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Original Article

ORIGINAL ARTICLE

Left Brain Asymmetry of the Planum Temporale in a Nonhominid Primate: Redefining the Origin of Brain Specialization for Language

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Abstract

The planum temporale (PT) is a critical region of the language functional network in the human brain showing a striking size asymmetry toward the left hemisphere. Historically considered as a structural landmark of the left-brain specialization for language, a similar anatomical bias has been described in great apes but never in monkeys—indicating that this brain landmark might be unique to Hominidae evolution. In the present in vivo magnetic resonance imaging study, we show clearly for the first time in a nonhominid primate species, an Old World monkey, a left size predominance of the PT among 96 olive baboons (*Papio anubis*), using manual delineation of this region in each individual hemisphere. This asymmetric distribution was quasi-identical to that found originally in humans. Such a finding questions the relationship between PT asymmetry and the emergence of language, indicating that the origin of this cerebral specialization could be much older than previously thought, dating back, not to the Hominidae, but rather to the Catarrhini evolution at the common ancestor of humans, great apes and Old World monkeys, 30–40 million years ago.

Key words: baboons, brain evolution, hemispheric specialization, MRI

Introduction

Hemispheric "asymmetry" or "specialization" of the brain has been well described in a host of vertebrates (Rogers et al. 2013) including human and nonhuman primates. Such a phenomenon reflects the better aptitude of one hemisphere over the other for a given cognitive/motor function and/or interhemispheric anatomical differences (Josse and Tzourio-Mazoyer 2004). In humans, the lateralization of the language networks within the brain is one of the most representative and well-known expressions of hemispheric specialization. Indeed a large majority of people shows functional asymmetries toward the left hemisphere for most language functions (e.g., phonology, semantics, or sentence processing) (Vigneau et al. 2011). The planum temporale (PT), a cerebral region located within the Sylvian fissure, is considered as one of the functional epicenters of the language network because it is in part overlapping with Wernicke's area (Mesulam 1998) and contains auditory association cortex (Brodmann's area 22 or area Tpt) (Galaburda et al. 1978). Many study demonstrated the specific significance of the PT in the left hemisphere in a variety of auditory and language-related processes (Shapleske et al. 1999), including the main perceptive component of the audio–motor loop for phonological processing (Vigneau et al. 2006). Left hemisphere lesion of this region was associated with severe deficits in language comprehension and production (Wernicke 1874; Dronkers et al. 2004; Borovsky et al. 2007). In addition, direct structure–function relationship was showed between the left PT's size and functional asymmetry of language tasks (Josse et al. 2003, 2006). Interestingly, in 1968, Geschwind and Levitsky (Geschwind and Levitsky 1968) demonstrated that the PT showed a striking left anatomical asymmetry: its length being larger in the left hemisphere than the right in 65% of 100 postmortem brains. With the advent of magnetic resonance imaging (MRI) in the 1990s, the neuroanatomical PT asymmetry was further confirmed by noninvasive in vivo morphometric analyses in large cohorts (Shapleske et al. 1999). This evidence of structural asymmetry for a cortical key-region for language has received particular attention because of its assumed relation with language functional lateralization (Geschwind and Levitsky 1968), as supported by several studies (Foundas et al. 1994; Moffat et al. 1998). Moreover, anatomical symmetry or reversed asymmetry has been related to language impairment and poor verbal ability (Gauger et al. 1997; Eckert et al. 2001; Altarelli et al. 2014). However, such a relationship between anatomical and functional PT lateralization remain unclear according to some other studies (Jäncke and Steinmetz 1993; Dorsaint-Pierre et al. 2006; Eckert et al. 2006; Keller et al. 2011; Greve et al. 2013; Kolinsky et al. 2014). We are thus far from understanding the exact role of the PT size asymmetry with respects to language. While this inconsistency of findings questions its role as a marker of functional hemispheric specialization for language, this structural feature of the brain seems to be probably influenced by numerous factors interacting with language specialization such as gender and handedness (Chiarello et al. 2004, 2009; Dos Santos Sequeira et al. 2006), which might confound the big picture.

