



# Asymmetries in cerebral width in nonhuman primate brains as revealed by magnetic resonance imaging (MRI)

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## Abstract

A comparative study of asymmetries in cerebral width was conducted in a sample of great apes, Old World and New World monkeys. The brains of all subjects were scanned using magnetic resonance imaging (MRI) and the first axial slice above the third ventricle was identified. Measures of cerebral width were taken at distances of 10% and 30% of the length from the occipital and frontal poles. Cerebral widths were measured from the midline to the lateral surface of the brain for each area. The great apes exhibited a right-frontal and left-occipital directional asymmetry in cerebral width. In contrast, no significant mean directional asymmetries were found in either the Old or New World monkeys. The results in the great apes are consistent with previous reports of petalia asymmetries and suggest that the use of MRI is a valid approach to the assessment of neuroanatomical asymmetries in primates. © 2000 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

Neuroanatomical asymmetries in the human brain are thought to underlie the expression of specific behavioral or physiological functions. In humans, neuroanatomical asymmetries have been reported for length of the sylvian fissure, size of the planum temporale, size of the pars triangularis, and volume of the globus pallidus, among other neuroanatomical features [17]. The asymmetries in the peri-sylvian area are the most well documented in humans because of their functional association with language processing [7,8,26]. There has been considerable interest in the topic of nonhuman neuroanatomical asymmetries since the earliest reports of neuroanatomical asymmetries in humans. Several early reports indicated the presence of certain neuroanatomical asymmetries in nonhuman species but

were limited because of either incomplete brain tissue or small sample sizes [1,24]. Recently, neuroanatomical asymmetries have been reported in a host of animal species including rodents, cats, dogs, and nonhuman primates [2,5,10,11,18,22].

There have been two general approaches to the assessment of neuroanatomical asymmetries in nonhuman primates. One approach has been to directly measure volumes of brain regions or lengths of various fissures from either post-mortem tissue or endocasts. For example, Yeni-Komshian and Benson [27] compared the length of the sylvian fissure in the left and right hemispheres of rhesus monkey, chimpanzee and human cadaver brains and reported that the left sylvian fissure is longer than the right in humans and chimpanzees but not monkeys. In a more recent study, Heilbronner and Holloway [11] reported that macaques and squirrel monkeys exhibit longer left than right sylvian fissure length, a finding that contradicts the earlier observations of Yeni-Komshian and Benson. Falk and colleagues [3,6] have similarly measured

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fissure lengths in different primate species but they have taken their measurements from endocranial casts (i.e., endocasts) and not from actual brain tissue. The most consistent asymmetries have been reported in the frontal lobe where the sulcus principalis and lateral orbital sulcus were found to be longer in the right compared to the left hemisphere.

A second measure of overall brain asymmetry in human and nonhuman primates is petalia pattern. Petalias refer to anterior-posterior protrusions of one hemisphere compared to the other. In nonhuman primates, petalia asymmetries have largely been examined using endocasts while in humans petalia asymmetries have been measured using CT scans, X-rays and endocasts (see ref. [19] for review). The most common petalia asymmetry found in humans is a left-occipital, right-frontal bias. That is to say, the left hemisphere protrudes posteriorly further than the right hemisphere while the anterior portion of the right hemisphere protrudes further forward compared to the left hemisphere. LeMay [19] reported that great apes ( $n = 24$ ) exhibited left-occipital and right-frontal protrusions whereas Old ( $n = 21$ ) and New ( $n = 43$ ) World monkeys exhibited only the left-occipital protrusion. In contrast to LeMay [19], Falk et al. [6] reported a significantly higher proportion of right frontal petalia asymmetries but no asymmetries in petalia within the occipital lobe in a sample of rhesus monkey endocasts. In a subsequent study, Cheverud et al. [3], reported that the left-occipital was more prominent when accompanied by a right-frontal petalia in a sample of rhesus monkey endocasts.

Based on the published findings, different methodological approaches to measuring neuroanatomical asymmetries have produced, to some extent, different findings. For example, though studies of post-mortem tissue indicate that the sylvian fissure is longer on the left than right in great apes, the results in monkeys have been equivocal (i.e. [6,11]). One potential problem with the use of endocasts is that the posterior regions of the skull do not cast as well as the frontal region. This may result in measurement error. Therefore, the use of cadaver brains is preferable to the use of endocasts. But shrinkage of tissue in fixed post-mortem specimens could similarly result in measurement error. Moreover, the pragmatic limitations of obtaining post-mortem tissue, particularly for great ape brain specimens, precludes timely collection of large data sets.

