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RESEARCH ARTICLE

Planum Temporale Asymmetries in Primates: A Comparative Study in Great Apes and Monkeys

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ABSTRACT

Objectives: Most human brains exhibit left hemisphere asymmetry for planum temporale (PT) surface area and gray matter volume, which is interpreted as cerebral lateralization for language. Once considered a uniquely human feature, PT asymmetries have now been documented in chimpanzees and olive baboons. The goal of the current study was to further investigate the evolution of PT asymmetries in nonhuman primates.

Materials and Methods: We measured PT surface area in chimpanzees (*Pan troglodytes*, $n = 90$), bonobos (*Pan paniscus*, $n = 21$), gorillas (*Gorilla gorilla*, $n = 34$), orangutans (*Pongo* spp., $n = 33$), olive baboons (*Papio anubis*, $n = 105$), rhesus macaques (*Macaca mulatta*, $n = 144$), and tufted capuchins (*Sapajus apella*, $n = 29$) from magnetic resonance imaging scans.

Results: Our findings reveal significant leftward biases in PT surface area among chimpanzees, gorillas, olive baboons, rhesus macaques, and capuchins. We did not find significant population-level asymmetries among orangutans and bonobos, which could be due, in part, to small sample sizes. We also detected significant age effects for rhesus macaques only, and no significant sex effects for any species.

Discussion: The observation of a population-level leftward bias for PT surface area among not only hominids (chimpanzees and gorillas), but also two cercopithecoids (olive baboons and rhesus macaques) and one platyrrhine (tufted capuchins) suggests that PT lateralization was likely present in some early anthropoid primate ancestors and relatives. This provides further evidence that human brains have since undergone changes to the size and connectivity of the PT in response to selection for the cognitive processes needed to support the evolution of language and speech.

1 | Introduction

In the human brain, the planum temporale (PT) is the bank of tissue that lies posterior to Heschl's gyrus and overlaps with Wernicke's area (which includes Brodmann area 22), a brain region associated with language functions, as well as other higher-order cognitive functions (Damasio and Geschwind 1984; Geschwind and Levitsky 1968; Griffiths and Warren 2002; Josse et al. 2009; Mazoyer et al. 2014; Spocter et al. 2012, 2010; Wernicke 1874). In humans, the PT is one of

Summary

- We observed significant leftward biases in planum temporale (PT) surface area among two great apes, two cercopithecoids, and one platyrrhine.
- These findings add to a growing body of evidence suggesting that PT lateralization is not unique to humans.
- Based on the evidence presented here, we can hypothesize that PT lateralization was likely present in some early anthropoid primates, as well.

the most studied and well-documented neuroanatomical asymmetries in the brain with findings consistently reporting that between ~70% and 75% of subjects exhibit a left hemisphere bias in size (Foundas, Leonard, and Heilman 1995; Galaburda et al. 1987; Galaburda, Sanides, and Geschwind 1978; Knaus et al. 2006; Kulynych et al. 1994). Similar population-level leftward asymmetries have also been reported for the gray matter volume of the posterior superior temporal gyrus, including the PT (Knaus et al. 2004; Shapleske et al. 1999). Clinically, it has been suggested that atypical asymmetry of the PT is associated with a number of neurodevelopmental and neuropsychiatric disorders such as schizophrenia, autism, and dyslexia (Altarelli et al. 2014; Barta et al. 1997; Beaton 1997; Carrion-Castillo et al. 2020; Kwon et al. 1999; Rojas et al. 2005).

To what extent nonhuman primates exhibit population-level behavioral and brain asymmetries is a matter of significant scientific inquiry. The comparative interest in lateralization stems, in part, from early theories on the origins of language. Because language is functionally lateralized to the left hemisphere in a majority of humans, early theories suggested that language and hemispheric specialization coevolved after the split from the common ancestor of humans and chimpanzees/bonobos (Annett 2002; Bradshaw and Rogers 1993; Corballis 1992; Crow 2004; Warren 1980). A plethora of data published in the past 30–40 years has challenged this historical perspective. There is now considerable evidence across the animal kingdom demonstrating population-level behavioral asymmetries (Atkinson et al. 2015; Caspar et al. 2022; Ocklenburg and Gunturkun 2018; Rogers, Vallortigara, and Andrew 2013; Strockens, Gunturkun, and Ocklenburg 2013), but data on neuroanatomical or neurofunctional asymmetries remain less clear, though this may, in part, be attributable to fewer studies on the topic and smaller sample sizes within species (Becker and Meguerditchian 2022; Hopkins 2022).

With specific reference to the PT, previous studies in chimpanzees have demonstrated significant population-level leftward asymmetries in surface area, gray matter volume, and at the cytoarchitectural level of analysis (Gannon et al. 1998; Hopkins and Nir 2010; Hopkins et al. 2008; Spocter et al. 2010, 2020). Moreover, population-level leftward asymmetries in the PT surface area of chimpanzees have been found to be consistent between two genetically independent samples, suggesting that findings are repeatable (Spocter et al. 2020). Thus, the available data suggest that population-level leftward asymmetries are robust and evident across multiple levels of neural structure. Furthermore, Hopkins and Nir (2010) found that chimpanzees with a right-hand preference for gestural communication had significantly greater leftward asymmetries for PT gray matter compared to ambiguously- and left-handed subjects. Interestingly, handedness for noncommunicative functions was not associated with asymmetries in PT surface area or gray matter volume. This suggests PT gray matter asymmetries may predict functional asymmetries—particularly, the handedness of gestural communication—in chimpanzees. Significant leftward asymmetries in the PT have also been reported for surface area and gray matter in olive baboons, including among individuals <6 months of age, suggesting that these asymmetries are evident early in life (Becker et al. 2022, 2021; Marie et al. 2018). In addition, Becker et al. (2024) found that among these olive baboons, a left PT asymmetry at birth predicted right-handedness for gestures later in life but had no effect on handedness for noncommunicative actions. This observed PT asymmetry at birth and its association with handedness for gestural communication later in life may reflect continuity between human and nonhuman primates regarding the phylogeny and ontogeny of brain specialization for language and communication (Becker et al. 2024).

Studies on PT asymmetries in other nonhuman primate species remain less clear (Bogart et al. 2012; Lyn et al. 2011). For instance, in rhesus macaques, a leftward PT asymmetry was reported using voxel-based morphometry by Xia et al. (2020), but these patterns were not consistent over developmental time periods. In two separate studies using region-of-interest methods in samples of rhesus macaques, no population-level asymmetries in the PT were found (Gannon, Kheck, and Hof 2008; Lyn et al. 2011; Xia et al. 2020), but the sample sizes were relatively small. Additional nonhuman primate data on PT asymmetries among bonnet macaques and vervets also failed to reveal significant population-level asymmetries in the PT, but again, these studies involved smaller samples (Lyn et al. 2011).

Here, we tested for population-level PT asymmetries in seven nonhuman primate taxa, including four great apes (chimpanzees, bonobos, gorillas, and orangutans), two cercopithecoids (olive baboons and rhesus macaques), and one platyrrhine (tufted capuchins). These species were selected for analysis because relatively large sample sizes of structural MRI data are currently available. Besides chimpanzees, there is only a single study that has examined PT asymmetries in other great ape species (bonobos), and no population-level bias was found (Hopkins, Lyn, and Cantalupo 2009). We hypothesized that if PT asymmetries were evident among the great apes, then bonobos, gorillas, and orangutans would exhibit leftward asymmetries similar to chimpanzees and humans. In addition, we measured PT surface area asymmetries in olive baboons to determine if the previously reported leftward asymmetry in this species could be replicated in a second, independent sample. We also measured PT surface area in rhesus macaques to determine whether the inconsistent findings from previous studies were potentially due to a lack of statistical power. Finally, we measured PT surface area in tufted capuchins to examine whether population-level asymmetries in PT could be observed in platyrrhine primates, as well. We want to emphasize that the goal of this study was not to investigate the evolution of language or language capabilities, but rather to examine temporal cortex asymmetries in nonhuman primates—specifically within the PT.