Whether PT asymmetry is human-specific and exclusively related to the emergence of language during human evolution has been questioned by paleoneurological research in more distant hominoids and nonhuman primate brain research. Because of the impossibility to study cortical asymmetries in the brains of our ancestors, PT asymmetries were first inferred from fossil endocasts using indirect measures of interhemispheric differences in length or posterior angulation of the Sylvian fissures. Those endocast studies described left-hemispheric asymmetries from those indirect measures in Homo neanderthalensis, Homo erectus pekinensis/soloensis (LeMay 1976; Holloway 1980) and Homo habilis (Tobias 1987). In nonhuman primates, the assessment of hemispheric differences in the Sylvian fissures of postmortem brains has shown consistent findings in great apes while inconsistent results were found in monkeys or lesser apes species (LeMay 1976; Yeni-Komshian and Benson 1976; Heilbroner and Holloway 1988; Falk et al. 1990; Gannon et al. 2008). Whether such indirect measures based on the Sylvian fissure are reliable to reflect real PT asymmetries have been questioned in both humans (Foundas et al. 1999) and great apes (Cantalupo et al. 2003). Direct measures of the surface/volume of the PT were then favored in nonhuman primates. Interestingly, leftward structural PT asymmetry were found in chimpanzees according to different quantification methods (Hopkins and Nir 2010) and, although less documented, in other great apes such as Bonobos, Gorillas, and Orangutans (Cantalupo et al. 2003). These different methods included (1) manual delineation of PT landmarks on *postmortem* brains (Gannon et al. 1998) or (2) on in vivo MRI scans (Hopkins et al. 1998) as well as (3) voxel-based morphometry on MRI scans (Hopkins et al. 2008). In contrast, similar studies in more distant primates species than Hominidae, such as Old World and New World monkeys, are relatively sparse and did not reveal any hemispheric size predominance of the PT (Hopkins et al. 1998; Gannon et al. 2008; Lyn et al. 2011). These collective findings suggest that the origins of this structural landmark of left-hemispheric specialization for language might date to the common ancestor of Hominidae at 14–17 million years ago (Hopkins et al. 1998; Lyn et al. 2011).

In the present anatomical MRI study, we investigated asymmetries of the PT in an unstudied Old World monkey species, the baboon (*Papio anubis*). In vivo images were noninvasively acquired in 96 anesthetized subjects (60 females and 36 males). Using a similar PT delineation method than that used in humans (Larsen et al. 1989), great apes and Old World monkeys (Lyn et al. 2011), its surface area was manually traced in each hemisphere of each individual. Individual and population-level neuroanatomical asymmetries of this critical region for language were thus assessed as well as the potential effects of brain volume, age, and gender.

Materials and Methods

Imaging Protocol

From December 2012 to January 2015, in vivo imaging was performed with a 3 T whole-body imager MEDSPEC 30/80 ADVANCE (Bruker) located at the Marseille Functional MRI Center (Institut de Neuroscience de la Timone). Whole brain anatomical MRI data were acquired using a Rapid-Biomed surface antenna on top of head for reception. High-resolution structural T1-weighted image was provided thanks to 2 MPRAGE sequences depending on acquisition of a female/young male (time repetition: 9.4 ms; time echo: 4.3 ms; flip angle: 30°; inversion time: 800 ms; field of view: 108 × 108 × 108 mm; isotropic voxel size: 0.6 mm^3) or an adult male (same parameters except for field of view: 126 × 126 × 126 mm and isotropic voxel size: 0.7 mm^3).