Recent imaging technology, such as magnetic resonance imaging (MRI), offers a reasonable solution to some of the methodological problems associated with measuring brain asymmetry in primates [28]. Specifically, structural MRI is a non-invasive technique that can provide a detailed representation of neural structures in living organisms. Although not entirely free of its own drawbacks, MRI is advantageous compared

with endocasts and conventional post-mortem analyses for a number of reasons. First, shrinkage is not a factor in normal living tissue. Second, the ability to re-slice in different planes and measurement in both surface and internal anatomy provides a level of versatility not possible with either conventional post-mortem procedures or endocasts. Third, because MRI does not require euthanasia, anatomical measures can be potentially correlated with functional aspects of behavior within individuals.

In the current study, we report data on the presence of cerebral width asymmetries in great apes and monkeys using MRI. We have focused on measurements of cerebral width because the previous findings on petalia asymmetries in nonhuman primates allow us to generate specific hypotheses about our results. Specifically, if the petalia asymmetries in nonhuman primates are due to changes in the widths of the hemisphere then direct measurements of cerebral width should be consistent with reported petalia asymmetries. To date, no studies have directly measured cerebral widths from different regions of the brain in nonhuman primates for comparison to reported petalia asymmetries. Specifically, on the basis of reported right-frontal and left-occipital petalia asymmetries in great apes [19], we hypothesized that great apes would exhibit wider left posterior portions of the brain and wider right anterior brain regions. Likewise, Old and New World monkeys should exhibit wider left posterior portions of the brain but no width asymmetry in the anterior region.

## 2. Methods

### 2.1. Subjects

Magnetic resonance images (MRI) were collected in a sample of 19 adult great apes including nine chimpanzees (*Pan troglodytes*), four orangutans (*Pongo pygmaeus*), two gorillas (*Gorilla gorilla gorilla*) and four bonobos (*Pan paniscus*). Additionally, scans were collected in a sample of 15 adult Old World monkeys including nine rhesus monkeys (*Macaca mulatta*), two baboons (*Papio papio*) and four sooty mangabeys (*Cercocebus torquatus atys*) and eight adult New World monkeys including four capuchin (*Cebus apella*) and four squirrel (*Samiri sciureus*) monkeys. The distribution of sexes between taxonomic groups was eight females and 11 males (great apes), five females and 10 males (Old World monkeys) and three females and five males (New World monkeys). All subjects were housed at the Yerkes Regional Primate Research Center (YRPRC).

## 2.2. Procedure

Prior to transportation for scanning, the subjects were immobilized with ketamine injection (10 mg/kg) and subsequently anesthetized with propofol (10–20 mg/kg/h) following standard veterinary procedures used at the YRPRC. Subjects were then transported by van to the MRI facility at Emory University Hospital located about one mile from the YRPRC. The subjects remained sedated for the duration of the scans as well as the time needed for transport between YRPRC and Emory hospital (total time approximately 2 h). After completing the MRI, the nonhuman primate subjects were returned to Yerkes and temporarily housed in a single cage for 6–12 h to allow the effects of the anesthesia to wear off before being returned to their home cage and cagemates.

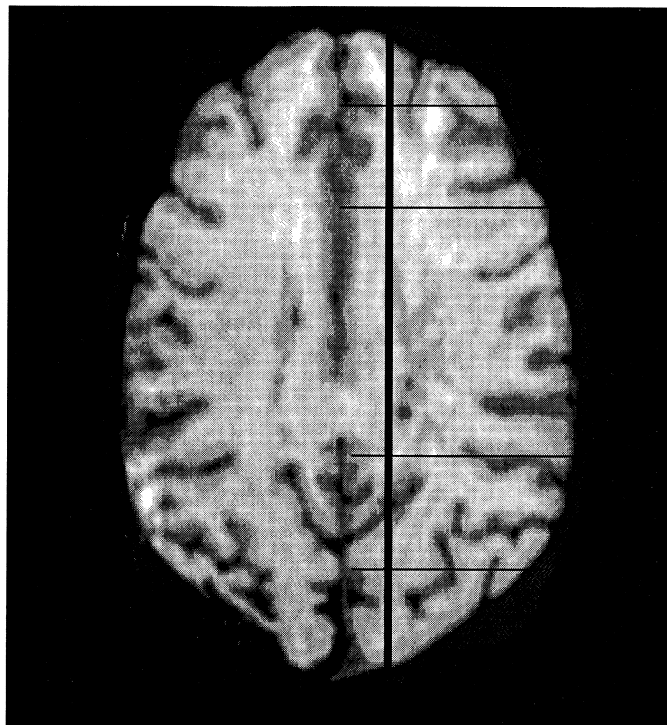
At the MRI facility, the animals were placed in the scanner chamber and their heads were fitted inside the head coil. This project involved using two MRI machines (Phillips, Model NT), each with 1.5-Tesla superconducting magnets, housed at Emory University hospital. For all subjects, T1-weighted images were collected in the axial plane using a gradient echo protocol (pulse repetition=19.0 ms, echo time=8.5 ms, slice thickness 1.2 mm, slice overlap=0.6 mm, number of signals averaged=8 and a  $256 \times 256$  matrix). These