2 | Methods

2.1 | Study Subjects

Our sample included magnetic resonance images from 90 chimpanzees (*Pan troglodytes*), 21 bonobos (*Pan paniscus*), 34 western lowland gorillas (*Gorilla gorilla*), 33 orangutans (*Pongo* spp.), 105 olive baboons (*Papio anubis*), 144 rhesus macaques (*Macaca mulatta*), and 29 tufted capuchins (*Sapajus apella*) (Table 1). Although the subspecies composition of the chimpanzees in our study has not been directly identified, it is likely that the vast majority are *Pan troglodytes verus* (Western chimpanzees), based on findings from Ely et al. (2005), which revealed that 95% of African-born founders in the U.S. captive chimpanzee population were *P.t. verus*, with minimal representation from other subspecies. All apes were housed at zoos, research centers, and sanctuaries in the United States until they died of natural causes, and postmortem MRIs were later obtained. The fixed specimens are now curated by the National Chimpanzee Brain Resource (https://www.chimpanzeebrain.org/) and the Great Ape Neuroscience Project. All olive baboons and a subset of the rhesus macaques ($n = 102$) were housed at the Michale E. Keeling Center for Comparative Medicine and Research (Bastrop, TX). Seven of the rhesus macaques were housed at Georgia State University (Atlanta, GA), and the remaining 35 rhesus macaques were housed at the Wisconsin National Primate Research Center ($n = 24$) and the Harlow Center for Biological Psychology ($n = 11$) (Madison, WI). The capuchins were housed at Hiram College (Hiram, OH), Northeastern Ohio Universities College of Medicine (Rootstown, OH), the College of Wooster (Wooster, OH), and the University of Pittsburgh (Pittsburgh, PA). All subjects studied in vivo were socially housed and were fed a diet of commercial primate chow, fresh produce, and other supplementary foods with ad libitum access to water.

All in vivo experimental procedures were carried out according to the National Institutes of Health guidelines for animal research and were approved by the Institutional Animal Care and Use Committee at each institution. This research complied with the U.S. National Research Council's Guide for the Care and Use of Laboratory Animals, the U.S. Public Health Service's Policy on Humane Care and Use of Laboratory Animals, and the Guide for the Care and Use of Laboratory Animals.

TABLE 1 | Description of subject characteristics, including sample size, sex, and age.

Species	Total *N*	# Males	# Females	Age range (years)
Pan troglodytes	90	45	45	3–55
Pan paniscus	21 (2 unknown sex)	8	11	3–62
Gorilla gorilla	34	17	17	3–61
Pongo spp.	33	18	15	6–60
Papio anubis	109	17	92	0.5–21
Macaca mulatta	144	78	66	0.8–32
Sapajus apella	29	9	20	2–21

2.2 | Image Collection and Processing

Among the great ape sample, all magnetic resonance images were collected postmortem except for those from 4 bonobos, 2 gorillas, and 4 orangutans (Rilling and Insel 1999b). All of these apes died from natural causes. At the time of death, subjects ranged in age from 3 to 62 years (mean = 33, SD = 13.4). Brains were extracted by the resident pathologist within 12 h of death and were fixed in 10% formalin for at least 2 weeks before MRI acquisition. All postmortem brains were scanned with either 4.7 or 7 Tesla magnets and transverse T2-weighted MR images were collected through the entire brain using a gradient echo protocol (pulse repetition = 22.0 s, echo time = 78.0 ms, number of signals averaged = 8–12) and a 256 × 192 matrix was reconstructed to 256 × 256. A small proportion of bonobo ($n = 4$), gorilla ($n = 2$), and orangutan ($n = 4$) subjects included in this study were scanned in vivo (Rilling and Insel 1999b). Before scanning, these subjects were anesthetized with ketamine (10 mg/kg) and scanned in a supine position using a human head coil. Throughout the scan, subjects received a continuous intravenous (iv) infusion of propofol (10–20 mg/kg/h) for anesthesia. Head motion was minimized by stabilizing with foam cushions and elastic straps. T1-weighted MR images of the entire brain were acquired with a 1.5 T Phillips NT scanner (Philips Medical Systems, The Netherlands) using a gradient echo protocol (slice thickness = 1.2 mm, slice interval = 0.6 mm [in most cases], repetition time = 19.0 ms, echo time = 8.5 ms, number of signals averaged = 8), and a 256 × 256 matrix was constructed. The field of view was adjusted to include the entire brain in each subject, and it varied as a function of brain size. Consequently, pixel size ranged from 0.47 to 0.78 mm^2 (Rilling and Insel 1999b).

In vivo T1-weighted MRI scans were collected in the olive baboon (*P. anubis*), rhesus macaque (*M. mulatta*), and tufted capuchin (*S. apella*) samples. For all the baboons and 102 rhesus macaques, T1-weighted images were collected on a Phillips Achieva 1.5-Tesla scanner. Following experimental protocols intended to minimize pain and distress, subjects were immobilized by intramuscular (im) injection of ketamine HCl (5–10 mg/kg body weight) followed by anesthetization with isoflurane inhalation (1%–3%) per standard institutional guidelines before being placed in the scanner chamber in a supine position. T1-weighted images were collected using a 3D Turbo sequence (repetition time = 0.017, TE = 0.0037, number of signals averaged = 10, voxel resolution = 0.8). For seven rhesus macaques, subjects were placed in the scanner chamber in a supine position with their head inside the head coil and scanned using a 3-Tesla scanner (Siemens Trio, Siemens Medical Solutions USA

Inc., Malvern, PA, USA). T1-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 × 320). For 35 rhesus macaques, T1-weighted images were collected using a 3D gradient echo sequence (repetition time = 11.4 ms, echo time = 5.4 ms, number of signals averaged = 2, matrix size = 256 × 224).

All capuchins were scanned using a Siemens 3-Tesla Allegra Scanner. For these scans, subjects were initially immobilized with one of two methods: (a) im injections of ketamine (7 mg/kg) and medetomidine (0.06 mg/kg) and a subcutaneous (sq) injection of atropine (0.05 mg/kg) or (b) im injections of ketamine (25 mg/kg) and acetylpromazine (1 mg/kg) and a sq injection of atropine (0.05 mg/kg). An iv catheter was then placed in the saphenous vein. Subjects were given a bolus of propofol (2–5 mg/kg) intravenously; a constant iv drip (250–350 μg/kg/min) maintained anesthesia. Subjects were placed into the scanner chamber and their heads were fitted inside a 16- or 12-cm head coil. Sagittal T1-weighted 3D MPRAGE MR images were acquired through the entire brain (TR = 1500 ms, TE = 3.04 ms, no echo-train, number of signals averages = 3). Slices were obtained as 0.05-mm-thick contiguous sections with a matrix size of 256 × 256 and a field of view of 128 mm × 128 mm, resulting in a final voxel size of 0.05 mm × 0.05 mm × 0.05 mm. At the cessation of the scan, subjects that received the combination of ketamine and medetomidine injections were administered the reversal agent, atipamezole (0.06 mg/kg), via im injection.

