

Cerebral volumetric asymmetries in non-human primates: A magnetic resonance imaging study

Dawn L. Pilcher

Yerkes Regional Primate Research Center, Atlanta, USA

Elizabeth A.D. Hammock

Emory University, Atlanta, USA

William D. Hopkins

Yerkes Regional Primate Research Center, Atlanta, and Berry College, Rome, USA

Magnetic resonance images (MRI) were collected in a sample of 23 apes, 14 Old World monkeys, and 8 New World monkeys. The total area or volume of the anterior and posterior cerebral regions of each hemisphere of the brain was measured. The results indicated that a rightward frontal and leftward occipital pattern of asymmetry was present at a population level in the great ape sample. Population-level cerebral asymmetries were not revealed in the sample of New or Old World monkeys. The total area or volume of the planum temporale, which was localised only in the great apes, was also measured in both hemispheres. A leftward planum temporale asymmetry was evident at the population level in the great apes. It was hypothesised that the rightward frontal and leftward occipital asymmetries would correlate with leftward planum temporale asymmetries. This hypothesis was based on the assumption that, similar to development of the human brain, the non-human primate brain “torques” during development due to a growth gradient which progresses anterior to posterior, ventral to dorsal, and right to left. The results of this study confirmed the predicted relationship between cerebral volume and the planum temporale asymmetries. This supports the hypothesis that the great ape brain may develop in a “torquing” manner, producing similar anatomical asymmetries as reported in humans.

Address correspondence to Dr William Hopkins, Division of Psychobiology, Yerkes Primate Research Center at Emory University in Atlanta, Georgia 30329, USA. Email: Ircbh@rmy.emory.edu or whopkins@berry.edu

This work was supported in part by NIH grants RR-00165, NS-29574, NS-36605, and HD-38051. Significant proportions of the MRI scans were collected during many hours of dedication from Drs Jim Rilling, Tom Insel, and Lori Marino. Special thanks are also directed to Brent Swenson and the rest of the vet staff for assisting in the care of the animals during scanning.

The relationship between neuroanatomy and behaviour in humans has been of scientific interest for over a century. Early discovery of language-related neuroanatomical asymmetries and the unique capability of the left hemisphere to organise linguistic information are what began the burgeoning field of neuropsychology (Eggert, 1977; Geschwind & Levitsky, 1968; Goodglass & Quadfasel, 1954; Wada & Rasmussen, 1960). The left hemisphere's capacity for the storage and processing of language has been associated with specific volumetric and indirect cortical measures of the posterior temporal region. The region of the pars triangularis, pars opercularis, and planum temporale are larger in the left compared to the right hemisphere (Foundas et al., 1996; Geschwind & Levitsky, 1968; Penhune, Zatorre, MacDonald, & Evans, 1996). Structures such as Heschl's gyrus, which is more pronounced in the left than the right hemisphere, and the Sylvian fissure, which is longer in the left than the right hemisphere, are also evidence of the distinct anatomy of this language-dominant cerebral hemisphere (Campain & Minckler, 1976; Leonard, Puranik, Kuldau, & Lombardino, 1998; Rubens, Mahowald, & Hutton, 1976; Yeni-Komshian & Benson, 1976).

Asymmetries of the planum temporale and sulci in the temporal region have been reported in the human brain as early as 29 weeks of gestation. Chi, Dooling, and Gilles (1977a, b) reported that in over half of their subjects (foetuses between 10 and 44 weeks gestation) the left planum temporale was larger than the right. It was also reported that the right central sulcus, the right superior temporal gyrus, and the right superior frontal gyrus appear one to two weeks before those on the left hemisphere of the fetal brain (Chi et al., 1977a, b). The temporal course of cerebral development that creates these hemispheric asymmetries, which reportedly occurs within the last trimester, seems to follow a consistent pattern in humans (Chi et al., 1977a, b).

Until recently, it was assumed that neuroanatomical asymmetries were traits unique to humans and directly associated with language acquisition. Brain asymmetries in non-human primates were reported more than 100 years after lateralisation in humans was discovered when Groves and Humphrey (1973) observed a leftward asymmetry in the length of the skull for a sample of mountain gorillas. Yeni-Komshian and Benson (1976) were the first to report neuroanatomical asymmetries by directly measuring the sulci of the non-human primate brain. The length and direction of lateral fissures have been used as a quantitative measure for inferring three-dimensional asymmetry in cerebral size and shape of both human and non-human primates. Formalin-fixed brain specimens are often used to measure lateral morphological asymmetries, such as sulci and petalia. Yeni-Komshian and Benson (1976) reported that the length of the Sylvian fissure (SF), which was measured from the brains of 25 chimpanzees (*Pan troglodytes*) and 25 rhesus monkeys (*Maccaca mulatta*), was longer in the left than right hemisphere for 80% of the chimpanzee sample, but only 44% of the rhesus sample. In contrast, when Heilbronner and Holloway (1988) measured

the length of the SF in 96 formalin-preserved brains of five species of Old and New World monkeys, four species displayed significant left population-level asymmetry (rhesus monkeys, *Macaca mulatta*; long-tail monkeys, *Macaca fascicularis*; cotton-top tamarins, *Saguinus oedipus*; and marmosets, *Callithrix jacchus*). The sample of squirrel monkeys (*Saimiri sciureus*) did not display any asymmetry in the SF (Heilbroner & Holloway, 1988). Furthermore, when petalia asymmetries of 17 chimpanzee brain specimens were scored from photographs, 11 subjects had a wider left than right occipital petalia and 6 had a wider right occipital region (LeMay, 1976).

