gradient echo	MPRAGE T1-weighted	MPRAGE T1-weighted	3DSPGR T1-weighted
Repetition time (ms)	19	2300	1900	30
Echo time (ms)	8.5	4.4	4.38	6
Flip angle		8	15	20
Field of view (mm)	180	200	80	180
Data matrix size	256 × 256	320 × 320	256 × 256	256 × 256

Fig. 2. Upper panel (a) is a coronal view of aT1-weighted MRI and GM segmented volume at the anterior border of the PT. The red line indicates the tracing of the grey matter beneath the SF as displayed on the T1-weighted and segmented volume. (B) Same as above but the tracing occurred 10 mm posterior to the anterior border. For all slices in which the SF was present, using a freehand tool, a line was drawn along the inferior edge of the SF from the most lateral to medial portion of the sulcus, corresponding to the most medial visible grey matter. All the grey matter forming the inferior bank of the gyrus was then traced along the lateral-medial axis.

Table 3
PT grey matter volumes, PT_AQ and ABS_PT values for each species.

| | PT | | | | | | | |
	Right	Left	Total	PT_AQ	ABS_PT	#L	#NB	#R
Chimpanzees	438.95 (9.91)	510.79 (10.16)	949.74 (18.35)	−.159 (.02)	.209 (.019)	60	6	16
Vervets	119.49 (13.57)	119.99 (14.20)	239.48 (25.64)	−.002 (.02)	.122 (.024)	16	9	17
Rhesus	197.67 (19.19)	195.33 (20.08)	388.00 (36.26)	.040 (.040)	.222 (.040)	10	3	8
Bonnet	168.87 (22.71)	181.54 (23.76)	350.40 (42.91)	−.052 (.050)	.163 (.050)	11	0	4

Values for the right, left and total PT volume are in mm³. Numbers in parentheses are standard errors. #L = number of left lateralized subjects, #R = number of right lateralized subjects and #NB = number of subjects with no bias.

were scanned in the 3.0 Tesla scanner were compared to those scanned in the 1.5 Tesla scanner and no significant differences were found for either total grey matter volume $t(80) = −1.81$, $p > .05$, PT_AQ $t(80) = −1.16$, $p > .05$ or PT_GM_Ratio $t(80) = −1.95$, $p > .05$. Therefore, both set of chimpanzee scans were combined into a single group. The mean GM volumes for the left and right PT for each species, as well as the PT_AQ values, can be found in Table 3.

2.2. Comparative analysis of direction and strength of PT asymmetries

To test for species differences in lateralization we performed a one-way analysis of co-variance with the PT_AQ values serving as the dependent variable and species serving as the between-groups variable. Age was the covariate. We found a significant main effect for species $F(3, 155) = 6.415$, $p < .001$. Subsequent post hoc analysis indicated that the chimpanzees had significantly larger left hemisphere asymmetry in the PT (as reflected in lower PT_AQ values) compared to all other species. No significant differences in PT_AQ values were found between the rhesus, bonnet and vervet monkeys. One sample t-tests were also conducted within each species and significant population-level leftward asymmetries were found for the chimpanzees $t(81) = −6.94$, $p < .001$, but not for the rhesus $t(20) = .049$, $p > .05$, bonnet $t(14) = −.05$, $p > .05$ or vervet monkeys $t(42) = −.12$, $p > .05$. The mean PT_AQ values for each species are shown in Table 3 and scatterplots of the left and right PT grey matter volumes within each species are shown in Fig. 3a–d. We have also provided scatterplots of the relation between total brain volume and the PT_AQ values for each species in Fig. 4a–d.