For all monkeys scanned in vivo, after MRI acquisition, the subjects remained alone until they recovered from anesthesia and then were returned to their home cage and social group.

2.2.1 | Surface Area Measurement

We include both ex vivo and in vivo scans in this dataset because previous studies have measured PT asymmetries in chimpanzees using both in vivo and ex vivo scans and have shown that results are comparable (Hopkins and Nir 2010). Since magnet strength influences the contrast of gray and white matter, we would not want to compare absolute gray matter volumes or surface area without using identical scanning protocols. However, because subjects' left and right hemispheres would be subjected to the same scanning conditions, the inclusion of in vivo and ex vivo scans in a study comparing asymmetries, specifically within individuals, is appropriate.

Before tracing, all images were imported into *Analyze 14.0* and transformed into 0.625 isotropic voxel dimensions and realigned in the anterior commisure- posterior commisure axis. PT surface area was quantified in the coronal plane. Because Heschl's gyrus is not always detectable for monkeys, we followed methods previously used with baboons, vervets, and macaques, in which the anterior border of the PT was defined as the most anterior slice immediately after the insula closed (i.e., when the insular sulcus disappeared posteriorly) (Lyn et al. 2011; Marie et al. 2018). We used this method for all taxa so that we could use the same landmarks. The posterior border was defined as

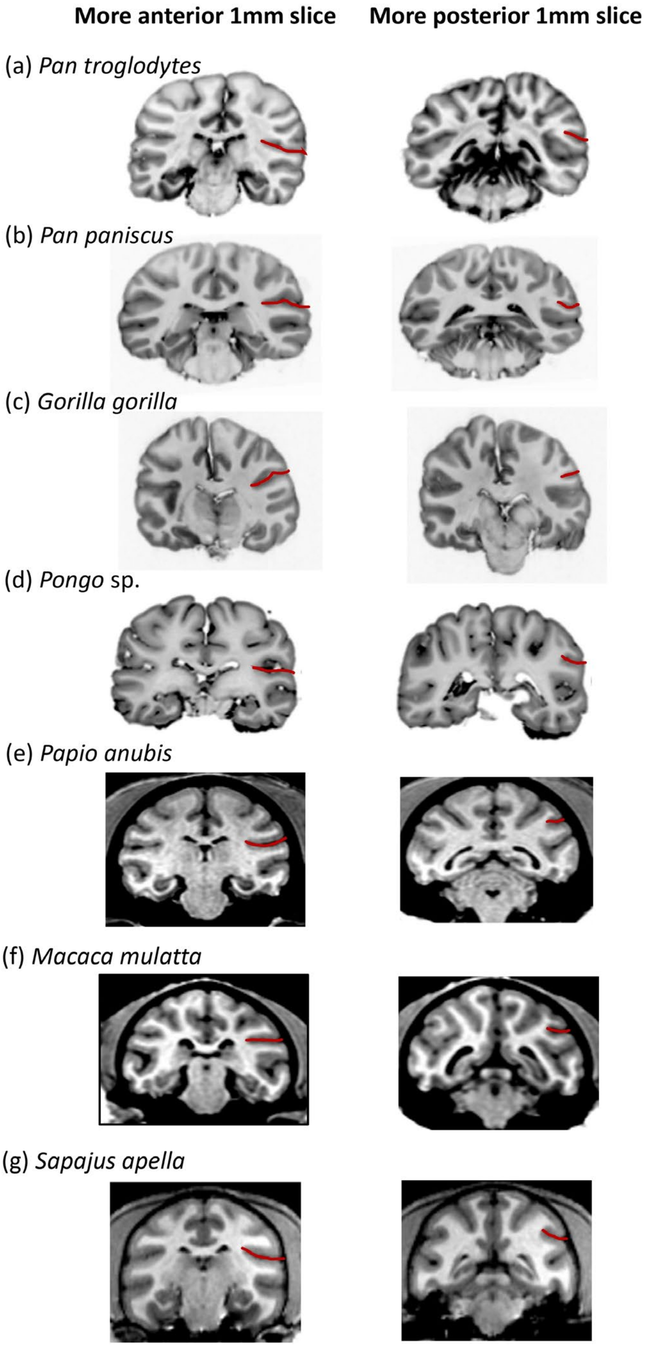

FIGURE 1 | Coronal view of 1 mm slices of a T2-weighted MRIs from a chimpanzee (*Pan troglodytes*), bonobo (*Pan paniscus*), gorilla (*Gorilla gorilla*), and orangutan (*Pongo* sp.) and T1-weighted MRIs from an olive baboon (*Papio anubis*), rhesus macaque (*Macaca mulatta*), and tufted capuchin (*Sapajus apella*). Here, the contrast of the T2-weighted images has been inverted to make them visually comparable to the T1-weighted images. In the Measure component of Analyze 14.0, a mouse-driven cursor was used to trace a line from the most medial point of the Sylvian fissure to the most lateral point, following the most ventral edge of the Sylvian fissure (represented by the red line, which is extra thick here for illustrative purposes). This step was repeated on each slice, moving posteriorly until the Sylvian fissure fell out of view. PT surface area was measured to the closest 0.1 mm, and measurements were taken on every slice in which the Sylvian fissure was visible. PT surface area (in mm^2) was calculated as the sum of all PT measures within a hemisphere.

the last slice in which the sylvian fissure was visible. Using the *Measure tool* of *Analyze 14.0* in the coronal plane, a computer cursor was used to trace a line from the most medial point of the sylvian fissure to the most lateral point, following the most ventral edge of the sylvian fissure. This step was repeated on each slice, moving posteriorly until the Sylvian fissure was no longer visible (Figure 1). The depth between the medial and lateral landmarks of the sylvian fissure was measured to the closest 0.1 mm on each virtual slice. PT surface area (in mm^2) was calculated as the sum of all PT measures within a hemisphere. Before data collection, intra-rater reliability for the one experimenter was assessed through intraclass correlation coefficients in the left and right hemispheres (0.999 for the left hemisphere and 0.999 for the right hemisphere).

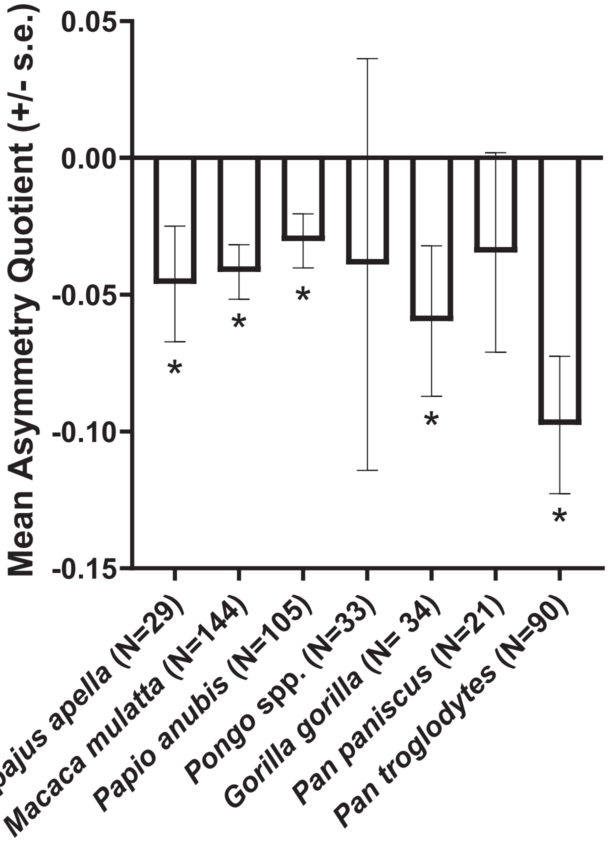

FIGURE 2 | Mean PT surface area asymmetries among the taxa included in this study. The boxes show the mean asymmetry quotient (AQ) for each taxon. The whiskers represent the standard error of the mean. * indicates significant *t*-test results at a level of $p < 0.05$ when testing if the mean AQ for each taxon significantly differed from 0.0.