scan parameters were based on preliminary studies and provided excellent resolution of the brain areas of interest. The archived data were stored on optical diskettes and transported to a Sun Sparc work station for post-image processing.

## 2.3. Measurement of cerebral width

In order to measure cerebral width and length, the MRI scans were aligned along the midline in the coronal and axial planes and along the anterior-posterior commissure in the sagittal plane. Following the procedure of Kertesz et al. [16] with humans, the scans were reformatted and “cut” in the axial plane in 1 mm slices. The first axial slice above the third ventricle was identified and the length of each hemisphere was determined by measuring from the frontal to the occipital pole, 5 mm lateral to the midline. Midline was defined by placing a point in the middle of the interhemispheric cleft at the frontal and occipital poles and connecting a straight line between these points. Four regional width measurements were taken corresponding to 10% and 30% of the length from the frontal and occipital pole within each hemisphere. These were collectively referred to as the anterior-frontal (10% from frontal pole), posterior-frontal (30% from the frontal pole), parietal (30% from occipital pole)

## Axial View of Brain for Cerebral Width Measure



Anterior Frontal

Posterior-Frontal

Parietal

Occipital

Fig. 1. Axial view of chimpanzee brain from MRI scan.

and the occipital lobe (10% from occipital pole). Widths were measured from the midline to the lateral surface of the brain (in tenths of a mm). Intra-rater reliability was assessed in 25% of the sample by one of the investigators who was blind to both the subject and orientation of the hemispheres (left or right). The test-retest correlation coefficients for the right-frontal, right-occipital, left-frontal and left-occipital widths were 0.975, 0.978, 0.988, and 0.996, respectively. Inter-rater reliability was obtained for 25% of the sample from the two investigators whom, though not blind to subject and hemispheric orientation, made their measurements independently of each other. The inter-rater reliability correlation coefficient for the sample was 0.976. An illustration of the axial view of a chimpanzee MRI scan can be seen in Fig. 1. For each subject and region, an asymmetry quotient (AQ) was derived following the formula  $[AQ = ((R - L / R + L) * 0.5)]$ . This formula took into account variation in brain size as a potential covariate in the magnitude of asymmetry. Positive AQ values reflected a rightward bias and negative values reflected a leftward bias. The absolute value of the AQ score reflected the magnitude of the bias. The AQ data were analyzed using parametric statistics (*t*-tests, repeated measures analysis of variance).

### 3. Results

Depicted in Table 1 are the individual AQ data for each region and subject in the entire sample. The mean AQ score for each taxonomic group and measured brain area of interest can be seen in Fig. 2. To assess the pattern of asymmetries, one-sample *t*-tests were conducted for each brain region and taxonomic group (see Fig. 2). In the great apes, the left occipital lobe was significantly wider than the right,  $t(18) = -3.43$ ,  $p < 0.01$ , and the right anterior-frontal lobe was significantly wider than the left,  $t(18) = 2.94$ ,  $p < 0.05$ . Also, the left parietal lobe was wider than the right,  $t(18) = -1.83$ ,  $p < 0.10$ , and the right posterior-frontal region was wider than the left, but both of these effects achieved borderline significance,  $t(18) = 2.05$ ,  $p < 0.07$ . In the Old World monkeys, no significant left-right differences in width were evident for the anterior-frontal  $t(14) = -0.14$ ,  $p > 0.10$ , posterior-frontal  $t(14) = 0.81$ ,  $p > 0.10$ , parietal  $t(14) = 1.38$ ,  $p > 0.10$  and occipital regions  $t(14) = -0.80$ ,  $p > 0.10$ . In the New World monkeys, the right occipital  $t(7) = 2.24$ ,  $p < 0.08$  and right posterior-frontal  $t(7) = 1.99$ ,  $p < 0.08$  regions were wider than the left counterpart, but these effects were marginally significant. For the anterior-frontal  $t(7) = -0.62$ ,  $p > 0.10$  and parietal  $t(7) = -0.62$ ,  $p > 0.10$  regions, no significant directional biases were found. Within each taxonomic group, independent