For each MRI session, minimally invasive premedication was realized with an intramuscular injection of ketamine (10 mg/kg) at the Station de Primatologie and subjects remained sedated during transportation to the MRI center. Once arrived at the MRI center, the focal subject was further sedated with an intramuscular injection of tiletamine and zolazepam (Zoletil™, 7 mg/kg) and acepromazine (Calmivet™, 0.2–0.5 mg/kg). The latter injection was needed to provoke a myorelaxation and avoid snoring or motions. Finally, anesthesia was maintained during the whole experiment thanks to a drip irrigation setup including tiletamine, zolazepam (Zoletil™, 4 mg/kg/h) and NaCl (0.9% of 4 mL/kg/h) without any use of endotracheal tube. Cardiovascular and respiratory functions were monitored, respectively, with a SpO_2 device placed on the lower lip and a respiratory belt (mechanical captor). Each subject was placed in ventral decubitus position in the MRI scanner and head of the subject was maintained using foam positioners, cushions and Velcro strips to maintain straight the head and reduce potential motion occurrences. At the end of the MRI session, baboons were put back in their social group at the Station de Primatologie.

Subjects

Among the 106 baboons selected for MRI sessions, 96 baboons (60 females and 36 males) were included in final analyses because of the exclusion of 10 subjects due to MRI artifacts (motion, aliasing, or truncation). The age ranges from 2.4 to 26.6 years (mean of 12.1 ± 6.15 SD). Olive baboons being considered as sexually mature around 4 years old for females and 5 years old for males (Leigh 2009; Onyango et al. 2013), the current population included 58 female and 26 male adults (87.5% of the population). All subjects were free from developmental problems, neurological antecedents, and brain abnormalities.

Baboons are housed at the Station de Primatologie CNRS (UPS 846, Rousset, France; Agreement number for conducting experiments on vertebrate animals: D13-087-7). All subjects are born in captivity from 1 (F1) or 2 generations (F2) and live in social groups with free access to outdoor areas connected to indoor areas. Enclosures are enriched by wooden platforms and vertical structures. Baboons are fed 4 times a day with monkey pellets, seed mixture, fresh vegetables, and fruits. Water is available ad libitum. The experimental procedure complied with the current French laws and the European directive 86/609/CEE.

Preprocessing of Anatomical MRI

Each individual anatomical MRI was manually oriented using ANALYZE 12.0 software (AnalyzeDirect, Inc.: http://analyzedirect.com/analyze-12-0/) according to the plane defined by the anterior and posterior commissures and the interhemispheric fissure plane. Images were corrected for noise thanks to the spatially adaptive nonlocal means denoising filter (Manjón et al. 2010) from VBM8 toolbox included in SPM8 (http://www.fil.ion.ucl.ac.uk/) as well as for bias field inhomogeneity using the N4 bias field removal tool (Tustison et al. 2010) from ANTs software (default parameters, http://stnava.github.io/ANTs/). Gray matter, white matter, and cerebrospinal fluid volumes of each subject were extracted with SPM8 in a subsample of 88 baboons using their segmented T1 provided by a previous study conducted in ANTs (see Love et al. (2016) for a full description). Brain volume was then computed in each of the 88 subjects from the sum of the volumes of the 3 compartments.

Manual Delineation of the PT

The surface area of the PT homolog was measured in the coronal plane following the procedures used in humans (Larsen et al. 1989), great apes (Hopkins et al. 1998; Cantalupo et al. 2003), and their adaptation to Old World monkeys (Lyn et al. 2011). The individual T1-weighted volumes were imported into ANALYZE. The region of interest was manually traced in the coronal plan in the individual native space with the ANALYZE tool "Volume Edit" using a touchpad-driven pointer (Wacom Cintiq® 13HD). Coronal rather than sagittal sections are used because they provide the best direct assessment of the full depth of the sylvian fossa, of which the planum is its floor (Shapleske et al. 1999). The delineation method of the PT was performed as followed. Whereas the posterior border of the PT was defined by the most caudal slice showing the Sylvian fissure, the definition of its anterior border in the baboons required to follow the specific delineation adaption to Old World monkeys from Lyn et al.'s method (Lyn et al. 2011). While in humans the anterior border of the PT is delimited by the Heschl's sulcus, Heschl's gyrus is not really detectable in the monkey species notably macaques (Hackett et al. 2001; Lyn et al. 2011). Indeed while in some baboon hemispheres, a slight cortical elevation was present somewhat where the Heschl's gyrus is located in humans, we could not identify reliable anatomical landmarks highlighting its borders (see Supplementary Material S1). In fact, at its posterior border, the sulcus notch was completely inconsistent between subjects but also between hemispheres of the same subject. Thus, to define the anterior border of the PT in the baboons, instead of using this inconsistent or invisible Heschl's sulcus, we used the most anterior slice right after the insula closed, namely when the insular sulcus totally disappeared posteriorly (Lyn et al. 2011). This border corresponds to the posterior second half of the "Heschl's gyrus embryo" in the antero-posterior direction, when this "embryo" was present. Consequently, because of the lack of reliable Heschl's gyrus borders in baboons, the present planum delineation using the posterior termination of the insular sulcus might include a piece of Heschl's gyrus in the antero-lateral direction. It might also miss a limited piece of the PT which is, in humans, in-between the lateral part of the Heschl's sulcus and this posterior insular sulcus termination (see Altarelli et al. 2014). In each slice, the tracing was drawn from the most medial portion of the Sylvian fissure to the most lateral point, following the most ventral edge of the fissure. Then, this step was repeated on the next 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. Then, a surface area was generated for each slice and further combined across all slices for each hemisphere independently in a given subject (Fig. 1, see Supplementary Material S2).