2.3 | Data Analysis

For each subject, an asymmetry quotient was computed following the formula [$AQ = (R - L)/((R + L) \times 0.5)$]. Positive AQ values reflected rightward asymmetries, while negative values indicated a leftward bias. Each subject was also classified as being left- ($AQ \leq -0.0250$), right- ($AQ \geq +0.025$), or nonlateralized/"ambiguously-lateralized" ($AQ > -0.0249$ and $AQ < +0.0249$) based on the sign and strength of the AQ values. Tests for population-level asymmetries were performed using one-sample *t* tests and chi-square goodness-of-fit tests with alpha set to $p < 0.05$. Comparisons between species were conducted using nonparametric Kruskal–Wallis or Mann–Whitney *U* tests. To test whether species differed in the magnitude of PT asymmetry, independent of direction, we calculated the absolute value of the AQ score (ABS_AQ) for each subject and compared these values across species and taxa. Finally, to test for allometric effects, we ran a Pearson correlation between the degree of asymmetry detected in this study and the average brain size for each species.

3 | Results

The mean AQ values are presented in Figure 2 and Table 2. The number of left-, right-, and nonlateralized subjects within each species is shown in Table 3. The one-sample *t* tests revealed significant leftward asymmetries for the chimpanzees $t(89) = -3.886$, $p = 0.0002$, gorillas $t(33) = -2.167$,

TABLE 2 | Planum temporale descriptive statistics including mean left surface area (mm^2), mean right surface area (mm^2), and mean asymmetry quotient (AQ). AQ scores were computed for each subject using the formula [$AQ = (R - L)/((R + L) \times 0.5)$]. An AQ score ≤ -0.0250 indicates a leftward bias, an $AQ \geq +0.025$ indicates a rightward bias, and an AQ > -0.0249 or $< +0.0249$ indicates no bias. One-sample *t* tests with alpha set to $p < 0.05$ were used to assess population-level asymmetries (i.e., whether the mean AQ for each species significantly differed from 0.00).

Species	Total *N*	Mean left (mm^2)	Mean right (mm^2)	Mean AQ	*t*	*p*
Pan troglodytes	90	299.98	271.26	−0.0976	−3.886	0.0002
Pan paniscus	21	252.99	247.04	−0.0345	−0.095	0.355
Gorilla gorilla	34	307.79	292.24	−0.0574	−2.167	0.038
Pongo spp.	33	194.08	181.01	−0.0389	−0.517	0.609
Papio anubis	109	256.90	249.25	−0.0311	−3.253	0.002
Macaca mulatta	144	170.21	163.43	−0.0428	−4.165	< 0.0001
Sapajus apella	29	213.32	203.83	−0.0460	−2.175	0.038
Apes	179	276.47	255.88	−0.0715	−3.599	< 0.0001
Monkeys	283	208.02	200.62	−0.0386	−5.799	< 0.0001

TABLE 3 | Planum temporale surface area asymmetry results. Asymmetry quotient (AQ) scores were computed for each subject using the formula $[AQ = (R - L)/((R + L) \times 0.5)]$. This table presents the number of subjects from each taxon who were left-lateralized (#L: $AQ \leq -0.0250$), right-lateralized (#R: $AQ \geq +0.025$), or nonlateralized/"ambiguously-lateralized" (#A: $AQ > -0.0249$ or $AQ < +0.0249$) for PT surface area. Chi-square goodness-of-fit tests with alpha set to $p < 0.05$ were used to determine whether the distribution of left-, right-, and ambiguously-lateralized subjects significantly differed from the expected distributions. Subsequent binomial z-scores with alpha set to $p < 0.10$ were computed to compare the frequency of left- and right-lateralized subjects.

Species	#L	#A	#R	χ^2	p	L vs. R z-score	p
Pan troglodytes	57	11	22	39.64	< 0.0001	3.83	0.0001
Pan paniscus	10	3	8	3.93	0.1403	0.24	0.8145
Gorilla gorilla	19	7	8	8.12	0.0172	1.92	0.0522
Pongo spp.	18	1	14	14.84	0.0006	0.53	0.5966
Papio anubis	55	25	29	15.34	0.0005	2.73	0.0060
Macaca mulatta	80	23	41	36.86	< 0.0001	3.45	0.0005
Sapajus apella	16	6	7	6.52	0.0384	1.67	0.0931

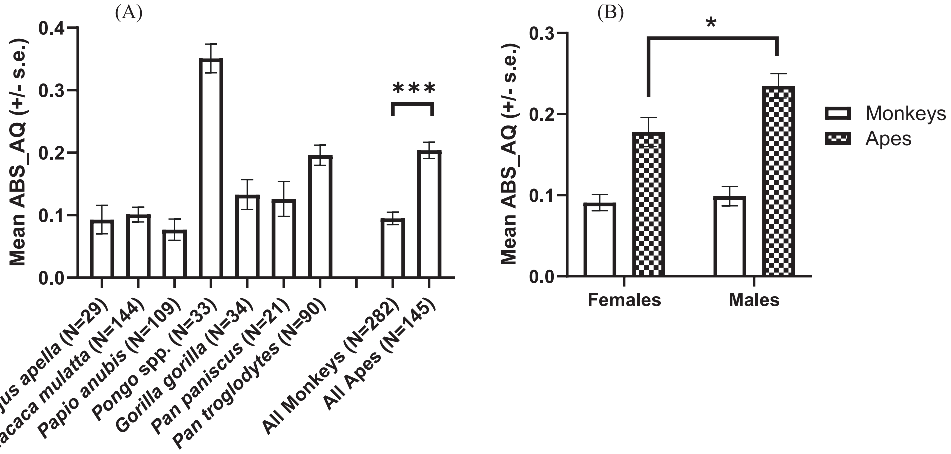

FIGURE 3 | Mean absolute asymmetries (ABS_AQ) for each taxon (a) and sex (b) depicted by boxes. Whiskers show the standard error of the mean. We used analyses of covariance to compare ABS_AQ scores between taxons, taxonomic groups (monkeys vs. apes), and sexes while controlling for age. *** indicates significance at a level of $p < 0.001$ and * indicates significance at a level of $p < 0.05$ for these analyses.

$p = 0.038$, baboons $t(108) = -3.253$, $p = 0.002$, rhesus macaques $t(143) = -4.165$, $p < 0.0001$, and capuchins $t(28) = -2.175$, $p = 0.038$. No significant population-level bias was found for the bonobos $t(20) = -0.095$, $p = 0.355$ or orangutans $t(32) = -0.517$, $p = 0.609$, although they all showed leftward asymmetry on average (Table 2). The qualitative data largely supported the results of the one-sample t tests. Chi-square goodness-of-fit tests revealed that, aside from the bonobos, the distribution of left-, right-, and nonlateralized subjects was not random. Subsequent binomial z-scores with alpha set to $p < 0.10$ showed that the frequency of left- compared to right-lateralized subjects was significantly higher in the chimpanzees, gorillas, baboons, rhesus macaques, and capuchins (Table 3).