sample *t*-tests failed to reveal significant sex differences in asymmetry for any brain region.

In addition, the cerebral width data within each taxonomic group were analyzed using a one-way

Table 1

Individual asymmetry quotient (AQ) data for each brain region and subject in the sample<sup>a</sup>

Common		Hemispheric region			
Family name	Sex	AF	PF	PAR	OCCP
<i>Cebidae</i>					
Capuchin	Male	0.143	0.063	0.014	-0.012
Capuchin	Male	-0.161	0.015	-0.046	-0.063
Capuchin	Female	0.060	0.000	-0.021	0.026
Capuchin	Female	0.034	0.000	0.058	0.033
Squirrel	Male	0.032	-0.015	0.036	0.101
Squirrel	Male	-0.142	0.007	0.041	0.149
Squirrel	Male	-0.049	0.026	0.007	0.075
Squirrel	Female	0.066	0.085	0.052	0.091
<i>Cercopithecidae</i>					
Mangabey	Male	0.242	0.129	-0.032	-0.115
Mangabey	Male	0.025	-0.021	-0.013	-0.068
Mangabey	Male	-0.008	0.005	-0.009	-0.079
Mangabey	Female	0.035	-0.017	0.026	0.026
Baboon	Male	0.000	0.066	0.007	-0.073
Baboon	Male	-0.082	-0.027	-0.082	-0.132
Rhesus	Male	-0.008	0.005	-0.009	-0.079
Rhesus	Male	-0.047	-0.009	0.036	0.025
Rhesus	Male	-0.122	-0.093	0.028	0.011
Rhesus	Male	-0.048	0.079	0.020	-0.046
Rhesus	Female	-0.026	-0.038	0.000	0.055
Rhesus	Female	-0.062	0.000	0.045	-0.011
Rhesus	Male	-0.053	0.072	0.077	0.136
Rhesus	Female	0.045	0.040	0.039	0.068
Rhesus	Male	0.065	-0.021	0.079	0.053
<i>Pongidae</i>					
Bonobo	Male	0.033	0.021	-0.016	-0.046
Bonobo	Female	0.129	0.030	-0.026	-0.033
Bonobo	Female	0.078	0.047	-0.005	0.027
Bonobo	Male	0.114	-0.049	-0.015	-0.025
Chimpanzee	Male	0.104	0.086	0.036	-0.043
Chimpanzee	Male	0.030	0.010	-0.058	-0.019
Chimpanzee	Male	0.074	0.080	-0.037	-0.018
Chimpanzee	Female	0.041	0.076	-0.048	-0.080
Chimpanzee	Female	0.035	0.030	-0.007	-0.034
Chimpanzee	Male	0.008	0.024	0.039	-0.011
Chimpanzee	Female	0.040	0.040	-0.054	-0.081
Chimpanzee	Female	0.022	0.052	0.034	-0.137
Chimpanzee	Male	-0.074	-0.103	-0.094	-0.180
Gorilla	Male	0.048	0.005	0.027	-0.090
Gorilla	Female	-0.087	-0.025	-0.018	-0.061
Orangutan	Male	0.038	0.017	0.005	0.048
Orangutan	Female	0.065	0.068	0.027	0.073
Orangutan	Male	0.033	0.021	-0.016	-0.046
Orangutan	Male	-0.031	-0.022	-0.077	-0.145

<sup>a</sup> AF — anterior frontal, PF — posterior frontal, PAR — parietal lobe, OCCP — occipital lobe. For each subject and region, an asymmetry quotient (AQ) was derived following the formula  $[AQ = ((R - L / R + L) * 0.5)]$ . Positive AQ values reflected a rightward bias and negative values reflected a leftward bias. The absolute value of the AQ score reflected the magnitude of the bias.