Latex casts of the braincase (endocasts) have also been used to measure lateral surface asymmetries of the brain. Holloway and DeLa Coste-Lareymondie (1982) ordinally scored (leftward, rightward, or no asymmetry) the frontal and occipital petalia from the endocasts of gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and orangutans (*Pongo pygmaeus*). Petalia asymmetries in the occipital pole were reported for 91 of 135 great apes, with 65 having a left hemisphere bias (Holloway & DeLa Coste-Lareymondie, 1982). Asymmetries in the frontal pole were reported for 65 of 135 great apes, with 53 exhibiting a right hemisphere bias (Holloway & DeLa Coste-Lareymondie, 1982). The occurrence of a combined right frontal and left occipital petalia asymmetry was reported in only 34 of 135 of the great apes (Holloway & DeLa Coste-Lareymondie, 1982). Another study reported that when measuring the central sulcus, rectus principal, and lateral orbital sulcus of 335 rhesus monkey endocasts, an elongated and rightward orbital and dorsolateral frontal lobe was present (Falk et al., 1990).

To date, the evidence of neuroanatomical asymmetries in sulci and petalia is relatively consistent among samples of great apes, while the evidence in Old and New World monkeys is inconsistent (see Table 1 for a review of the relevant literature on neuroanatomical asymmetries in non-human primates). This issue is important because the differences in neuroanatomical asymmetries may reflect phylogenetic discontinuity in the brain organisation of primates. Differences in methodology, however, preclude any direct comparison. For example, difficulty locating the median border of smaller brains, poor casting of the occipital region in endocasts (Falk, 1987; LeMay, Billig, & Geschwind, 1982), and difficulty identifying sulcal endpoints due to shrinkage caused by chemical preservation (Heilbroner & Holloway, 1988; Falk, 1986) may influence measurement of asymmetries in some species and not others. With the development of imaging technologies, particularly magnetic resonance imaging (MRI), procedural differences can be minimised as a potential confounding source of between-species variation in morphological asymmetries (Hopkins & Marino, 2000; Hopkins, Marino, Rilling, & MacGregor, 1998; Hopkins & Rilling, 2000; Rilling & Insel, 1998).

The primary focus of this study was to investigate the applicability of the Lateralised Neuroembryologic Gradient Hypothesis (LNGH) proposed in human

TABLE 1
Studies that investigated neuroanatomical asymmetries in nonhuman primates

<i>Author(s)</i>	<i>Species/Method</i>	<i>Results</i>
<i>Great Apes</i>		
Groves & Humphrey (1973)	21 mountain gorillas/skull length	left half of skull longer
Gannon et al. (1998)	18 chimpanzee cadavers/PT area	larger left PT
Hopkins et al. (1998)	21 apes MRI/PT volume	larger left PT
Hopkins & Marino (2000)	19 chimpanzees MRI/frontal & occipital width	leftward occipital; rightward frontal
Holloway & De La Coste-Lareymondie (1982)	135 ape endocasts/qualitative score of petalias	65 leftward, 26 rightward occipital; 53 rightward, 12 leftward frontal petalia
LeMay (1976)	28 great ape cadaver photos/occipital petalia and width	rightward occipital petalia; leftward width
Zilles et al. (1996)	9 chimpanzee cadavers/differences in chimerics of hemispheric petalias	no differences in petalias
Yeni-Komishan & Benson (1976)	25 chimpanzee cadavers/SF length	left SF longer
<i>NW and OW Monkeys</i>		
LeMay (1976)	9 NW and 21 OW monkey cadaver photos/occipital petalia, occipital width	no differences in petalia; leftward occipital width in OW monkeys
Hopkins & Marino (2000)	8 NW and 15 OW monkeys MRI/frontal and occipital width	no differences in occipital or frontal width
Falk et al. (1990)	335 rhesus endocasts/sulci length	right rectus longer, left central sulcus longer, right orbital sulcus longer, no difference in length of SF
Falk (1978)	88 endocasts of 8 genera of OW monkeys/sulci length	right SF and right STS longer
Falk et al. (1986)	10 rhesus endocasts, CT/SF length	left SF longer
Yeni-Komishan & Benson (1976)	25 rhesus cadavers/SF length	no differences in SF
Heilbronner & Holloway (1988)	20–30 of 4 species monkey cadavers/SF length	left SF longer

PT = Planum Temporale; MRI = Magnetic Resonance Imaging; SF = Sylvian Fissure; STS = Superior Temporal Sulcus; OW = Old World; NW = New World.