For each individual, from the left (L) and the right (R) PT surface areas, an Asymmetry Quotient (AQ) was computed, $AQ = (R - L) / [(R + L) \times 0.5]$, the sign indicating the direction of asymmetry (negative: left side, positive: right side) and the value, the strength of asymmetry. In addition, according to classification criteria used previously in humans and great apes (Hopkins and Nir 2010), the AQ were also used to classify the individuals as left-hemispheric biased ($AQ \leq -0.025$), right biased ($AQ \geq 0.025$), or nonbiased ($-0.025 < AQ < 0.025$).

In order to evaluate the robustness of our manual tracing data, a second rater blind to the side (images being randomly flipped on half of the subsample) measured the PT for evaluating the interraters reliability in 20 subjects for both left and

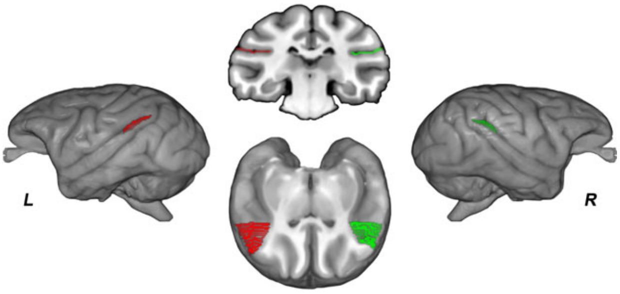

Figure 1. PT's asymmetry quantification in the baboon brain. Top, coronal section passing through the left (red) and right (green) PT; left, lateral view of a 3D render of the left hemisphere; right, lateral view of the right hemisphere; bottom, oblique section oriented along the Sylvian Fissure (L: left; R: right). Note the clear leftward asymmetry of the PT surface area in this individual on the bottom oblique section.

right hemispheres (i.e., 40 tracing). We also made use of a brain template previously computed in a subsample (89 individuals) of the same baboons (Love et al. 2016). This template has been built using the standard ANTs pipeline based on the use of an initial target image that is an average of the sample and is thus unbiased towards the brain morphometry of any individual. We assume that quantifying the PT asymmetry on this template would give a good indication of the population-level structural asymmetry of this region in those 89 baboons. We thus manually delineated the left and the right PT surface area on the template and computed the asymmetry. The anatomical landmarks used to quantify the PT were as identifiable on the brain template as on the individual images.

Statistical Analysis

To assess significance of asymmetry, we first explored the distributions of the left and right surface area of the PT, and their mean subtraction, testing if it was different from 0 with a Student's *t*-test in the full sample of 96 baboons. The same analysis was then conducted on the AQ.