Analysis of the PT asymmetries based on the classification criteria largely confirmed the previous findings. The number of left-, right- and no biased subjects within each species are shown in Table 3. A chi-square test of independence revealed a significant association between species and PT asymmetry $X^2(6, N = 160) = 18.68$, $p < .006$. Two observations are of note from these data. First, as can be seen in Table 3, the number of left-lateralized chimpanzees was significantly higher than the number of right-lateralized $X^2(1, N = 76) = 25.47$, $p < .006$ whereas left-right comparisons within bonnet $X^2(1, N = 15) = 3.27$, n.s, rhesus $X^2(1, N = 18) = .222$, n.s. and vervet $X^2(1, N = 33) = .030$, n.s. monkeys were not significantly different. Second, within each species, a significant majority of the individuals showed an asymmetry, at least according to the cut-points employed in this study (chimpanzees = 93%; bonnet = 100%, rhesus = 86% and vervet = 76%). A Fishers exact test was performed to compare the distribution of lateralized and non-lateralized subjects (because we did not meet the assumptions of chi-square due to low expected values in some cells) and we failed to find significant differences in the proportion of lateralized individuals between species.

In our next analysis, we considered whether species differences were evident in the strength or magnitude of asymmetries in the PT as reflected in the ABS_PT scores. As with the previous analysis, we performed a one-way analysis of co-variance but with the ABS_PT values serving as the dependent variable and species serving as the
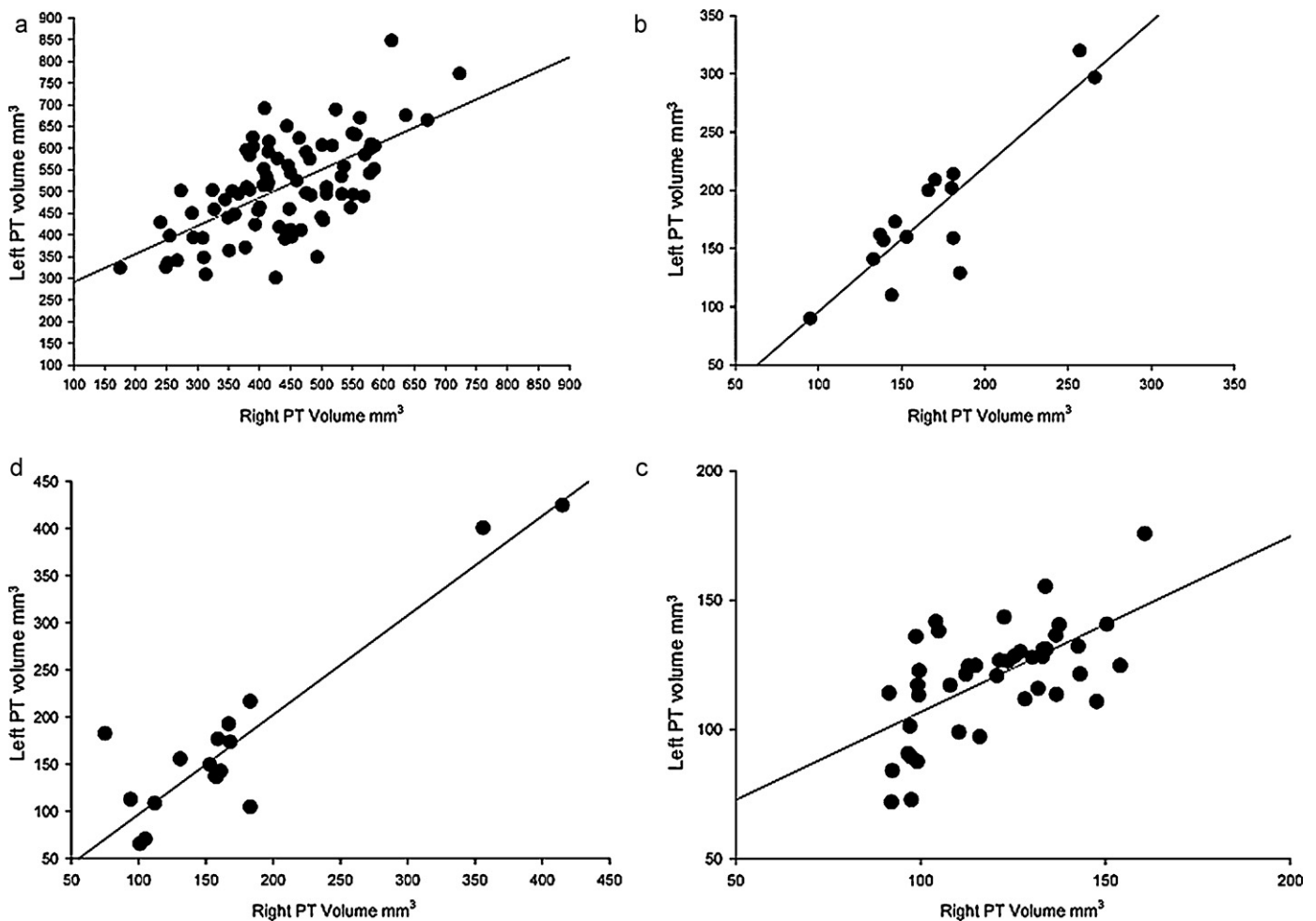
Fig. 3. Scatterplots of the left and right PT grey matter volumes for each species. (a) Chimpanzees, (b) Bonnet monkeys, (c) Rhesus monkeys, (d) Vervet monkeys.