studies to explain left-occipital and right-frontal volumetric asymmetries found in non-human primates. This hypothesis suggests that the brain develops in an anterior–posterior, ventral–dorsal and right–left direction (Best, 1988), which allegedly accounts for rightward frontal and leftward occipital asymmetries. To test the applicability of the LNGH in non-human primates, we adopted the procedures developed for human subjects to measure right and left cerebral volumetric asymmetries for the frontal and occipital regions (Weinberger, Luchins, Morihisa, & Wyatt, 1981). In addition, volumetric measures of the planum temporale were used from a previous study of the same sample of apes to correlate with the cerebral volume measures (Hopkins et al., 1998). Specifically, Hopkins et al. (1998) reported that, with the use of MRI, great apes show a population-level leftward asymmetry in the volume of the planum temporale, a finding consistent with other studies that used non-human primate cadaver specimens (Gannon, Holloway, Broadfield, & Braun, 1998). If the torquing of the developing brain results in a rightward frontal and leftward occipital pattern of asymmetry, it is predicted that this pattern will correlate with a resulting leftward planum temporale asymmetry. This hypothesis was tested by correlating PT volume with cerebral volume from each of the regions of interest.

METHOD

Subjects

Magnetic resonance images were collected in a sample of 23 lesser and great apes, which included 9 chimpanzees (*Pan troglodytes*), 4 orangutans (*Pongo pygmaeus*), 2 gorillas (*Gorilla gorilla*), 4 bonobos (*Pan paniscus*), and 4 gibbons (*Hylobates lar*). MRI scans were also collected from 14 Old World monkeys, which included 8 rhesus monkeys (*Macaca mulatta*), 2 baboons (*Papio papio*), and 4 mangabeys (*Cercocebus torquatus atys*), and 8 New World monkeys, which included 4 capuchin (*Cebus apella*) and 4 squirrel monkeys (*Samiri sciureus*) monkeys. These subjects were members of a captive colony that is maintained at the Yerkes Regional Primate Research Center (YRPRC) in Atlanta, Georgia, USA. The distribution of sex within each family was 10 females and 9 males for the great apes (*Pongidae*), 2 females and 2 males for the lesser apes (*Hylobatidae*), 3 female and 5 male New World monkeys (*Cebidae*), and 5 females and 9 males for the Old World monkeys (*Cercopithecidae*).

Procedure

The subjects were first immobilised by ketamine injection (10mg/kg) and subsequently anaesthetised with propofol (40–60 mg/kg/h) following standard procedures at YRPRC. Subjects were transported by van to the MRI facility at Emory University Hospital. The subjects remained anaesthetised for the duration of the scans as well as the time needed to travel between YRPRC and Emory

Hospital (total time ~ 2 h). At the MRI facility, apes were placed in the scanner chamber with their head fitted inside the head coil while monkeys were placed with their head fitted inside the knee coil. Scan duration, a function of brain size, was approximately 40 to 80 minutes. This project involved using two MRI machines (Phillips, Model 51), each with 1.5-Tesla super conducting magnets. For all subjects, T1-weighted images were collected in the transverse plane using a gradient echo protocol (pulse repetition = 19.0 ms, echo time = .6 mm, number of signals averaged = 8 and a 256×256 matrix). These scan parameters were used based on preliminary studies and provided excellent resolution of the brain areas of interest to this study. After completing MRI procedures, the subjects were returned to YRPRC and temporarily housed in a single cage for 6–12 h to allow the effects of the anaesthesia to wear off, after which they were returned to their home cage. The archived data were stored on optical diskettes and transported to a Sun Sparc work station and YRPRC for post-image processing. The scans were aligned in the coronal, sagittal, and transverse planes and cut into 1 mm coronal slices using multiplanar reformatting software (Easy Vision). A mouse-driven computer-guided cursor was used to measure volume of the defined regions. Measurements were made using NIH-Image developed for use in the Windows platform (Scion Corporation, Frederick, Maryland).

Cerebral volume measurement

The methodology used in humans by Weinberger et al. (1981) was followed for measurement of volumetric cerebral asymmetries. Using Easy Vision multiplanar reformatting software, the brain was aligned in the coronal, sagittal, and transverse planes and cut into 1 mm frontal and occipital coronal slices using the following landmarks. The first sagittal section that displayed the genu of the corpus callosum identified the posterior border of the frontal region. Identifying the sagittal midpoint between the posterior border of the corpus callosum (splenium) and the lateral surface of the occipital pole (Figure 1) approximated the anterior border of the occipital region. Subcortical structures, such as the cerebellum, were not included in cerebral volumetric measures. The frontal and occipital regions were traced with an area tool in successive 1 mm coronal slices (in tenths of mm; see Figure 2). The total number of slices in each region was divided equally to distinguish anterior and posterior regions of the frontal and occipital lobes. If the region had an un even number of slices, an additional slice was added to the outer poles, or the anterior frontal region and the posterior occipital region. Dividing these regions allowed for two measurements of the frontal and occipital regions. The area measures from each coronal image within a hemisphere were summed to derive a volumetric estimate of the anterior frontal (frontal1), posterior frontal (frontal2), anterior occipital (posterior1) and posterior occipital (posterior2) regions. Inter-rater reliability was assessed for the volume of the four regions of the left and right hemispheres for 10 subjects.