repeated measures analysis of variance. Brain region served as the repeated measure variable. For this analysis, in the great apes, a significant interaction was found between asymmetry in cerebral width and region  $F(3,54)=18.62$ ,  $p < 0.001$ . Post-hoc analyses using Bonferroni corrected correlated  $t$ -tests indicated that cerebral width of the occipital lobe differed significantly from the anterior-frontal  $t(18)=6.24$ ,  $p < 0.001$  and posterior-frontal  $t(18)=5.06$ ,  $p < 0.001$  measures. Additionally, the width of the parietal lobe differed significantly from the width of the anterior  $t(18)=4.20$ ,  $p < 0.002$  and posterior  $t(18)=3.67$ ,  $p < 0.002$  portions of the frontal lobe. No difference in widths were found between the two anterior regions (anterior and posterior frontal lobe) and the two posterior regions (parietal and occipital lobe). No significant differences were found in cerebral width for either the Old World or New World monkeys. Descriptively, in 13 of the 19 great apes, the right frontal lobe was wider than the left and the left occipital lobe was wider than the right. In contrast, only two of the 15 Old World monkeys and one of the eight New World monkeys showed this pattern of width differences in both the frontal and occipital lobe.

#### 4. Discussion

The results of this study are the first to quantitat-

ively confirm that great apes possess both a significantly wider right than left frontal lobe and a significantly wider left than right occipital lobe. Furthermore, no significant directional asymmetries in cerebral width were found for either Old or New World monkeys. The present findings in monkeys are not consistent with the endocast data reported by Falk and her colleagues [3,6] nor the petalia data presented by LeMay [19]. One reason for the discrepancy between the present findings and those of Falk et al. [6] may be that our sample size was relatively small compared with that of Falk et al. [6]. Based on the data presented in Fig. 2 showing a nonsignificant trend toward a left-occipital lobe bias, at least in the Old World monkeys, it may be that our failure to find a significant leftward-occipital asymmetry is due to insufficient statistical power. A second reason for the discrepancy between the present findings and Falk et al. [6] may be the fact that in the present study cerebral width was measured in the central region of the brain (i.e., the first axial slice above the third ventricle) whereas Falk et al. [6] measured cerebral width from endocasts and were therefore limited to surface features. The magnitude of difference in cerebral width may be greater on the surface of the brain compared to the central portion. This possible explanation warrants further investigation.

In contrast to the results with the Old and New World monkeys, the present results for great apes are

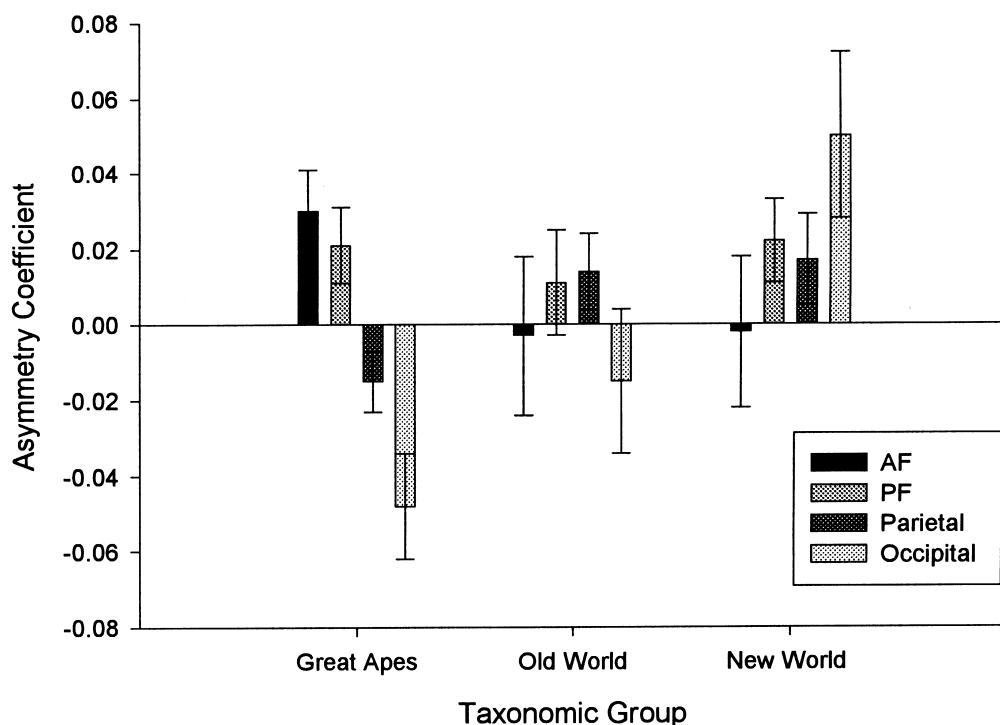


Fig. 2. Mean and (standard error) AQ values for each taxonomic group and brain region. Negative values reflect a left hemisphere bias and positive values reflect right hemisphere bias. The absolute values reflect the magnitude of bias.