between-groups variable. Age was the covariate. We found a significant main effect for species $F(3, 155) = 3.171$, $p < .03$. The mean ABS_PT values for each species are shown in Table 3. Post hoc analysis indicated that chimpanzees and rhesus monkeys were more lateralized than vervet monkeys but did not differ from the bonnet monkeys. These results are consistent with the data reported in Table 3 showing that the proportion of individuals with no bias was higher in the vervet monkeys compared to the other species, notably the chimpanzees and bonnet monkeys. Interestingly, while the rhesus macaques showed similar levels of individual asymmetry, these were equally divided among those that were left- and right-biased (See Table 3).

2.3. Grey matter ratio in PT size

We next examined whether species differences were evident in the proportion of grey matter comprising the PT region when adjusted for differences in the whole brain grey matter. To be conservative in our estimates of the comparison in the relative proportion of grey matter in the different species, for this analysis we included only those chimpanzees that were scanned at 1.5 Tesla ($n = 16$), which was the same magnet strength as the scans obtained in all three monkey species. We performed a one-way analysis of covariance with the PT_GM_Ratio measure serving as the dependent measure while species served as the between groups factor. Age was the covariate. The analysis revealed a significant main effect for species $F(3, 89) = 4.55$, $p < .001$. Post hoc analysis indicated that chimpanzees had significantly lower PT_GM_Ratio values than all

other species and none of the monkey species differed significantly from each other. The mean PT_GM_Ratio measure for each hemisphere and species is shown in Fig. 5. Separate ANOVAs were run on the PT-R_GM_Ratio and the PT-L_GM_Ratio with the same results [PT-R, $F(3, 89) = 5.92$, $p < .001$; PT-L $F(3, 89) = 3.23$, $p < .05$]. Chimpanzees had relatively smaller grey matter volumes for the left and right PT compared to the rhesus, bonnet and vervet monkeys. These findings suggest that the size of the PT area is overall smaller in the chimpanzees than in the monkey species.

3. Discussion

The first aim of this study was to directly compare the grey matter volumes and asymmetry of the PT region between chimpanzees and monkeys by using identical procedures. When these procedures are used, chimpanzees show population-level leftward asymmetries in the PT region, confirming earlier findings (Hopkins & Nir, 2010). However, none of the three monkey species showed population-level asymmetries in the PT region. Thus, there appear to be phylogenetic differences in the evolution of PT asymmetries with their emergence occurring after chimpanzees split from Old World monkeys some 30 million years ago.