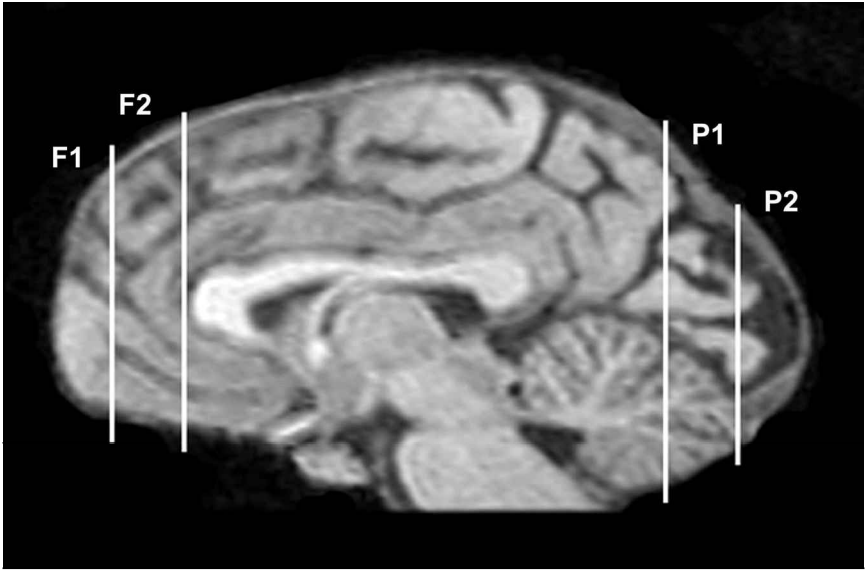


Figure 1. Sagittal view of a common chimpanzee MRI scan that specifies the parameters used during cerebral volumetric measures. The white lines indicate the borders of frontal1 (F1), frontal2 (F2), posterior1 (P1), and posterior2 (P2).

The two raters were blind to the orientation of the brain and region of assessment. The inter-rater correlation coefficients for the left and right hemispheres were .981 and .994, respectively.

PT measurement

PT measures were used from a study completed by Hopkins et al. (1998). Although PT measures from both the coronal and sagittal plane were collected, only coronal measures were used in this study to maintain a consistent plane in the assessment of asymmetries in the cerebral hemispheres. On successive 1 mm coronal slices, two raters determined the presence or absence of Heschl's gyrus (HG) in the left and right cerebral hemispheres. The HG could not be identified in the New or Old World monkeys, therefore these subjects were not included in PT analyses. If the HG was present, then the area measures were taken following the procedures of Larsen, Hoein, Lundberg, and Odegaard (1990) in which the depth of the Sylvian fissure was measured from the surface of the brain to lateral portion of HG (in tenths of mm). Summing the width measures of the PT from each slice within a hemisphere derived an estimate of total area. This value was added to the number of slices, in which HG could be identified within a hemisphere, to derive an estimate of the PT volume for each hemisphere.

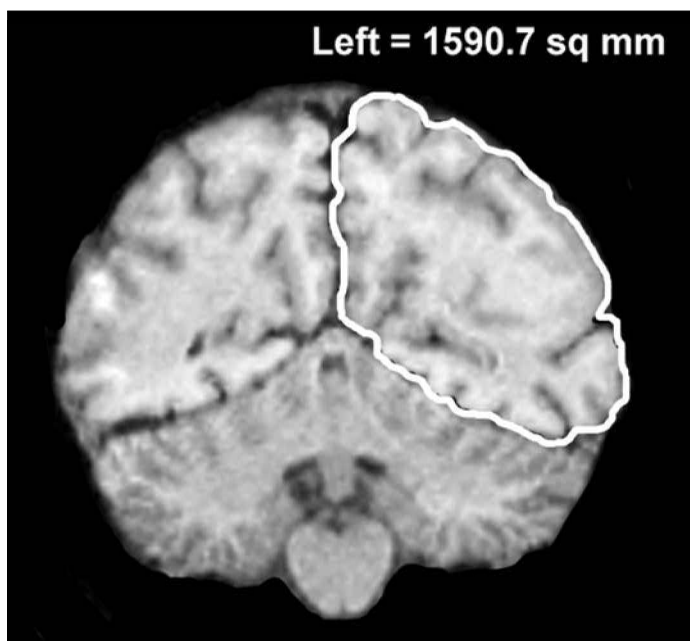


Figure 2. Coronal view of a common chimpanzee MRI scan that indicates the borders used when tracing each cerebral hemisphere. In this example, the left hemisphere was traced with an area tool, which has an area of 1590.7 square mm.

Data analysis

Log transformed data were used in analyses of cerebral volume in order to meet the assumption of linearity and normalise the distribution for across-species analyses. For the cerebral and PT asymmetry measures, the log value of the raw left and right hemisphere value in each region was used for determining the asymmetry quotient (AQ) in each region. The AQ was calculated using the formula $(R-L)/((R+L)*.5)$. The sign of the resulting value indicated the direction of asymmetry (positive value = right hemisphere bias; negative value = left hemisphere bias). The absolute value of the AQ reflected the magnitude of asymmetry. An AQ was derived for the PT area and each cerebral region (frontal1, frontal2, posterior1, and posterior2).

