

Planum Parietale of Chimpanzees and Orangutans: A Comparative Resonance of Human-Like Planum Temporale Asymmetry

PATRICK J. GANNON,^{1*} NANCY M. KHECK,² ALLEN R. BRAUN,³ AND RALPH L. HOLLOWAY⁴

¹Department of Otolaryngology, Mount Sinai School of Medicine, New York, New York

²Department of Medical Education, Mount Sinai School of Medicine, New York, New York

³National Institutes of Health, National Institute on Deafness and Other Communication Disorders, Bethesda, Maryland

⁴Department of Anthropology, Columbia University, New York, New York

ABSTRACT

We have previously demonstrated that leftward asymmetry of the planum temporale (PT), a brain language area, was not unique to humans since a similar condition is present in great apes. Here we report on a related area in great apes, the planum parietale (PP). PP in humans has a rightward asymmetry with no correlation to the L>R PT, which indicates functional independence. The roles of the PT in human language are well known while PP is implicated in dyslexia and communication disorders. Since posterior bifurcation of the sylvian fissure (SF) is unique to humans and great apes, we used it to determine characteristics of its posterior ascending ramus, an indicator of the PP, in chimpanzee and orangutan brains. Results showed a human-like pattern of R>L PP ($P = 0.04$) in chimpanzees with a nonsignificant negative correlation of L>R PT vs. R>L PP ($CC = -0.3$; $P = 0.39$). In orangutans, SF anatomy is more variable, although PP was nonsignificantly R>L in three of four brains ($P = 0.17$). We have now demonstrated human-like hemispheric asymmetry of a second language-related brain area in great apes. Our findings persuasively support an argument for addition of a new component to the comparative neuroanatomic complex that defines brain language or polymodal communication areas. PP strengthens the evolutionary links that living great apes may offer to better understand the origins of these progressive parts of the brain. Evidence mounts for the stable expression of a neural foundation for language in species that we recently shared a common ancestor with. © 2005 Wiley-Liss, Inc.

Key words: brain language areas; evolution; polymodal language; primates; dyslexia; comparative neurobiology; great apes

Abbreviations: AG, angular gyrus; CS, central sulcus; cm, centimeters; G-V, gestural visual communication; HG, Heschl's gyrus; HISF, horizontal limb of the sylvian fissure (lateral fissure); IP, inferior parietal gyrus; L, left hemisphere; PCS, postcentral sulcus; parSF, posterior ascending ramus (limb) of the sylvian fissure; pdrSF, posterior descending ramus (limb) of the sylvian fissure (lateral fissure); SMG, supramarginal gyrus; SyP, sylvian point; STG, superior temporal gyrus; V-A, vocal auditory communication.

*Correspondence to: Patrick J. Gannon, Department of Otolaryngology, Annenberg 10 (1189), Mount Sinai School of Medicine, 5th Avenue at 100th Street, New York, NY 10029. Fax: 212-831-3700. E-mail: patrick.gannon@mssm.edu

Received 16 August 2005; Accepted 17 August 2005

DOI 10.1002/ar.a.20256

Published online 7 October 2005 in Wiley InterScience (www.interscience.wiley.com).

The evolutionary origin of human brain language areas is an issue that has captured the interest of many groups of scientists, in particular comparative and paleoneurologists, physical anthropologists, primatologists, linguists, and paleolinguists. Some have addressed this subject by studying the human fossil record to capture the only direct evidence from human ancestors (Holloway, 1976, 1983; Tobias, 1987; Tattersall, 2004). In this report, we have used the comparative approach to assess the anatomic representation of a newly described area of the brain, the planum parietale, which is thought to be involved with polymodal language functions in humans. First we will briefly review current thinking of some key components in the comparative functional anatomy armamentarium for evolutionary origins of brain language areas, the sylvian fissure, the planum temporale, and the planum parietale.

The comparative approach has proven to be a useful complement to assess the expression and transition of key neural elements within an evolutionary framework. Using this approach, the expression of human-like features in homologous brain regions of primates may indicate that a precursor condition was present in a common ancestor possibly many millions of years ago. However, the comparative approach also recognizes the fact that evolution is based on the concept of a foundation that underlies a subsequent species-specific and progressive building plan. As such, homologous brain regions, although similarly rooted, may have adapted differently to encompass the unique form of the communication demands within otherwise closely genetically related species.