The evidence reported here of phylogenetic differences in population-level (or species-level) directional asymmetries in this brain region is unclear. There are several possible explanations. First, systematic lateralized input during pre- or post-natal development could have long-term effects on the development of brain asymmetry. For example, Previc (1991) has suggested that during
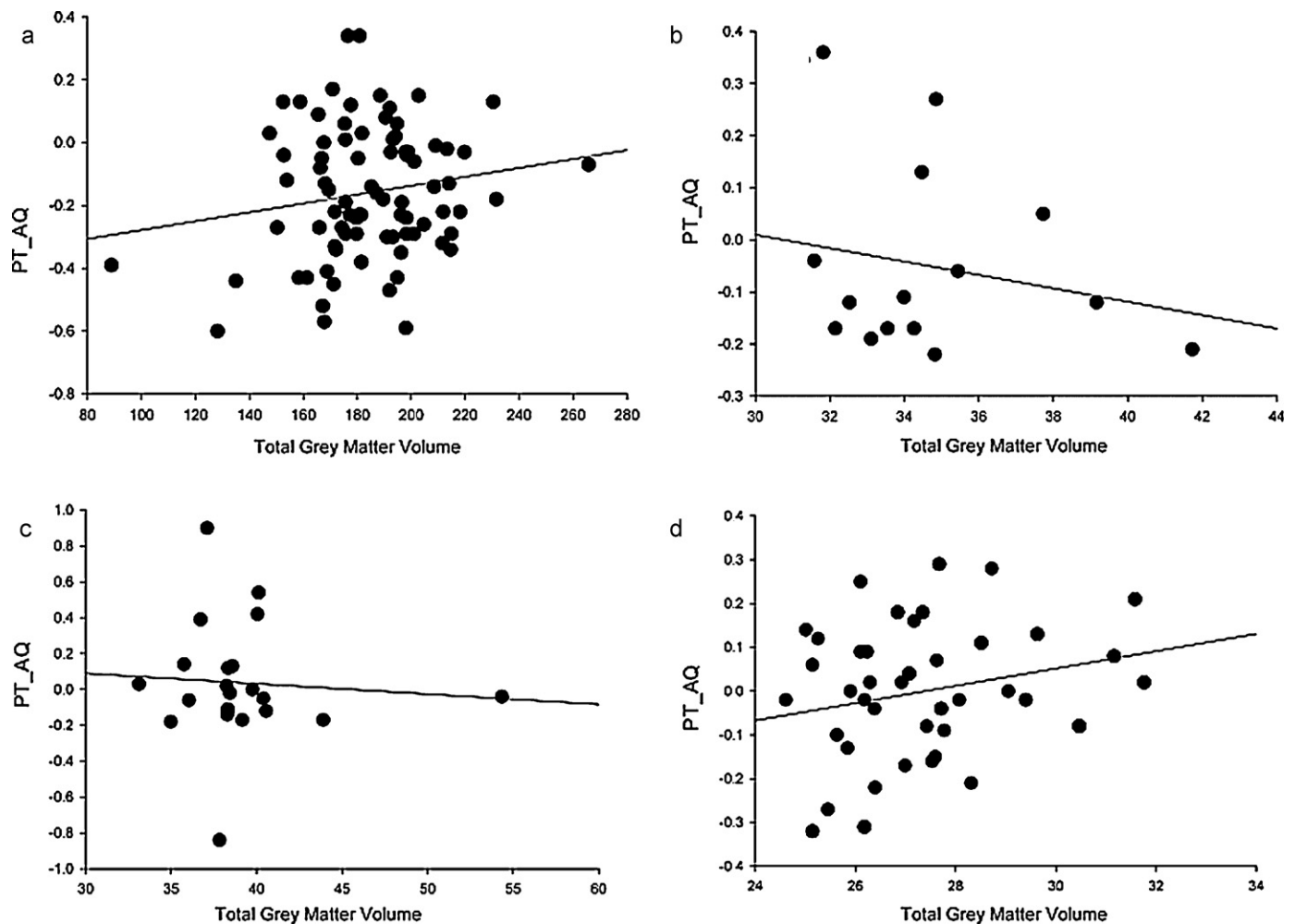
Fig. 4. Scatterplots of the PT_AQ values and total grey matter brain volumes for each species. (a) Chimpanzees, (b) Bonnet monkeys, (c) Rhesus monkeys, (d) Vervet monkeys.