RESULTS

Analyses of cerebral volumetric asymmetries

Direction. In terms of qualitative assessment, the frequency of leftward and rightward AQ values can be seen in Table 2 for each cerebral region between taxonomic family. One-sample *t*-tests were then performed on the AQ values of

TABLE 2
 Frequency of rightward and leftward AQ values for each cerebral region between taxonomic family

	<i>Frontal1</i>		<i>Frontal2</i>		<i>Posterior1</i>		<i>Posterior2</i>	
	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>
Apes	15	8	14	9	6	17	9	14
OWM	9	5	6	8	7	7	5	9
NWM	3	5	3	5	5	3	4	4

OWM = Old World Monkey; NWM = New World Monkey

each region and taxonomic family. The mean AQ scores for each region and taxonomic family can be seen in Figure 3. Within the ape sample, population-level left hemisphere biases were found for the posterior1 $t(22) = 3.73$, $p < .01$ and posterior2 $t(22) = 2.20$, $p < .03$ regions. No population-level asymmetries were found for either frontal region. Analyses of the Old and New World monkey data failed to reveal any significant population-level asymmetries for any regions.

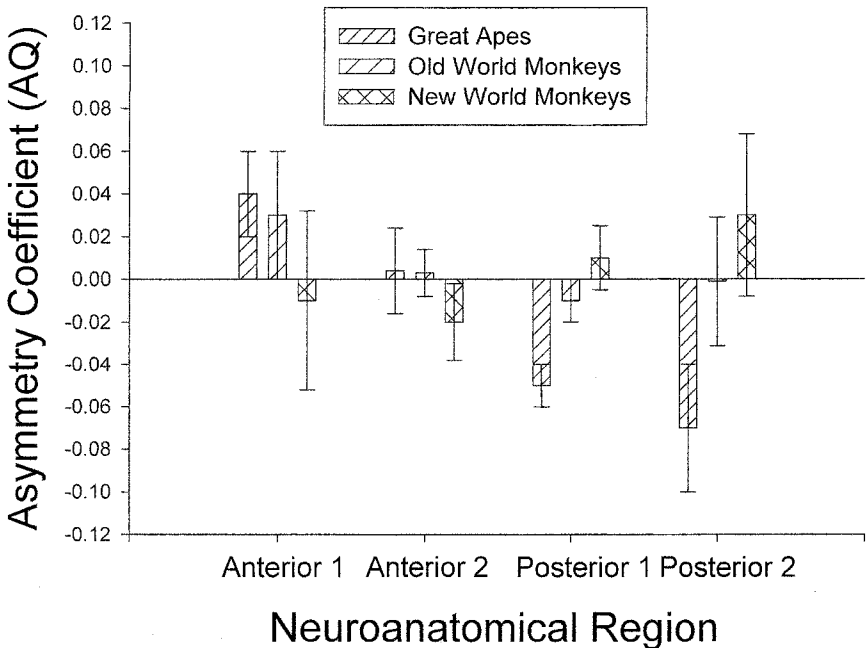


Figure 3. Mean AQ score (and standard error), or direction of asymmetry for each cerebral region between families (A1 = anterior frontal; A2 = posterior frontal; P1 = anterior occipital; P2 = posterior occipital).

Strength. In the next analysis, we compared species on strength of laterality to determine whether any directional differences were due to inherent differences in the magnitude of asymmetry. An analysis of variance was performed with the absolute value of frontal1, frontal2, posterior1, and posterior2 serving as the dependent variables. The between-group variable was taxonomic family. A significant difference between families was found for the posterior2 region $F(2, 42) = 7.04, p < .001$. The mean absolute value of the AQ scores for each cerebral region and family can be seen in Figure 4. Post-hoc analyses using Tukey's HSD indicated that the apes were significantly more lateralised in the posterior2 region than both the Old and New World monkeys. No significant differences were found between the remaining two families.

Relationship between cerebral volume and planum temporale

A one sample t -test revealed a population-level leftward asymmetry in the PT $t = (19) 3.24, p < .01$. In terms of qualitative assessment of asymmetry, the AQ values of the PT were leftward for 16 subjects and rightward for the remaining 4