Then in 88 baboons, for which Brain volume was documented, Age, Brain volume, Sex, and the interaction Age x Brain volume were entered as the main factors of a repeated measures MANCOVA of left and right PT surface area, the corresponding within-subject "Side" effect standing for the significance of PT asymmetry. All interactions with Side were included, as well as the Age x Brain volume interaction. Cerebral volume ranged from 137.51 to 208.17 cm^3 (mean of 175.31 cm^3 ± 16.02 SD) and was not correlated with age ($r = -0.13$, $P < 0.19$). As expected, brain volume differed between males and females (respectively 188.24 vs. 168.62 mm^3, $t(87) = 6.3$, $P < 0.0001$). Post hoc analysis included a linear regression of combined left and right PT surface areas as predicted by brain volume, a linear regression of both left and right PT surface areas as predicted by the residuals of a linear fit between brain volume and age, to characterize the effect of the interaction Age x Brain volume. We also performed 2 linear regressions separately on the left or right PT measurements, and the brain volume to explore the interaction Side x Brain volume. We also performed a ANCOVA on the AQ including Age, Brain volume, Sex, and the interaction Age x Brain volume as factors. Additionally, we also performed correlation analysis between the AQ and the left/right PT surface area independently in left- or right-biased baboon categories to explore which side was driving the asymmetry as well as if this relationship was different between the 2 categories. Sex having no significant effect in any analysis, it was finally removed.

Finally a correlation between the tracings and another set of tracings from a second rater (20 baboons) was performed to investigate interrater reliability and measurement consistency. All statistical analysis was completed with JMP9 Pro (SAS Institute, Inc.).

Results

Population-Level PT Asymmetries

Analyses of the raw surface areas of the PT showed a significant difference between the left and the right PT (left hemisphere: mean = 144.81 mm^2 ± 21.2 SD; right hemisphere: mean = 134.50 mm^2 ± 19.9 SD, $t(95) = 5.62$, $P < 0.0001$). According to the AQ scores, a significant degree of population-level asymmetry toward the left hemisphere was found for the PT surface area (Mean.AQ = −0.07 ± 0.13 SD, $t(95) = 5.38$, $P < 0.0001$). Categorization of individual AQ showed a majority of left-biased individuals: 60 baboons exhibited a left-hemispheric bias (62.5%) whereas 25 exhibited a right bias (26%) and 11 no bias (11.5%). The number of left-biased individuals was significantly greater than the number of right-biased ($\chi^2 = 14.84$, $P < 0.0001$) and nonbiased individuals ($\chi^2 = 37.20$, $P < 0.0001$).

Effect of Brain Volume and Age

The MANCOVA with repeated measure applied to left and right raw PT surface areas revealed a significant Side x Brain volume interaction [$F(1,85) = 4.09$, $P = 0.05$], and main effects of Side [$F(1,85) = 2.66$, $P = 0.07$], Brain volume [$F(1,85) = 8.11$, $P = 0.006$], and Age [$F(1,85) = 3.34$, $P = 0.07$]. The main effect of Side demonstrates that the asymmetry of the PT surface area was significant when taking into account Age and Brain volume. The main effect of Age was explained by a decrease in the combined left and right PT surface area with age ($r = -0.22$; $P = 0.04$). The Side x Brain volume interaction reveals that the bigger the brain volume at the individual level, the larger is the leftward asymmetry of the PT, as confirmed by post hoc correlation ($r = -0.22$; $P = 0.04$). The main effect of Brain volume indicates a relationship with the combined left and right PT surface areas ($r = 0.32$, $P = 0.003$), but brain volume and the left PT surface area were more closely related ($r = 0.37$, $P = 0.0004$) than brain volume and right PT surface area ($r = 0.2$, $P = 0.07$).

Similarly to the previous analysis, the ANCOVA on the AQ revealed a main effect of brain volume [$F(1,85) = 3.41$, $P = 0.07$]. The larger the brain volume, the more negative is the AQ indicating a larger left bias of the PT ($r = 0.21$; $P = 0.05$). There was no effect of age and the interaction Age x Brain Volume was not significant. Moreover, as can be seen in Figure 2, in the 60 left-biased baboons, the AQ was correlated with the left PT surface area ($r(60) = -0.37$; $P = 0.003$) and the right ($r = 0.24$, $P = 0.06$), whereas in the 25 right-biased baboons, only the correlation of the AQ with the left PT surface area approaches conventional level of significance ($r(25) = -0.34$, $P = 0.09$).