3.1 | Sex and Age Effects Within Each Species

Spearman rank-order correlations revealed a significant association between age and AQ values in rhesus macaques ($r = 0.182$, $p = 0.021$), with older animals exhibiting a smaller leftward bias. However, no significant associations were found between age and the AQ scores among chimpanzees ($r = 0.107$, $p = 0.325$), bonobos ($r = -0.417$, $p = 0.086$), gorillas ($r = 0.013$, $p = 0.943$), orangutans ($r = -0.020$, $p = 0.914$), baboons ($r = -0.033$, $p = 0.731$), or capuchins ($r = -0.079$, $p = 0.696$). In addition, Mann–Whitney U tests revealed no significant sex differences in AQ values among chimpanzees ($U = 1044.0$, $p = 0.799$), bonobos ($U = 40.0$, $p = 0.797$), gorillas ($U = 173.0$, $p = 0.339$), orangutans ($U = 107.0$, $p = 0.325$), baboons ($U = 818.5$, $p = 0.760$), rhesus macaques ($U = 2661.0$, $p = 0.849$), or capuchins ($U = 91.0$, $p = 0.875$).

3.2 | Comparisons Between Species

Though all taxa in this study exhibited a negative mean AQ, indicating a leftward bias, Kruskal–Wallis tests revealed a significant difference in mean AQ between the ape sample and the cercopithecoid/platyrrhine sample ($H = 5.116$, $p = 0.024$), but not between all species ($H = 9.018$, $p = 0.173$), only the ape species ($H = 1.923$, $p = 0.589$), or only the cercopithecoid/platyrrhine species ($H = 1.009$, $p = 0.604$).

3.3 | Absolute Asymmetries and Allometric Effects

Using analyses of covariance, we compared the ABS_AQ scores between taxa, primate groups (ape or cercopithecoid/platyrrhine), and sexes while controlling for age. Significant main effects were found for taxa $F(5,451) = 13.879$, $p < 0.001$, group $F(1, 446) = 31.601$, $p < 0.001$, and sex $F(1, 446) = 7.232$, $p = 0.007$, as well as a two-way interaction between group and sex $F(1,446) = 3.996$, $p = 0.046$. Age was not a significant covariate. The mean ABS_AQ value for each sex and taxon is shown in Figure 3. Overall, apes had higher ABS_AQ values than cercopithecoids/platyrrhines, and males had higher ABS_AQ values than females. However, this sex effect was driven by the apes and not the cercopithecoids/platyrrhines, with male apes showing a higher ABS_AQ than female apes. When considering each species, as shown in Figure 3, all the ape species had higher ABS_AQ values than the non-ape species, with the orangutans showing the most lateralized PT asymmetries. Regarding potential allometric effects on PT asymmetries, we did not find a significant association between mean cerebral volumes (reported in Ardesch et al. 2022 and Rogers et al. 2007) and mean AQ values (from this study) $r = 0.472$, df = 7, $p = 0.284$.

4 | Discussion

Our findings reveal significant leftward biases in PT surface area among chimpanzees, gorillas, olive baboons, rhesus macaques, and capuchins. We did not find significant population-level asymmetries among orangutans and bonobos, but both species showed a trend toward leftward asymmetries. The lack of statistical significance for the bonobos and orangutans could partially be due to their small sample sizes, which resulted in a lack of statistical power. For instance, our bonobo sample actually exhibited a larger leftward asymmetry, on average, than the rhesus macaque sample, but the bonobo sample had fewer subjects, and therefore, this asymmetry was not found to be significant. Alternatively, the greater phenotypic variation in PT asymmetry quotients (and therefore less chance of statistical significance) in bonobos and orangutans compared to the other great apes could be due to differences in the divergence dates of the populations sampled in our study. The great ape brains included in our study do not represent all subspecies and represent varying levels of genetic variation. According to estimates from Prado-Martinez et al. (2013), the divergence times for populations in our sample are as follows: bonobos (only one subspecies)—divergence ~0.8 million years ago, orangutans (Sumatran, Bornean, and hybrids)—divergence ~0.5 million years ago, chimpanzees (Western)—divergence ~0.3 million years ago, and gorillas (Western lowland)—divergence ~0.1 million years ago. It is, therefore, possible that normal genetic drift or other population genetic dynamics resulted in a greater range of phenotypic variation in small populations that have persisted over a longer time span (i.e., the bonobos and orangutans).

We detected significant age effects for rhesus macaques only. The significant age effects could be influenced by the large number of young rhesus macaques in this sample (40 subjects were between the ages of 8–32 years old; 104 subjects were under the age of 5). However, because the correlation coefficient was very low, it could possibly be a spurious result. We detected no significant sex differences in AQ for any of the taxa; however, we did find that male apes showed higher ABS_AQ values than female apes. While we do not have a definitive explanation for this finding, one speculation is that corpus callosum (CC) size may influence lateralization, and male apes may have larger CCs than females. There is also evidence that human female brains exhibit higher interhemispheric connectivity, which may affect asymmetry. Alternatively, there is evidence that larger brains are more asymmetric, so the sex differences we see could be related to males having larger brains on average. Regarding the size of the PT asymmetries, we found that asymmetry quotients significantly differed when comparing monkeys and apes; specifically, apes had greater leftward AQ values compared to the cercopithecoid and platyrrhine species.

4.1 | Repeatability

We note here that the chimpanzee ex vivo scans used in this study excluded any subjects that were previously included in reports of PT asymmetries measured from in vivo scans (Gilissen 2001; Hopkins and Nir 2010); thus, they are a third independent set of chimpanzee subjects that have been measured for PT asymmetries and, like previous studies, we found a statistically significant leftward bias for PT surface area. These findings further demonstrate the consistency in this asymmetry even when using different samples of chimpanzees and methods (i.e., ex vivo vs. in vivo scans). Our finding of a leftward asymmetry in PT surface area among chimpanzees also aligns with evidence from cytoarchitectural measures of area Tpt (part of Brodmann's area 22) in postmortem chimpanzee brains, which also exhibit a significant leftward asymmetry in volume and neuron count (Spocter et al. 2010).

The olive baboon findings reported here are also consistent with previous reports of leftward asymmetries among adults and infants of this species (Marie et al. 2018; Becker et al. 2021). Interestingly, our rhesus macaque results differ from previous studies that did not find a population-level PT asymmetry among rhesus macaques (Gannon, Kheck, and Hof 2008; Lyn et al. 2011); however, the Lyn et al. (2011) study measured gray matter volume rather than surface area, and included 21 rhesus macaques, compared to the 144 individuals in the current study. Likewise, the Gannon, Kheck, and Hof (2008) paper used postmortem brains and also had a relatively small sample size ($n < 20$). This suggests that rhesus macaques show a small to moderate leftward asymmetry in the PT, which requires relatively large samples to detect. These results are also consistent with at least one recent report of leftward PT asymmetries in rhesus macaques using voxel and surface-based analytic approaches (Xia et al. 2020).