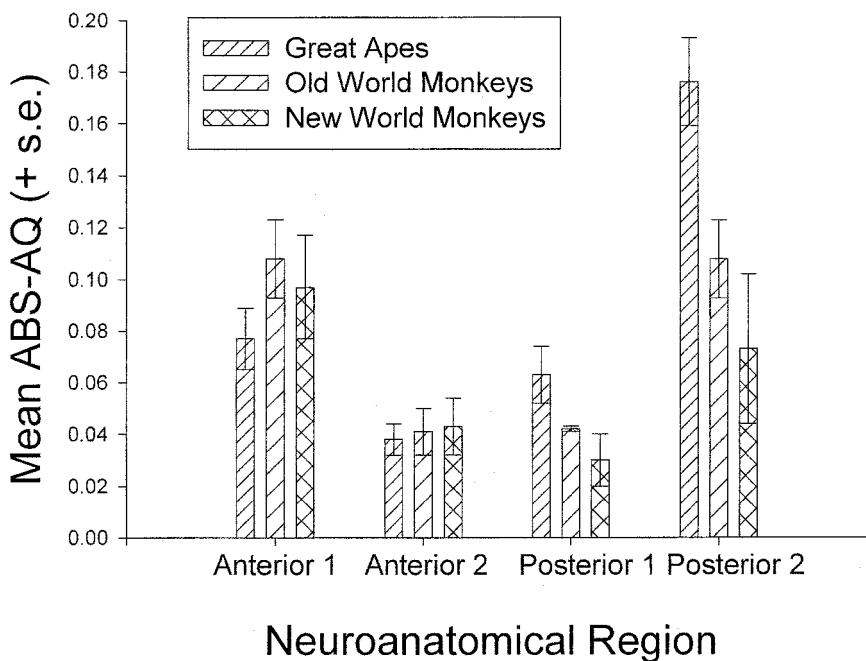


Figure 4. Mean absolute AQ score (and standard error), or strength of asymmetry for each cerebral region and for each family (A1 = anterior frontal; A2 = posterior frontal; P1 = anterior occipital; P2 = posterior occipital).

subjects. The AQ values of each cerebral region and the AQ values of the PT were correlated using a Pearson product-moment correlation. These results can be seen in Table 3. Significant positive correlations were found between the PT asymmetries and both the posterior1 and posterior2 regions. In contrast, a significant negative correlation was found between the frontal2 region and the PT asymmetry.

DISCUSSION

The results from this study reveal that, with the use of MRI, volumetric measures of cerebral asymmetries allow for predictions of asymmetry in other regions of interest, such as the PT in great apes. The apparent neuroanatomical asymmetries in this sample of great apes also support the applicability of the LNGH to the investigation of ontogeny of laterality in primates. A larger leftward occipital volume was evident at the population level in apes for P1 and P2, which is consistent with results found in humans by Weinberger et al. (1981). When the magnitude of this leftward volumetric asymmetry was compared across taxonomic families, only the posterior area of the occipital region (P2) was more lateralised in apes than in any other family. Volumetric asymmetries of both the frontal and occipital regions were significant predictors for patterns of PT asymmetry in the apes. Thus, when the anterior and posterior occipital regions (P1 and P2) exhibited a leftward asymmetry, the planum temporale also exhibited a leftward asymmetry. In contrast, a rightward asymmetry in the posterior frontal region predicted a leftward planum asymmetry. The anterior frontal region did not correlate with direction of PT asymmetry. The cerebral volume measures of the Old and New World monkeys did not exhibit any population-level asymmetries; however, these results should be interpreted with some caution due to the small sample size, particularly for the New World monkeys. (For a review of the literature on cerebral asymmetries in non-human primates relevant to this study see Table 1.)

TABLE 3
Correlation coefficients for the AQ values of cerebral volume and planum temporale in great apes

	<i>Cerebral Volume Region</i>			
	<i>Frontal1</i>	<i>Frontal2</i>	<i>Posterior1</i>	<i>Posterior2</i>
PT-AQ	0.281	-0.755	0.593	0.645
<i>N</i> =	15	15	15	15
<i>p</i> = (two-tailed)	0.311	0.001	0.02	0.009

The discontinuity in cerebral asymmetries of this sample of non-human primates may be indicative of at least two interrelated or independent hypotheses. The inconsistency in cerebral asymmetry within primates could be a mere reflection of different temporal courses in cerebral development. The results in this study suggest that the development of the ape brain follows a course similar to that proposed in the LNGH for human cerebral development. A study of asymmetries in the ape brain during foetal development would confirm the applicability of the LNGH. In terms of cerebral development of New and Old World monkeys and the lack of asymmetry reported in this study, the limited post-gestational brain and neurocranium growth in monkeys should be mentioned (Flugel, Schram, & Rohen, 1993; Sacher, 1982; Sacher & Staffeldt, 1974). The neonate human brain is only 25% the size of an adult human brain. Similar to the human newborn, the chimpanzee and bonobo brain complete about 65% of their growth after birth (Sacher, 1982; Sacher & Staffeldt, 1974). On the other hand, the brain of the capuchin and rhesus monkey neonate weighs between 40% and 48% of its mature adult weight (Sacher, 1982; Sacher & Staffeldt, 1974). Less post-natal developmental occurs in the monkey brain than the ape and human brain. The neurocranium of humans also continues to grow well into childhood, whereas the monkey's neurocranium stops growth at birth (Flugel et al., 1993). The authors were unable to find any studies on the post-natal growth of the neurocranium in apes.