Interrater Reliability and PT Asymmetry on the Brain Template

First, a second rater, blind to the side, confirmed the measures of the PT in a subsample of 20 individuals for both hemispheres (interrater correlation coefficient for 40 tracings was $r = 0.72$, $P < 0.0001$). Second, a left bias of the PT was found on the brain template computed from 89 individuals (Love et al. 2016), for both the raw surface area (left PT surface area = 161.28 mm^2, right PT surface area = 132.12 mm^2) and the AQ (−0.20). Both analyses indicate the robustness of the leftward population-level asymmetry of the PT.

Discussion

We demonstrate, for the first time in a nonhominid species, a clear left-hemispheric size predominance of the PT at a population-level in 96 baboons, which is robust and consistent across interrater measures as well as with leftward PT asymmetry assessed in the related baboon brain template made from 89 subjects.

Towards a Continuity of PT Asymmetry Among Primates

These findings, revealed in the largest sample size ever used to investigate PT asymmetry in monkeys, clearly speak for a

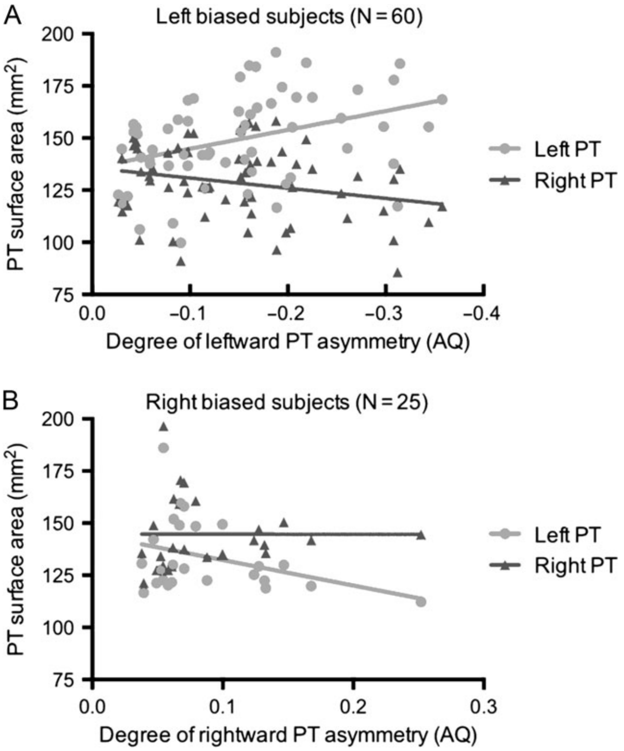

Figure 2. Scatter plots of the Asymmetry Quotient as a function of the left or right PT surface area in both left-biased (*A*) and right-biased subjects (*B*). AQ: Asymmetry Quotient (negative AQ values indicate leftward anatomical asymmetry, positive AQ values indicate rightward anatomical asymmetry).

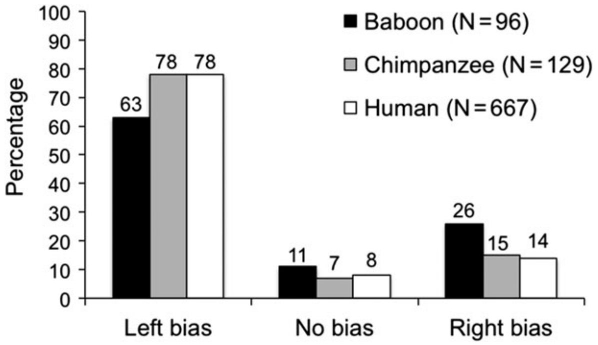

Figure 3. Distribution of primate subjects as a function of the direction of their PT asymmetry in baboons and previous studies conducted in chimpanzee and humans. Chimpanzee data from Hopkins and Nir reported with asymmetry quotient categorization (Hopkins and Nir 2010), human data from Shapleske et al. (1999).