prenatal development, gravitational forces associated with locomotion induces shearing of the otolithic nerves in the developing fetus, particularly during the last trimester, which has a long-term effects on the development of asymmetries in auditory processing. In humans, Previc (1991) argues that because most human fetuses are oriented in the same way (the right ear faces out from the womb) during the last trimester, this induces similar asymmetries within the population. Extending the assumptions of Previc's theory to all primates, it could be argued that during prenatal development, chimpanzee fetuses similarly show consistent orienting asymmetries and this induces similar asymmetries across individuals whereas the consistent prenatal fetal positions are not present in Old World monkeys. Unfortunately, there are no published data in nonhuman primates on fetal position during prenatal development, so at present it is impossible to test this hypothesis.

It is also possible that postnatal factors influence the development of brain asymmetries and that this may explain some species differences in brain asymmetries. For example, there are well-documented effects of early handling on the development of behavioral and brain asymmetries in rats (Denenberg & Yutzey, 1985). In humans, Michel (1981) has suggested that early head orientation asymmetries may lead to the development of functional and neuroanatomical asymmetries that favor the left hemisphere. A significant proportion of neonates show rightward orienting asymmetries, which Michel suggests leads to greater right hand-eye stimulation, differentially stimulating the left half of the brain. Previous studies have shown that neonatal chimpanzees also have

rightward asymmetries in head orientation (Hopkins & Bard, 1995) as well as other hand-to-mouth activities (Fagot & Bard, 1995; Hopkins & Bard, 1993; Hopkins, Bard, & Griner, 1997; Hopkins, Bard, Jones, & Bales, 1993) which is consistent with the hypothesis of Michel (1981). There are no reports of a direct link between early
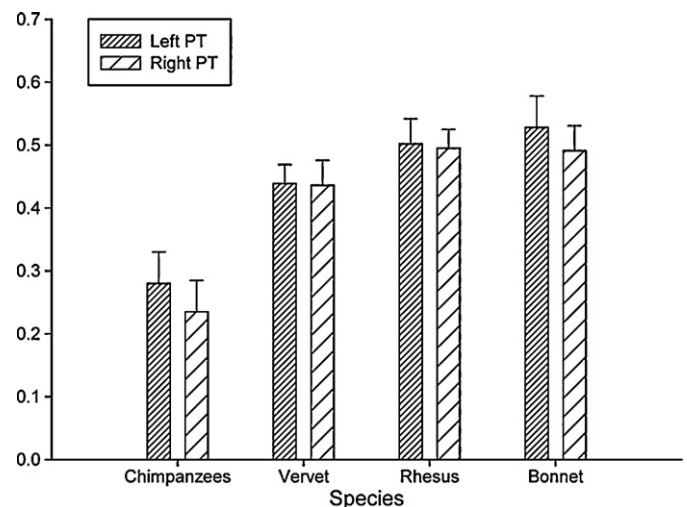

Fig. 5. Mean left and right PT_GM_Ratio (±s.e.) for each species. Values include only the subset of chimpanzees that were scanned at 1.5 Tesla.

head orientation and PT asymmetries however; thus, this notion awaits further investigation.

Similarly, Hopkins (2004) has suggested that early maternal cradling biases can influence the development of behavioral (and possibly brain) asymmetries and that species differences in maternal cradling and infant head position may explain some phylogenetic differences in handedness. Several investigators have reported significant leftward asymmetries in maternal cradling in great apes (Damerose & Hopkins, 2002; Damerose & Vauclair, 2002; Hopkins & De Lathouwers, 2006; Hopkins et al., 1993; Manning, Heaton, & Chamberlain, 1994; Nishida, 1993; Tomaszycki, Cline, Griffin, Maestripieri, & Hopkins, 1998; Zhao, Gao, Li, & Wantanabe, 2008) and there is at least one report that maternal cradling preferences predict the development of hand preferences of the offspring (Hopkins, 2006). In contrast, there little evidence of population-level biases in infant cradling or nipple preferences in Old World monkeys. Indeed, in rhesus monkeys, it has been reported that nipple preferences by offspring alternate between birth seasons, which indicates that it is highly variable within the same individual females (Jaffe et al., 2006). Again, however, there are no longitudinal studies on this topic and therefore this hypothesis remains speculative at this point in time.