Although the cerebral asymmetries of a human appear at 29 weeks gestation, the brain remains plastic and malleable long after birth, which may also be the case with the great apes (Sacher, 1982; Sacher & Staffeldt, 1974). This post-natal plasticity makes the brain susceptible and vulnerable to environmental and biological change, both of which may contribute to increasing brain asymmetry (Chi et al., 1977a,b; Sacher, 1982; Sacher & Staffeldt, 1974). The increased laterality as one ascends the primate order could also be interpreted as a progression in the efficiency and capability for higher cognitive functions in the primate brain, a second potential hypothesis (Best, 1988; Hopkins & Rilling, 2000; Rilling & Insel, 1998). This second hypothesis is based on the assumption that lateralisation of the brain is directly related to functional capabilities. However, a recent study challenges this notion that the factors that determine the direction of brain and functional asymmetry are homologous (Kennedy et al., 1999). In this study, it was reported that three subjects with situs inversus totalis, who were right-handed and left-hemisphere language-dominant, had reversed petalia asymmetries (i.e., leftward frontal and rightward occipital petalia; Kennedy et al., 1999). The relationship between laterality of the brain and functional laterality is a topic of ongoing investigation in both human and non-human primate research.

Establishing reliable and valid methods of measuring neuroanatomical asymmetries across non-human primates continues to be a challenge. Although differences in methodology have generally revealed similar results in apes, this

is not the case in monkeys. Rightward frontal and leftward occipital cerebral or petalia asymmetries have been reported somewhat consistently in apes with the use of preserved brains, endocasts and, more recently, MRI (Hopkins & Marino, 2000; Holloway & De La Coste-Lareymondie, 1982; see Table 1). The leftward planum temporale has also been reliably reported in great ape cadaver brains and from MRI scans (Gannon et al., 1998; Hopkins et al., 1998; see Table 1). Unfortunately, the same results have not been confirmed across methodologies for New and Old World monkeys (see Table 1). For example, inconsistent results were displayed in a single study when formalin-fixed brain tissue and photographs of the same specimens were used to measure the lateral length of the SF (Heilbroner & Holloway, 1988). Significant leftward asymmetry was found when the brains were measured directly, but these results were not replicated on the two-dimensional photograph (Heilbroner & Holloway, 1988).

Although there are some limitations, MRI offers a non-invasive means by which to potentially correlate functional with neuroanatomical asymmetries, a central interest in both human and non-human primate comparative neuropsychology. The findings reported in this study confirm previous evidence of cerebral asymmetries in great apes and reveal new evidence of using these asymmetries to predict related asymmetries, which has not yet been reported in the literature. Further studies, which include larger sample sizes and comparable methodology, will hopefully resolve the inconsistencies reported in cerebral asymmetries of New and Old World monkeys and allow for between-species comparisons.

Manuscript received 13 March 2000

Revised manuscript received 17 July 2000

REFERENCES

- Best, C. (1988). The emergence of cerebral asymmetries in early human development: A literature review and a neuroembryological model. In D.L. Molfese & S.J. Segalowitz (Eds.), *Brain lateralization in children: Developmental implications* (pp. 5–34). New York: Guilford Press.
- Campaigne, R., & Minckler, J. (1976). A note on the gross configurations of the human auditory cortex. *Brain Language*, 3, 318–323.
- Chi, J.G., Dooling, E.C., & Gilles, F.H. (1977a). Gyral development of the human brain. *Annals of Neurology*, 1, 86–93.
- Chi, J.G., Dooling, E.C., & Gilles, F.H. (1977b). Left-right asymmetries in the temporal speech areas of the human brain. *Archives of Neurology*, 34, 346–378.
- Eggert, G.H. (1977). *Wernicke's works on aphasia: A sourcebook and review*. The Hague: Mouton.
- Falk, D. (1978). Cerebral asymmetry in Old World monkeys. *Acta Anatomica*, 101, 334–339.
- Falk, D. (1986). Endocranial casts and their significance for primate brain evolution. In D.R. Swindler & J. Erwin (Eds.), *Comparative primate biology. Volume 1. Systematics, evolution and anatomy* (pp. 477–490). New York: Alan R. Liss, Inc.
- Falk, D. (1987). Hominid paleoneurology. *Annual Reviews of Anthropology*, 16, 13–30.