phylogenetic continuity of hemispheric specialization for this region between humans and a nonhominid primate. The proportion of left-biased baboons (62.5%) is quasi-identical to the one originally found in humans (65%) from a similar sample size by Geschwind and Levitsky (1968) and is consistent, although less pronounced, with a meta-analyses of human (Shapleske et al. 1999) and chimpanzee (Hopkins and Nir 2010) studies (Fig. 3). Although the distribution of right-, left-, no-biased subjects is similar across species, the degree of PT asymmetry is smaller in baboons. The percentage difference of the raw surface area between the left and the right PT is 2 times smaller in baboons (6.5%) than previous meta-analysis in chimpanzees (12.6%) and humans (13.2%) (Hopkins and Nir 2010). This latter finding suggests that, across brain evolution, this leftward asymmetry may not only exist in the phylogeny of Catarrhini but also tends to increase with the emergence of Hominidae and the increase in brain volume. Whether this change in the degree of PT asymmetry is related to primate phylogeny or increase in brain volume remains unclear. For instance, we found an effect of the brain volume on the PT asymmetry, which is consistent with a previous study in great apes (Pilcher et al. 2001), but see Hopkins et al. (1998). Nevertheless, this latter brain volume hypothesis is questioned by the small change in the percentage difference of the left and right PT surface areas between chimpanzees and humans (0.6%) despite their large difference in brain volume (chimpanzee: approximately 300–400 cm^3 in chimpanzees vs. 1300 cm^3 in humans) (Josse et al. 2006; Hopkins et al. 2009). Moreover, PT asymmetry has been documented in both human infants and preterm (e.g., Dubois et al. 2010; Hill et al. 2010; Glasel et al. 2011; Li et al. 2014) who have much smaller brain than adults, supporting the hypothesis that brain size in humans does not condition the emergence of this structural asymmetry.

Interestingly, as revealed by the correlation analysis between raw surface areas and AQ, our results show that, contrary to what was reported in humans (Galaburda et al. 1987), PT asymmetry toward the left hemisphere appears to be driven by both the increase in the left PT surface area and the decrease in the right one. In contrast, similarly than in humans, the PT asymmetry toward the right hemisphere is driven only by the decrease in the left PT surface area. Indeed by reappraising Geschwind and Levitsky's data and running similar correlational analyses between AQ and side, Galaburda et al. (1987) showed that leftward asymmetry was driven by a decrease in the right PT size while rightward asymmetry was supported by a decrease in the left PT size (Galaburda et al. 1987). This differential contribution of side between species for left-biased individuals might be critical for the evolution of PT asymmetry and/or language. Further comparative studies across primate species on this specific phenomenon are needed to understand the dynamic of the evolution of the PT asymmetry among primates and the respective evolutionary contribution of the left and right PT regions. In addition, such structural asymmetry was present regardless of the age of the subject (Side x Age interaction not significant while the age range was large, baboons being aged from 2.4 to 26.6 years old), suggesting it appears very early in the development of the baboons. The early development of this brain feature suggests a potentially strong influence of genetic factors on this brain organization in baboons as it has been suggested in humans by similar reports in preterm and newborns (e.g., Dubois et al. 2010; Hill et al. 2010; Glasel et al. 2011; Li et al. 2014).

Is PT Asymmetry Unique to Baboons Among Old World Monkeys?