4.2 | Absolute PT Asymmetry and Allometric Effects

More broadly, we found that apes had more lateralized PT asymmetries than the cercopithecoids and platyrrhines. These findings are consistent with studies examining the evolution of absolute asymmetries in relation to increasing brain size and reduced interhemispheric connectivity. Specifically, it has been demonstrated that primate species with larger brains have relatively smaller CC surface areas (Rilling and Insel 1999a). One consequence of the negative allometry between brain size and CC surface area is that the two hemispheres have become increasingly disconnected, which some have hypothesized led to increasing selection for specializations within the left and right hemispheres (Caminiti et al. 2013; Hopkins and Cantalupo 2008; Innocenti, Caminiti, and Hof 2010; Jäncke and Steinmetz 1996; Oliveras, Montiel, and Aboitiz 2001; Phillips et al. 2015). We do note that in this study, associations between brain size and absolute asymmetry are less evident. For example, orangutans have the highest ABS_AQ values compared to all other great ape species, but they do not have the largest brain volumes within the ape sample. Likewise, within the non-apes, baboons have the largest brains but have the lowest ABS_AQ values, albeit not significantly different from either the rhesus macaques or capuchin. Furthermore, we did not detect a significant association between mean cerebral volumes and mean AQ values. Future studies could contribute to this area of inquiry by examining associations between CC size and PT asymmetries.

5 | Summary

The human central nervous system is characterized by hemispheric specialization, which refers to cognitive, sensory, or motor functions that are differentially processed by the left and right hemispheres of the brain (Hopkins 2013). Language and handedness are the most well-studied examples of hemispheric specialization. Given the prevalence of leftward PT asymmetry in humans, as well as the PT's critical role in human language and speech, this region has been a targeted area for comparative studies of neuroanatomical asymmetry in nonhuman primates. However, PT is believed to have nonlanguage functions, as well, such as processing sounds that are spectrally and temporally complex, which are thought to be common in nature (reviewed by Griffiths and Warren 2002). Our goal was to examine temporal cortex asymmetries in nonhuman primates. In doing so, we observed a population-level leftward bias for PT surface area among not only great apes (chimpanzees and gorillas), but also two cercopithecoids (baboons and macaques) and one platyrrhine (capuchins). These findings provide additional support that hemispheric specialization, particularly in the PT, is not unique to humans. These findings suggest that PT lateralization was likely present in some anthropoid primate ancestors and relatives and that human brains have since undergone changes to the size and connectivity of the PT in response to selection for the cognitive processes needed to support the evolution of language and speech (Becker et al. 2022; Rilling et al. 2012, 2008). Given evidence that PT asymmetries are associated with hand preference for gestural communication in both chimpanzees (Hopkins and Nir 2010) and olive baboons (Becker et al. 2024), it would be useful for future studies to test for similar associations in additional primate species to better understand the functional significance of this phylogenetically shared PT asymmetry.

Author Contributions

Angela M. Achorn: formal analysis (lead), investigation (equal), visualization (equal), writing – original draft (equal), writing – review and editing (equal). **Michele M. Mulholland:** investigation (equal), methodology (equal), resources (equal), writing – original draft (supporting). **Chelsea M. Cox:** investigation (equal). **Kimberley A. Phillips:** funding acquisition (equal), investigation (equal), resources (equal), writing – original draft (supporting). **Allyson J. Bennett:** funding acquisition (equal), investigation (equal), resources (equal). **Peter J. Pierre:** funding acquisition (equal), investigation (equal), resources (equal), writing – original draft (supporting). **Chet C. Sherwood:** funding acquisition (equal), investigation (equal), resources (equal), writing – original draft (supporting), writing – review and editing (supporting). **Steven J. Schapiro:** investigation (equal), writing – original draft (supporting). **William D. Hopkins:** conceptualization (lead), data curation (equal), formal analysis (equal), funding acquisition (equal), investigation (equal), methodology (equal), project administration (lead), resources (equal), supervision (lead), visualization (equal), writing – original draft (equal), writing – review and editing (supporting).

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Ethics Statement

All experimental procedures were carried out according to the National Institutes of Health guidelines for animal research and were approved by the Institutional Animal Care and Use Committee at each institution. We appreciate the assistance of veterinarians and care staff in all aspects of the care of the animals during scanning and recovery from the anesthesia.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information of this article. Magnetic resonance images for some subjects are available through The National Chimpanzee Brain Resource (https://www.chimpanzeebrain.org).

References

Altarelli, I., F. Leroy, K. Monzalvo, et al. 2014. "Planum Temporale Asymmetry in Developmental Dyslexia: Revisiting an Old Question." *Human Brain Mapping* 35: 5717–5735. https://doi.org/10.1002/hbm.22579.

Annett, M. 2002. *Handedness and Brain Asymmetry: The Right Shift Theory.* Hove: Psychology Press.

Ardesch, D. J., L. H. Scholtens, S. C. de Lange, et al. 2022. "Scaling Principles of White Matter Connectivity in the Human and Nonhuman Primate Brain." *Cerebral Cortex* 32: 2831–2842. https://doi.org/10.1093/cercor/bhab384.

Atkinson, E. G., J. Rogers, M. C. Mahaney, L. A. Cox, and J. M. Cheverud. 2015. "Cortical Folding of the Primate Brain: An Interdisciplinary Examination of the Genetic Architecture, Modularity, and Evolvability of a Significant Neurological Trait in Pedigreed Baboons (Genus *Papio*).” *Genetics* 200: 651–666. https://doi.org/10.1534/genetics.114.173443.

Barta, P., G. Pearlson, L. B. Brill, et al. 1997. “Planum Temporale Asymmetry Reversal in Schizophrenia: Replication and Relationship to Gray Matter Abnormalities.” *American Journal of Psychiatry* 154: 661–667. https://doi.org/10.1176/ajp.154.5.661.

Beaton, A. A. 1997. “The Relation of Planum Temporale Asymmetry and Morphology of the Corpus Callosum to Handedness, Gender and Dyslexia: A Review of the Evidence.” *Brain and Language* 60: 255–322. https://doi.org/10.1006/brln.1997.1825.

Becker, Y., K. K. Loh, O. Coulon, and A. Meguerditchian. 2022. “The Arcuate Fasciculus and Language Origins: Disentangling Existing Conceptions That Influence Evolutionary Accounts.” *Neuroscience & Biobehavioral Reviews* 134: 104490. https://doi.org/10.1016/j.neubiorev.2021.12.013.

Becker, Y., and A. Meguerditchian. 2022. “Structural Brain Asymmetries for Language: A Comparative Approach Across Primates.” *Symmetry* 14: 876. https://doi.org/10.3390/sym14050876.

Becker, Y., R. Phelipon, D. Marie, et al. 2024. “Planum Temporale Asymmetry in Newborn Monkeys Predicts the Future Development of Gestural Communication's Handedness.” *Nature Communications* 15: 4791. https://doi.org/10.1038/s41467-024-47277-6.

Becker, Y., R. Phelipon, J. Sein, L. Velly, L. Renaud, and A. Meguerditchian. 2022. “Planum Temporale Grey Matter Volume Asymmetries in Newborn Monkeys (*Papio anubis*).” *Brain Structure & Function* 227: 463–468. https://doi.org/10.1007/s00429-021-02278-9.

Becker, Y., J. Sein, L. Velly, et al. 2021. “Early Left-Planum Temporale Asymmetry in Newborn Monkeys (*Papio anubis*): A Longitudinal Structural MRI Study at Two Stages of Development.” *NeuroImage* 227: 117575. https://doi.org/10.1016/j.neuroimage.2020.117575.