consistent with the petalia asymmetries reported by LeMay [19] and are consistent with cerebral width asymmetries in humans as reported by Kertesz et al. [16] using the same procedures. Taken together, these results suggest that these petalia asymmetries are manifestations of the position and rotation of the cerebral cortex within the skull.

The functional significance of the greater left occipital width and right frontal width remains unclear. A preliminary analysis of the correlation between hand preference in apes and the cerebral width measures taken in this study failed to reveal a significant association [13]. Notwithstanding, the general pattern of neuroanatomical asymmetries observed in the apes compared to the Old World and New World monkeys is consistent with recent reports on hand preference in these taxonomic families. For at least some measures of hand preference, such as bipedal reaching [25] and coordinated bimanual actions [4,12,23,24], great apes are more right-handed compared to the other taxonomic families. Thus, at one level of analysis, functional differences in asymmetry appear to map onto neuroanatomical differences but this conclusion assumes that differences among species in the direction of hand preference are indeed real rather than an artifact of certain testing circumstances or situations. McGrew and Marchant [20] have recently argued that there is no compelling evidence that hand preferences in nonhuman primates resemble hand preferences in humans based on a meta-analysis of the existing data. One limitation of the meta-analysis performed by McGrew and Marchant [20] was that it was executed only on studies that met a number of a priori assumptions and arbitrary criteria and therefore a number of studies which directly challenged their position were excluded from the analysis. In addition, many of the criteria and assumptions that McGrew and Marchant [20] used for their meta-analysis can be questioned on theoretical and empirical grounds [14]. For example, McGrew and Marchant [20] argue that only humans show consistent hand preferences across multiple measures of hand preference (i.e., true handedness) while nonhuman hand preference is task specific. The suggestion that humans show the same hand preferences on all tasks is not supported by the evidence [14]. To more definitively resolve these issues, what is needed are studies which attempt to directly correlate functional and neuroanatomical asymmetries in the same individuals.

Additionally, we can speculate that the asymmetries evident in the present great ape sample may reflect similar processes to those that have led to recent findings of posterior temporal lobe, and specifically, planum temporale, asymmetries in great apes [9,15]. Consistent with this hypothesis is the lack of significant cerebral width patterns in the present Old and

New World monkey sample and the finding of no posterior temporal lobe asymmetry patterns in monkeys similar to those in great apes [9,15].

In conclusion, the results of the present study indicate that, in great apes, the right frontal lobe is wider than the left and the left occipital lobe is wider than the right. Old and New World monkeys did not show any consistent directional biases in cerebral width. Based on the high image quality, sensitivity in measurement and application to a wide range of non-human primate species, the use of structural MRI for further comparative study of neuroanatomical asymmetries in primates appears to have much potential. Moreover, the application of MRI to quantitative studies of comparative brain anatomy may offer new insights into phylogenetic changes in the organization of the central nervous system (e.g., [21]) that have not been adequately studied.

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### References

- [1] Bailey P, Bonin VG, McCulloch WS. The isocortex of the chimpanzee. Urbana, IL: Illinois University Press, 1950.
- [2] Bradshaw J, Rogers LJ. The evolution of lateral asymmetries, language, tool use and intellect. San Diego: Academic Press, 1993.
- [3] Cheverud JM, Falk D, Hildebolt C, Moore AJ, Helmkamp RC, Vannier J. Heritability and association of cortical petalia in rhesus monkeys (*Macaca mulatta*). *Brain, Behavior, and Evolution* 1990;35:368–72.
- [4] Colell M, Segarra MD, Sabater Pi J. Manual laterality in chimpanzees (*Pan troglodytes*) in complex tasks. *Journal of Comparative Psychology* 1995;109:298–307.
- [5] Diamond MC. Age sex and environmental influences. In: Geschwind NA, Galaburda Am, editors. *Cerebral dominance: the biological foundations*. Cambridge: Harvard University Press, 1984. p. 134–307.
- [6] Falk D, Hildebolt C, Cheverud J, Vannier M, Helmkamp RC,