Since all Old World monkey species such as baboons and macaques share the same Catarrhini common ancestor with humans, one could question the phylogenetical hypothesis of the emergence of PT asymmetry in Catarrhini given this asymmetry was found absent in macaques (Gannon et al. 2008; Gannon 2010; Lyn et al. 2011). In those studies, its absence was interpreted to be the result of a lack of structural landmarks in monkeys that prevented reliable delineation of the PT. Considering the theory that brain lateralization arose from increased brain size (Ringo et al. 1994), it has also been suggested that lower gyrification and smaller brain size in the macaque might affect the visibility of structural asymmetries in this region (Gannon et al. 2008). In accordance with this hypothesis, given the baboon brain is not only on average 2 times larger than macaques but also has a larger degree of gyrification (folding) (Kochunov et al. 2010), these differences in brain anatomy might explain the discrepancy. In contrast to baboons, interhemispheric differences in the PT in macaques might thus be too subtle to be seen at the macrostructural level of the brain (Gannon 2010). Another potential explanation might be found in the difference of sample size. Robust sample sizes are usually needed for reliably evaluating asymmetry at the population-level. Studies in macaques were conducted on relatively small samples, which may have induced statistical limitations for inferring any population-level asymmetries. It is thus not excluded that this asymmetry might actually be present in Old World monkeys but might not be visible in most species with small brain size, unless investigated at the cellular level as suggested by a histological study in 6 *postmortem* macaque brains (Gannon et al. 2008). Indeed histological analyses might help evaluating such subtle differences in this region. While leftward Tpt cellular asymmetries correlated with PT surface asymmetries in humans (Galaburda et al. 1978), a similar trend emerged in nonhuman primates, including rhesus monkeys and chimpanzee, despite results reported are not always consistent (Buxhoeveden and Casanova 2000; Buxhoeveden et al. 2001; Gannon et al. 2008; Spocter et al. 2010). One potential reason for inconsistency might be the small sample of postmortem brains involved in those studies.

Conclusion

More than 45 years after the pioneering finding of Geschwind and Levitsky in humans (Geschwind and Levitsky 1968), research on PT asymmetry in primates continues to question what we know about the evolution of the brain and language. The present finding of such a common brain anatomical asymmetry between a monkey species and the Hominidae stands for redefining the evolutionary origins of the anatomical organization of this language area. If this brain feature exists in baboons, one could question the relationship between PT asymmetry and organization of language. Indeed this finding in a “nonlinguistic” primate species provides additional supports to the idea that the PT asymmetry is definitively not sufficient for language and might not be a robust marker of language specialization. This hypothesis does not necessary mean than this structural feature of the brain has nothing to do with language. For instance, one potential explanation is that this cortical feature in monkeys, chimpanzees and humans may be related by potential common intentional cognitive properties between language in humans and the gestural communicative system of nonhuman primates (e.g., in chimpanzees: Leavens et al. 2004; in baboons: Bourjade et al. 2014). Specifically, in chimpanzees, variation of the PT structural asymmetry has been found to be driven by the direction of manual asymmetry (left-handed vs. right-handed) for intentional communicative gestures exclusively (Hopkins and Nir 2010; Meguerditchian et al. 2012); indicating that such neuroanatomical feature might have something to do with social cognition including intentional gestures. Thus according to this hypothesis, variation of degree of social cognition between baboons and hominid species including humans would explain their difference of degree of leftward PT asymmetry. Does this cortical feature might then constitute a landmark of social cognition in primate? Further investigation need to be done to address this question.

Nevertheless, the PT asymmetry does not make the baboons have a language-ready brain. In fact, this hypothesis of a lack of neural circuitry enabling language and sophisticated vocal control in monkeys has recently be highlighted by the finding showing that anatomical constraints of the vocal apparatus are not enough to prevent the baboons and monkeys to produce vowels (Fitch et al. 2016; Boë et al. 2017). Similarly having a leftward PT asymmetry is not enough to allow the baboons to have language, despite their intentional gestural communicatory system. Nevertheless, it is now not excluded that some of the brain circuitry involved in language might already be present in the baboon brain and that the prerequisites of the structural hemispheric specialization for the PT might precede the emergence of Hominidae and date back even to the Catarrhini 30–40 million years ago.

Authors’ Contributions

D.M. and A.M. prepared the paper. D.M. performed the tracing and analyzed data. A.M. supervised the study and MRI acquisitions. K.M. was the second rater. W.D.H. expertised method of tracing. M.R. designed MRI sequences, B.N. designed the baboons’ monitoring programs, J.-L.A. supervised and coordinated the MRI sessions. R.L. and A.B. developed the specific procedures of welfare, anesthesia, and preparation of baboons in the MRI machine. S.A.L. participated to MRI acquisition, image preprocessing, and manuscript editing.

Supplementary Material

Supplementary data is available at *Cerebral Cortex* online.

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