At the higher cognitive level, the key research issues are not related to whether complex vocal-auditory (V-A; spoken-heard) or gestural-visual (G-V; gestured/signed/written-seen) language is unique to humans since of course it is. Evolutionarily, the seminal question, at least for hominoids, is when might the neural foundation have become specialized to conduct lateralized higher-order associative processing of V-A, G-V, or even polymodal communication. This is particularly compelling since functional activation of human brain language areas seems to be equipotential across modalities (Emmorey et al., 2003).

A recent timely review and synthesis (Hauser et al., 2002) dealt with these important issues by separating the communicative repertoire of humans and nonhuman primates into two major categories, the faculty of language in the broad sense (FLB) and the narrow sense (FLN) (see also Pinker and Jackendoff, 2005). FLN alone was considered human-like since it involves recursive processes that provide "the capacity to generate an infinite range of expressions from a finite set of elements," which may perhaps represent interpretations of Chomsky's (1975) earlier compelling theories of the language organ and transformational grammar, in broader, more utilizable comparative terms. More recently, a newly conceptualized perspective on the human language organ was presented (Anderson and Lightfoot, 2000). However, here we use the standard *Merriam-Webster* dictionary definition of language as "a systematic means of communicating ideas or feelings by the use of conventionalized signs, sounds, gestures, or marks having understood meanings" to characterize primate communication within a broad comparative perspective.

Anatomic asymmetries of human cerebrocortical structures that are related to language functions or disorders in humans have long served as potential indicators of the

evolutionary foundation of neural specializations for communication, or species-specific language in nonhuman primates. Here we have continued our comparative anatomic analysis of brain language areas in representatives of closely related nonhuman primates, the great apes. Anatomic indicators of traditional human-like brain language areas such as the sylvian fissure, Heschl's gyrus, the areas of Wernicke and Broca, and the planum temporale and parietale may allow us to build a platform on which the cross-specific neurobiological origins of language can be logically reconstructed. As we review some of these anatomic indicators and examples of the functions and disorders that help characterize them in humans, the subsequent step to a comparative link is inherently speculative. However, in many cases, new avenues of exploration such as novel behavioral paradigms or utilization of functional imaging (PET or MRI) in living nonhuman primates may be strongly indicated to provide functional correlates of anatomic homologs.

Sylvian Fissure

A wealth of information has been derived from reports of the symmetry vs. asymmetry status of the sylvian fissure that adjoins receptive brain language area homologs in hominoids and other primates. As stated by LeMay (1976): "The most striking and consistently present cerebral asymmetries found in adult and fetal brains are in the region of the posterior end of the sylvian fissures—the areas generally regarded as being of major importance in language function." A study of humans demonstrated that sylvian fissure (SF) L>R asymmetry was present in almost 70% of brains (Rubens et al., 1976). This pronounced asymmetry, although present in newborns (Witelson and Pallie, 1973), becomes progressively pronounced through adolescence to adulthood and may be related to later expression of cognitive advancements during maturation (Sowell et al., 2002). This developmental occurrence has yet to be studied in great apes. One of the earliest comparative studies of the cerebral cortex of great apes and New and Old World monkeys showed no consistent pattern of SF asymmetry in apes where it was longer on the right in orangutans but on the left in chimpanzees (Cunningham, 1892). Another comparative report demonstrated that although humans showed marked leftward asymmetry of the SF, chimpanzees did also but to a lesser degree, whereas macaques showed no asymmetry (Yeni-Komshian and Benson, 1976). Similarly, it was reported that this condition was present in great apes, particularly common in orangutans and not surprisingly also in "fossil man" (LeMay, 1976). Our more recent studies of the sylvian fissure and the planum temporale (PT) area homolog (area Tpt) in two species of Old World monkeys showed that although there were no asymmetries at the gross anatomic level that would indicate leftward predominance of the homolog, there were significant L>R asymmetries and heterogeneity at the cytoarchitectonic level (Gannon et al., 1999, 2001a, 2001b; Kheck et al., 2000).