- Falk, D., Cheverud, J., Vannier, M.W., & Conroy, G.C. (1986). Advanced computer graphics technology reveals cortical asymmetry in endocasts of rhesus monkeys. *Folia Primatologia*, 46, 98–103.
- Falk, D., Hildebolt, C., Cheverud, J., Vannier, M., Helmkamp, C., & Konigsberg, L. (1990). Cortical asymmetries in frontal lobes of rhesus monkeys (*Macaca mulatta*). *Brain Research*, 512, 40–45.
- Flugel, C., Schram, K., & Rohen, R.W. (1993). Postnatal development of skull base, neuro- and viscerocranium in man and monkey: Morphometric evaluation of CT scans and radiograms. *Acta Anatomica*, 146, 71–80.
- Foundas, A.L., Leonard, C.M., Gilmore, R.L., Fennell, E.B., & Heilman, K.M. (1996). Pars triangularis asymmetry and language dominance. *Proceeding of the National Academy of Sciences*, 93, 719–722.
- Gannon, P.J., Holloway, R.L., Broadfield, D.C., & Braun, A.R. (1998). Asymmetry of chimpanzee planum temporale: Humanlike pattern of Wernicke's brain language area homologue. *Science*, 279, 220–222.
- Geschwind N., & Levitsky, W. (1968). Human brain: Left–right asymmetries in the temporal speech region. *Science*, 151, 186–187.
- Goodglass, H., & Quadfasel, F.A. (1954). Language laterality in left-handed aphasics. *Brain*, 77, 521–548.
- Groves, C.P., & Humphrey, N.K. (1973). Asymmetry in gorilla skulls: Evidence of lateralized brain function? *Nature*, 244, 53–54.
- Heilbronner, P.L., & Holloway, R.L. (1988). Anatomical brain asymmetries in New World and Old World monkeys: Stages of temporal lobe development in primate evolution. *American Journal of Physical Anthropology*, 76, 39–48.
- Holloway, R.L., & De La Coste-Lareymondie, M.C. (1982). Brain endocast asymmetry in pongids and hominids: Some preliminary findings on the paleontology of cerebral dominance. *American Journal of Physical Anthropology*, 58, 101–110.
- Hopkins, W.D., & Marino, L. (2000). Asymmetries in cerebral width in nonhuman primate brains as revealed by magnetic resonance imaging (MRI). *Neuropsychologia*, 38, 493–499.
- Hopkins, W.D., Marino, L., Rilling, J.K., & MacGregor, L.A. (1998). Planum temporale asymmetries in great apes as revealed by magnetic resonance imaging (MRI). *NeuroReport*, 9, 2913–2918.
- Hopkins, W.D., & Rilling, J.K., (2000). A comparative MRI study of the relationship between neuroanatomical asymmetry and interhemispheric connectivity in primates: Implication for the evolution of functional asymmetries. *Behavioral Neuroscience*, 114(4), 739–748.
- Kennedy, D., O'Craven, K., Ticho, B., Goldstein, A., Makris, N., & Henson, J. (1999). Structural and functional brain asymmetries in human situs inversus totalis. *Neurology*, 53(6), 1260–1265.
- Larsen, J.P., Hoehn, T., Lundberg, I., & Odegaard, H. (1990). MRI evaluation of the size and symmetry of the planum temporale in adolescents with developmental dyslexia. *Brain Language*, 39, 289–301.
- LeMay, M. (1976). Morphological cerebral asymmetries of modern man, fossil man and nonhuman primate. *Annals of the New York Academy of Sciences*, 280, 349–366.
- LeMay, M., Billing, M.S., & Geschwind, N. (1982). Asymmetries in the brains and skulls of nonhuman primates. In E. Armstrong & D. Falk (Eds.), *Primate brain evolution: Methods and concepts* (pp. 263–277). New York: Plenum Press.
- Leonard, C., Puranik, C., Kuldau, J., & Lombardino, L. (1998). Normal variation in the frequency and location of human auditory cortex landmarks. Heschl's gyrus: Where is it? *Cerebral Cortex*, 8, 397–406.
- Penhune, V., Zatorre, R., MacDonald, J., & Evans, A. (1996). Interhemispheric anatomical differences in human primary auditory cortex: Probabilistic mapping and volume measurement from magnetic resonance scans. *Cerebral Cortex*, 6, 661–672.

- Rilling, J.K., & Insel, T.R. (1998). The primate cortex in comparative perspective using magnetic resonance imaging. *Journal of Human Evolution*, 37, 191–223.
- Rilling, J.K., & Insel, T.R. (1999). Differential expansions of neural projection systems in primate brain evolution. *NeuroReport*, 10, 1453–1459.
- Rubens, A.B., Mahowald, M.W., & Hutton, J.T. (1976). Asymmetry of lateral (Sylvian) fissures in man. *Neurology*, 26, 620–624.
- Sacher, G.A. (1982). The role of brain maturation in the evolution of the primates. In E. Armstrong & D. Falk (Eds.), *Primate brain evolution: Methods and concepts* (pp. 97–112). New York: Plenum Press.
- Sacher, G.A. & Staffeldt, E. (1974). Relation of gestation time to brain weight for placental mammals. Implications for the theory of vertebrate growth. *American Naturalist*, 108, 593–615.
- Wada, J., & Rasmussen, T. (1960). Intracarotid injection of sodium amytal for the lateralization of cerebral speech dominance. Experimental and clinical observations. *Journal of Neurosurgery*, 17, 266–282.
- Weinberger, D.R., Luchins, D.J., Morihisa, J. & Wyatt, R.J. (1981). Asymmetrical volumes of the right and left frontal and occipital regions of the human brain. *Annals of Neurology*, 11, 97–100.
- Yeni-Komshian, G.H., & Benson, D.A. (1976). Anatomical study of cerebral asymmetry in the temporal lobe of humans, chimpanzees, and rhesus monkeys. *Science*, 192, 387–389.
- Zilles, K., Dabringhaus, A., Geyer, S., Amunts, K., Qu, M., Schleicher, A., Glissen, E., Schlaug, G., & Steinmetz, H. (1996). Structural asymmetries in the human forebrain and the forebrain of non-human-primates and rats. *Neuroscience and Biobehavioral Reviews*, 20(4), 593–605.

Copyright of *Laterality* is the property of Psychology Press (T&F) and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.