Lastly, of course, there could have been increasing selection in conformity in brain asymmetries because it offered some evolutionary advantages, as has been postulated by some (Vallortigara & Rogers, 2005). This increasing selection would have presumably had genetic consequences leading to specific genes that code for the development of brain asymmetries, such as those found in the PT. Studies in humans certainly suggest heritability of brain asymmetries, notably within the PT (Geschwind, Miller, DeCarli, & Carmeli, 2002; Thompson et al., 2001) but this issue has not been explored in nonhuman primates (but see Fears et al., 2009a, 2009b; Rogers et al., 2007). Based on the results reported here, the hypothesis would be that there are genes that bias the direction of PT asymmetries in humans and chimpanzees that are absent in vervet, rhesus and bonnet monkeys. One limitation with this explanation is that it is not obvious which factors were selected for that resulted in the emergence of brain asymmetries.

It should be noted that some have suggested that behavioral and brain asymmetries evolved as a consequence of increasing brain size. As such, as brain size increased in primates, the constraints on inter-hemispheric transfer speed became problematic, leading to the specialization of one hemisphere over the other for specific tasks (e.g. Aboitiz, Scheibel, Fisher, & Zaidel, 1992; Ringo, Doty, Demeter, & Simard, 1994). In support of these hypotheses are recent studies that have shown an inverse correlation between total brain volume and corpus callosum (CC) size in mammals (Oliveras, Montiel, & Aboitiz, 2001), as well as within the order Primates (Rilling & Insel, 1999a). Thus, though humans have the largest brain volume, they have a relatively small CC compared to other primates. In short, humans have a naturally greater "split-brain" compared to other primates, which some suggest led to greater functional and anatomical asymmetries within each hemisphere. At face value, our results provide partial support for this theory. Within our study, chimpanzees have the largest brain followed by macaques and vervets. In terms of their absolute asymmetries of the PT (taking the absolute value of the PT_AQ values), chimpanzees and rhesus macaques showed more individual asymmetries than vervet monkeys. Interestingly, based on previous studies on the corpus callosum (CC) size in these nonhuman primates (Hopkins & Phillips, 2010; Pierre, Hopkins, Taglialatela, Lees, & Bennett, 2008; Rilling & Insel, 1999a), the relative size of the CC (log CC area divided by the Log brain volume) in chimpanzees is much smaller (Mean = .956) compared to macaques (Mean = 1.08) and vervet monkeys (Mean = 1.079), which is consistent with the notion that chimpanzees have less interhemispheric connectivity than the Old World monkeys examined in this paper. Thus, the larger-brained chimpanzees had more asymmetrical grey matter PTs compared to the macaques and vervets which might be attributable to variation in interhemispheric connectivity. However, it must be recognized that although increasing brain size may explain phylogenetic variation in the magnitude of asymmetries it does not provide an adequate explanation for directional biases in PT asymmetry.

Another result from this study was a significant difference in the ratio in grey matter volume of the PT between species. Compared to the vervets and macaques, chimpanzees had a smaller grey matter volume of the PT after adjusting for total grey matter volume. These results are consistent with the general pattern of primate brain evolution, as well as temporal lobe evolution, in which white matter expansion outpaces that of grey matter, suggesting increasing connectivity in anthropoid apes compared to monkeys (Rilling & Insel, 1999b; Rilling & Seligman, 2002). One word of caution is warranted with respect to this interpretation based on the findings reported here. Although we restricted our analysis of the ratio of PT grey matter to those animals that were scanned with a T-1 weighted protocol on a 1.5 T machine, the scanner parameters did differ some between the samples. This may have influenced the resolution of grey and white matter differentiation within the species and may have skewed the data. We do not believe that this influenced our results; however, we cannot rule it out, and ideally, this analysis should be computed on samples of MRI scans that have employed the same scanner parameters.