Bogart, S. L., J. F. Mangin, S. J. Schapiro, et al. 2012. “Cortical Sulci Asymmetries in Chimpanzees and Macaques: A New Look at an Old Idea.” *NeuroImage* 61: 533–541. https://doi.org/10.1016/j.neuroimage.2012.03.082.

Bradshaw, J. L., and L. J. Rogers. 1993. *The Evolution of Lateral Asymmetries, Language, Tool-Use and Intellect*. San Diego: Academic Press.

Caminiti, R., F. Carducci, C. Piervincenzi, et al. 2013. “Diameter, Length, Speed, and Conduction Delay of Callosal Axons in Macaque Monkeys and Humans: Comparing Data From Histology and Magnetic Resonance Imaging Diffusion Tractography.” *Journal of Neuroscience* 33: 14501–14511. https://doi.org/10.1523/JNEUROSCI.0761-13.2013.

Carrion-Castillo, A., A. Pepe, X. Z. Kong, et al. 2020. “Genetic Effects on Planum Temporale Asymmetry and Their Limited Relevance to Neurodevelopmental Disorders, Intelligence or Educational Attainment.” *Cortex* 124: 137–153. https://doi.org/10.1016/j.cortex.2019.11.006.

Caspar, K. R., F. Pallasdies, L. Mader, H. Sartorelli, and S. Begall. 2022. “The Evolution and Biological Correlates of Hand Preferences in Anthropoid Primates.” *eLife* 11: e77875. https://doi.org/10.7554/eLife.77875.

Corballis, M. C. 1992. *The Lopsided Brain: Evolution of the Generative Mind*. New York: Oxford University Press.

Crow, T. 2004. “Directional Asymmetry Is the Key to the Origin of Modern *Homo sapiens* (the Broca-Annett Axiom): A Reply to Rogers' Review of the Speciation of Modern *Homo sapiens*.” *Laterality: Asymmetries of Body, Brain and Cognition* 9: 233–242. https://doi.org/10.1080/13576500342000374.

Damasio, A. R., and N. Geschwind. 1984. “The Neural Basis of Language.” *Annual Review of Neuroscience* 7: 127–147. https://doi.org/10.1146/annurev.ne.07.030184.001015.

Ely, J. J., B. Dye, W. I. Frels, et al. 2005. “Subspecies Composition and Founder Contribution of the Captive U.S. Chimpanzee (Pan Troglodytes) Population.” *American Journal of Primatology* 67: 223–241. https://doi.org/10.1002/ajp.20179.

Foundas, A. L., C. M. Leonard, and K. M. Heilman. 1995. “Morphological Cerebral Asymmetries and Handedness: The Pars Triangularis and Planum Temporale.” *Archives of Neurology* 52: 501–508. https://doi.org/10.1001/archneur.1995.00540290091023.

Galaburda, A. M., J. Corsiglia, G. Rosen, and G. F. Sherman. 1987. “Planum Temporale Asymmetry, Reappraisal Since Geschwind and Levitsky.” *Neuropsychologia* 25: 853–868. https://doi.org/10.1016/0028-3932(87)90091-1.

Galaburda, A. M., F. Sanides, and N. Geschwind. 1978. “Human Brain: Cytoarchitectonic Left–Right Asymmetries in the Temporal Speech Region.” *Archives of Neurology* 35: 812–817. https://doi.org/10.1001/archneur.1978.00500360036007.

Gannon, P. J., R. L. Holloway, D. C. Broadfield, and A. R. Braun. 1998. “Asymmetry of Chimpanzee Planum Temporale: Humanlike Pattern of Wernicke's Brain Language Area Homolog.” *Science* 279: 220–222. https://doi.org/10.1126/science.279.5348.220.

Gannon, P. J., N. Kheck, and P. R. Hof. 2008. “Leftward Interhemispheric Asymmetry of Macaque Monkey Temporal Lobe Language Area Homolog Is Evident at the Cytoarchitectural, but Not Gross Anatomic Level.” *Brain Research* 1199: 62–73. https://doi.org/10.1016/j.brainres.2007.12.041.

Geschwind, N., and W. Levitsky. 1968. “Human Brain: Left–Right Asymmetries in Temporal Speech Region.” *Science* 161: 837186–837187. https://doi.org/10.1126/science.161.3837.186.

Gilissen, E. 2001. “Structural Symmetries and Asymmetries in Human and Chimpanzee Brains.” In *Evolutionary Anatomy of the Primate Cerebral Cortex*, edited by D. Falk and K. R. Gibson, 187–215. Cambridge: Cambridge University.

Griffiths, T. D., and J. D. Warren. 2002. “The Planum Temporale as a Computational Hub.” *Trends in Neurosciences* 25: 349–355. https://doi.org/10.1016/s0166-2236(02)02191-4.

Hopkins, W. D. 2013. “Neuroanatomical Asymmetries and Handedness in Chimpanzees (*Pan troglodytes*): A Case for Continuity in the Evolution of Hemispheric Specialization.” *Annals of the New York Academy of Sciences* 1288: 17–35. https://doi.org/10.1111/nyas.12109.

Hopkins, W. D. 2022. “Neuroanatomical Asymmetries in Nonhuman Primates in the Homologs to Broca's and Wernicke's Areas: A Mini-Review.” *Emerging Topics in Life Sciences* 6: 271–284. https://doi.org/10.1042/ETLS20210279.

Hopkins, W. D., and C. Cantalupo. 2008. “Theoretical Speculations on the Evolutionary Origins of Hemispheric Specialization.” *Current Directions in Psychological Science* 17: 233–237. https://doi.org/10.1111/j.1467-8721.2008.00581.x.

Hopkins, W. D., H. Lyn, and C. Cantalupo. 2009. “Volumetric and Lateralized Differences in Selected Brain Regions of Chimpanzees (*Pan troglodytes*) and Bonobos (*Pan paniscus*).” *American Journal of Primatology* 71: 988–997. https://doi.org/10.1002/ajp.20741.

Hopkins, W. D., and T. Nir. 2010. “Planum Temporale Surface Area and Grey Matter Asymmetries in Chimpanzees (*Pan troglodytes*): The Effect of Handedness and Comparison With Findings in Humans.” *Behavioural Brain Research* 208: 436–443. https://doi.org/10.1016/j.bbr.2009.12.012.

Hopkins, W. D., J. P. Taglialatela, A. Meguerditchian, T. Nir, N. M. Schenker, and C. C. Sherwood. 2008. “Gray Matter Asymmetries in Chimpanzees as Revealed by Voxel-Based Morphometry.” *NeuroImage* 42: 491–497. https://doi.org/10.1016/j.neuroimage.2008.05.014.

Innocenti, G. M., R. Caminiti, and P. R. Hof. 2010. “Fiber Composition in the Planum Temporale Sector of the Corpus Callosum in Chimpanzee and Human.” *Brain Structure and Function* 215: 123–128. https://doi.org/10.1007/s00429-010-0274-9.

Jäncke, L., and H. Steinmetz. 1996. "Brain Size: A Possible Source of Interindividual Variabilty in Corpus Callosum Morphology." In *The Role of the Corpus Callosum in Sensory-Motor Integration: Anatomy, Physiology and Behavior*, edited by E. Zaidel, M. Iacoboni, and A. P. Pascual-Leone, 1–15. New York: Plenum Press.

Josse, G., G. Kherif, G. Flandin, M. L. Seghier, and C. J. Price. 2009. "Predicting Language Lateralization From Gray Matter." *Journal of Neuroscience* 29: 13516–13523. https://doi.org/10.1523/JNEUROSCI.1680-09.2009.