- Konigsberg L. Cortical asymmetries in the frontal lobe of rhesus monkeys (*Macaca mulatta*). *Brain Research* 1990;512:40–5.
- [7] Galaburda AM. Anatomical asymmetries. In: Geschwind NA, Galaburda AM, editors. *Cerebral dominance: the biological foundations*. Cambridge, MA: Harvard University Press, 1984. p. 11–25.
- [8] Galaburda AM. Anatomic basis of cerebral dominance. In: Davidson RJ, Hugdahl K, editors. *Brain asymmetry*. Cambridge, MA: MIT Press, 1995. p. 51–73.
- [9] Gannon PJ, Holloway RL, Broadfield DC, Braun AR. Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area homolog. *Science* 1998;279:220–2.
- [10] Groves CP, Humphrey NK. Asymmetry in gorilla skulls: evidence of lateralized brain function? *Nature* 1973;244:53–4.
- [11] Heilbronner PL, Holloway RL. Anatomical brain asymmetries in New World and Old World monkeys. Stages of temporal lobe development in primate evolution. *American Journal of Physical Anthropology* 1988;76:39–48.
- [12] Hopkins WD. Hand preferences for coordinated bimanual actions in 110 chimpanzees (*Pan troglodytes*): cross-sectional analysis. *Journal of Comparative Psychology* 1995;109:291–7.
- [13] Hopkins WD. Chimpanzee and human handedness: analogous or homologous processes? Paper presented at the annual meeting of the International Society of Primatology, Madison, Wisconsin (August), 1996.
- [14] Hopkins WD. On the other hand: Statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *International Journal of Primatology*, (in press).
- [15] Hopkins WD, Marino L, Rilling JK, MacGregor L. Planum temporale asymmetries in great apes as revealed by magnetic resonance imaging (MRI). *NeuroReport* 1998;9:2913–8.
- [16] Kertesz A, Black SE, Polk M, Howell J. Cerebral asymmetries on magnetic resonance imaging. *Cortex* 1986;22:117–27.
- [17] Kolb B, Whishaw IQ. *Fundamentals of human neuropsychology*. New York: Freeman, 1993.
- [18] Kolb B, Sutherland RJ, Nonneman AJ, Whishaw IQ. Asymmetry of the cerebral hemispheres of the rat, mouse, rabbit and cat: the right hemisphere is larger. *Experimental Neurology* 1982;78:348–59.
- [19] LeMay M. Asymmetries of the brains and skulls of nonhuman primates. In: Glick SD, editor. *Cerebral lateralization in nonhuman species*. New York: Academic Press, 1985. p. 223–45.
- [20] McGrew WC, Marchant LF. On the other hand: Current issues in and meta-analyses of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology* 1997;40:201–32.
- [21] Semendeferi K, Damasio H, Frank R, Van Hoesen GW. The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. *Journal of Human Evolution* 1997;32:375–88.
- [22] Tan U, Kutlu N. The end point of the sylvian fissure is higher on the right than the left in cat brain as in human brain. *International Journal of Neuroscience* 1993;268:11–7.
- [23] Westergaard GC, Suomi SJ. Hand preference for a bimanual task in tufted capuchin (*Cebus apella*) and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology* 1996;110:406–11.
- [24] Westergaard GC, Champoux M, Suomi SJ. Hand preferences in infant rhesus macaques. *Child Development* 1997;68:387–93.
- [25] Westergaard GC, Kuhn HE, Suomi SJ. Bipedal posture and hand preference in humans and other primates. *Journal of Comparative Psychology* 1998;112:55–64.
- [26] Witelson S. Anatomic asymmetry in the temporal lobe: its documentation, phylogenesis and relationship to functional asymmetry. *Annals of the New York Academy of Sciences* 1977;299:328–54.
- [27] Yeni-Komshian G, Benson D. Anatomical study of cerebral asymmetry in the temporal lobe of humans, chimpanzees and monkeys. *Science* 1976;192:387–9.
- [28] Zilles K, Dabringhaus A, Geyer S, Amunts K, Qu M, Schleicher A, Gilissen E, Schlaug G, Steinmetz H. Structural asymmetries in the human forebrain and the forebrain of nonhuman primates and rats. *Neuroscience and Biobehavioral Reviews* 1996;20:593–605.