The results reported here have implications for the interpretation of behavioral and functional imaging studies in apes and monkeys, particularly as it relates to the processing of species-specific vocalizations. First, several recent studies bonobos, macaques and vervets have documented individual and species differences in orienting asymmetries in response to species-specific vocalizations (Ghazanfar et al., 2001; Gil-da-Costa & Hauser, 2006; Hauser, Agnetta, & Perez, 1998; Taglialatela, 2004, 2007). The underlying assumption of some of these reports is that these behavioral asymmetries are associated with leftward asymmetries in Sylvian fissure lengths and planum temporale. That is to say, some have suggested that orienting asymmetries may be related to asymmetries in either the Sylvian fissure or PT. The absence of population-level asymmetries in the grey matter volume of the PT found in this study is not consistent with claims of population-level asymmetries in orienting asymmetries in macaques and vervets and suggests that the behavioral reports may require further examination (Teufel, Ghanzafar, & Fischer, 2010).

Second, functional asymmetries in the processing of species-specific sounds have been linked to the temporal lobe (including the PT region) in monkeys. For instance, lesions to the left posterior temporal lobe (but not the right) induce transient deficits in the discrimination of two types of "coo" calls in Japanese macaques (Heffner & Heffner, 1984). Somewhat contrarily, Poremba et al. (2004), utilizing positron emission tomography (PET), found rightward asymmetries in the posterior temporal lobe regions (including the PT region) and leftward asymmetries in the temporal pole in the processing of species-specific calls. Similarly, Taglialatela, Russell, Schaeffer, & Hopkins (2009) found rightward asymmetries in the PT region in the processing of species-specific sounds in three chimpanzees. All three of these studies clearly implicate the PT area in the processing of species-specific communication but the functional asymmetries differ from anatomical asymmetries, particularly in the chimpanzees. This suggests that the population-level asymmetries in anatomy are not necessarily linked to functional asymmetries or may be modulated by different dimensions of the vocalizations (i.e., whether they are involved in processing valence or semantics).

Finally, at least for chimpanzees, the anatomical results reported here are consistent with at least one report on cytoarchitectonic asymmetries. Spocter et al. (2010) recently measured the volume of areaTpt (Brodmann's area 22) in a sample of 12 post-mortem chimpanzee brains and found a significant leftward asymmetry, not unlike the grey matter anatomical asymmetries reported in this study. Gannon, Kheck, & Hof (2008) recently reported that 5 of 6 macaques showed a leftward asymmetry in the Tpt region when quantified cytoarchitectonically, while a larger sample of macaques ($n = 20$) failed to show asymmetries in the PT region based on anatomical measures. Our anatomical results in the macaques are consistent with the anatomical data reported by Gannon et al. (2008). Why there appears to be some potential discrepancy between the cytoarchitectonic and the anatomical findings in the macaques is not clear, but the discrepancy underscores the potential value of acquiring additional microstructural measurement data from macaques as well as great apes (Buxhoeveden & Casanova, 2000; Buxhoeveden, Switala, Roy, Litaker, & Casanova, 2001; Schenker et al., 2008).

In summary, our findings demonstrate species differences in directional asymmetries in the PT in four species of nonhuman primates. Chimpanzees show population-level leftward asymmetries while macaques and vervets failed to show any group level asymmetries. The hypothesized developmental mechanisms underlying PT asymmetries were similar in all species, suggesting that whatever mechanism led to the left-side asymmetries for the PT region, it began after the evolutionary split between apes and monkeys. Additional research is needed to understand the functional and behavioral consequences of the evolution of PT asymmetries in nonhuman primates.

Acknowledgements

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