Knaus, T. A., A. M. Bollich, D. M. Corey, L. C. Lemen, and A. L. Foundas. 2004. "Sex-Linked Differences in the Anatomy of the Perisylvian Language Cortex: A Volumetric MRI Study of Gray Matter Volumes." *Neuropsychology* 18: 738–747. https://doi.org/10.1037/0894-4105.18.4.738.

Knaus, T. A., A. M. Bollich, D. M. Corey, L. C. Lemen, and A. L. Foundas. 2006. "Variability in Perisylvian Brain Anatomy in Healthy Adults." *Brain and Language* 97: 219–232. https://doi.org/10.1016/j.bandl.2005.10.008.

Kulynych, J. J., K. Vladar, D. W. Jones, and D. R. Weinberger. 1994. "Gender Differences in the Normal Lateralization of the Supratemporal Cortex: MRI Surface-Rendering Morphometry of Heschl's Gyrus and the Planum Temporale." *Cerebral Cortex* 4: 107–118. https://doi.org/10.1093/cercor/4.2.107.

Kwon, J. S., R. W. McCarley, Y. Hirayasu, et al. 1999. "Left Planum Temporale Reduction in Schizophrenia." *Archives of General Psychiatry* 56: 142–148. https://doi.org/10.1001/archpsyc.56.2.142.

Lyn, H., P. Pierre, A. J. Bennett, S. Fears, R. Woods, and W. D. Hopkins. 2011. "Planum Temporale Grey Matter Asymmetries in Chimpanzees (*Pan troglodytes*), Vervet (*Chlorocebus aethiops sabaeus*), Rhesus (*Macaca mulatta*) and Bonnet (*Macaca radiata*) Monkeys." *Neuropsychologia* 49: 2004–2012. https://doi.org/10.1016/j.neuropsychologia.2011.03.030.

Marie, D., M. Roth, R. Lacoste, et al. 2018. "Left Brain Asymmetry of the Planum Temporale in a Nonhominid Primate: Redefining the Origin of Brain Specialization for Language." *Cerebral Cortex* 28: 1808–1815. https://doi.org/10.1093/cercor/bhx096.

Mazoyer, B., L. Zago, G. Jobard, et al. 2014. "Gaussian Mixture Modeling of Hemispheric Lateralization for Language in a Large Sample of Healthy Individuals Balanced for Handedness." *PLoS One* 9: e101165. https://doi.org/10.1371/journal.pone.0101165.

Ocklenburg, S., and O. Gunturkun. 2018. *The Lateralized Brain: The Neuroscience and Evolution of Hemispheric Asymmetries*. London: Academic Press.

Oliveras, R., J. Montiel, and F. Aboitiz. 2001. "Species Differences and Similarities in the Fine Structure of the Mammalian Corpus Callosum." *Brain, Behavior and Evolution* 57: 98–105. https://doi.org/10.1159/000047229.

Phillips, K. A., C. D. Stimpson, J. B. Smaers, et al. 2015. "The Corpus Callosum in Primates: Processing Speed of Axons and the Evolution of Hemispheric Asymmetry." *Proceedings of the Royal Society B: Biological Sciences* 282: 20151535. https://doi.org/10.1098/rspb.2015.1535.

Prado-Martinez, J., P. Sudmant, J. Kidd, et al. 2013. "Great Ape Genetic Diversity and Population History." *Nature* 499: 471–475. https://doi.org/10.1038/nature12228.

Rilling, J. K., M. F. Glasser, S. Jbabdi, J. Andersson, and T. M. Preuss. 2012. "Continuity, Divergence and the Evolution of Brain Language Pathways." *Frontiers in Evolutionary Neuroscience* 3: 11. https://doi.org/10.3389/fnevo.2011.00011.

Rilling, J. K., M. F. Glasser, T. M. Preuss, et al. 2008. "The Evolution of the Arcuate Fasciculus Revealed With Comparative DTI." *Nature Neuroscience* 11: 426–428. https://doi.org/10.1038/nn2072.

Rilling, J. K., and T. R. Insel. 1999a. "Differential Expansion of Neural Projection Systems in Primate Brain Evolution." *NeuroReport* 10: 1453–1459. https://doi.org/10.1097/00001756-199905140-00012.

Rilling, J. K., and T. R. Insel. 1999b. "The Primate Neocortex in Comparative Perspective Using Magnetic Resonance Imaging." *Journal of Human Evolution* 37: 191–223. https://doi.org/10.1006/jhev.1999.0313.

Rogers, J., P. Kochunov, J. Lancaster, et al. 2007. "Heritability of Brain Volume, Surface Area and Shape: An MRI Study in an Extended Pedigree of Baboons." *Human Brain Mapping* 28: 576–583. https://doi.org/10.1002/hbm.20407.

Rogers, L. J., G. Vallortigara, and R. J. Andrew. 2013. *Divided Brains: The Biology and Behaviour of Brain Asymmetries*. New York: Cambridge University Press.

Rojas, D. C., S. L. Camou, M. L. Reite, and S. J. Rogers. 2005. "Planum Temporale Volume in Children and Adolescents With Autism." *Journal of Autism and Developmental Disorders* 35: 479–486. https://doi.org/10.1007/s10803-005-5038-7.

Shapleske, J., S. L. Rossell, P. W. Woodruff, and A. S. David. 1999. "The Planum Temporale: A Systematic, Quantitative Review of Its Structural, Functional and Clinical Significance." *Brain Research Reviews* 29: 26–49. https://doi.org/10.1016/s0165-0173(98)00047-2.

Spocter, M. A., W. D. Hopkins, S. K. Barks, et al. 2012. "Neuropil Distribution in the Cerebral Cortex Differs Between Humans and Chimpanzees." *Journal of Comparative Neurology* 520: 2917–2929. https://doi.org/10.1002/cne.23074.

Spocter, M. A., W. D. Hopkins, A. R. Garrison, et al. 2010. "Wernicke's Area Homolog in Chimpanzees (*Pan troglodytes*): Probabilistic Mapping, Asymmetry and Comparison With Humans." *Proceedings of the Royal Society B: Biological Sciences* 277: 2165–2174. https://doi.org/10.1098/rspb.2010.0011.

Spocter, M. A., C. C. Sherwood, S. J. Schapiro, and W. D. Hopkins. 2020. "Reproducibility of Leftward Planum Temporale Asymmetries in Two Genetically Isolated Populations of Chimpanzees (*Pan troglodytes*)." *Proceedings of the Royal Society B: Biological Sciences* 287: 20201320. https://doi.org/10.1098/rspb.2020.1320.

Strockens, F., O. Gunturkun, and S. Ocklenburg. 2013. "Limb Preferences in Non-Human Vertebrates." *Laterality* 18: 536–575. https://doi.org/10.1080/1357650X.2012.723008.

Warren, J. M. 1980. "Handedness and Laterality in Humans and Other Animals." *Physiological Psychology* 8: 351–359. https://doi.org/10.3758/Bf03337470.

Wernicke, C. 1874. *Der Aphasische Symptomenkomplex*. Breslau: Max Cohn & Weigert.

Xia, J., F. Wang, Z. Wu, et al. 2020. "Mapping Hemispheric Asymmetries of the Macaque Cerebral Cortex During Early Brain Development." *Human Brain Mapping* 41: 95–106. https://doi.org/10.1002/hbm.24789.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.