It is well accepted that in humans the left SF courses more posteriorly and along a continuous horizontal trajectory than the right, which turns to course in a superior-posterior direction. This pattern occurs predominantly in right-handed humans who are left hemisphere-dominant for language functions. Further, it is also accepted that in these individuals the asymmetric configuration of the SF is due to the pronounced leftward asymmetry of the hor-

izontally oriented planum temporale language area. However, only recently has the significance of the superior-posterior course of the right SF been directly associated with rightward asymmetry of the planum parietale (Jäncke et al., 1994).

In humans, the sylvian fissure usually bifurcates posteriorly at the level of the sylvian point (SyP), the posterior conclusion of the horizontal portion. This bifurcation marks the origin of the posterior ascending ramus of the sylvian fissure (parSF) and several key studies have characterized the complexity of variation within this human morphologic trait and arrived at distinct classification systems. For example, Witelson and Kigar (1992) classified them as the S1 (parSF)/S2 (pdrSF) types while Ide et al. (1996) described combinations of these variants as the superior, inferior, symmetric, and inverted conditions. Steinmetz et al. (1990) named the variants type I, II, III, and IV based on the expression or absence of the two posterior horizontal and ascending rami and their association with other sulci such as the inferior postcentral sulcus (POCS): in type I, the parSF ascends posterior to the POCS; in type II, the parSF is absent so only the horizontal limb of the sylvian fissure (hLSF) is present; type III shows an additional sulcus interposed between the POCS and parSF, which creates an extra small gyrus; in type IV, the parSF is continuous with the postcentral sulcus (such that the supramarginal gyrus is absent). We have amalgamated these nomenclatures to distinguish variation in ape brains but primarily used that of Steinmetz et al. (1990). It is important to note that the posterior bifurcation of the SF (with the parSF and pdrSF) is unique to humans and the great apes and is not present in lesser apes or any other primate species where the horizontal limb of the sylvian fissure (hLSF), with no exception within normal variation, terminates at the sylvian point (SyP) (Gannon et al., 2001a, 2001b).

Supporting the concept of a comparative continuation in the anatomic signature for the PT and planum parietale (PP), Witelson and Kigar (1992) noted that the parSF was continuous with the hLSF and not the posterior descending ramus of the SF (pdrSF). The pdrSF was reported to be more diffuse in its association with the SF since it was not expressed as robustly as the parSF deep to the surface. Accordingly, only the parSF was defined as the *de facto* terminus of the SF. In a later report by Witelson et al. (1995) of the cytoarchitectonic signature of the language area PT (Brodmann's area 22 and area Tpt) (Galaburda et al., 1978a, 1978b; Galaburda and Sanides, 1980), it was also demonstrated that PP showed a similar cytoarchitectonic signature. These findings indicated that anatomical definitions of the PT should include the posterior vertical wall of the superior temporal gyrus (PP). However, this position prompts a seminal question: Does equivalence of cellular anatomy necessarily translate to functionality within and/or between hemispheres?

Planum Temporale

Since the classic report by Geschwind and Levitsky (1968), the planum temporale was placed prominently into the mainstream of asymmetric brain areas related to language functions. These authors state upfront: "It is generally accepted that the preponderance of the human left hemisphere in speech functions is not associated with significant structural differences between the two halves of the brain" (cited by them from: von Bonin, 1962). Al-

though functional lateralization has been well known for more than a century by aphasiology approaches, the PT serves as an anatomic model of the brains' adaptive and progressive fine-tuning of functional lateralization.

Studies have now demonstrated unequivocally that leftward asymmetry of the planum temporale is not unique to humans and is in fact evident in all the great apes (Gannon et al., 1998, 2001a; Hopkins et al., 1998). However, these comparative reports did and should not change our understanding of the role of this purported language area in humans. Instead, they simply grounded evolutionary interpretations and allowed for broader and more progressive perspectives to be developed. For example, a considerable part of the diversity across reports on the role of PT in language functions may be related to the wide variation of language tasks that are presented, and that "hemispheric specialization for language is multidimensional" (Josse and Tzourio-Mazoyer, 2004). Although such a multidimensionality has yet to be fully characterized, it may well also involve a role for the PP that is just beginning to become integrated within the framework of a functional mosaic along with the PT and beyond. It is always productive to integrate historic gems to broaden a comparative approach since, as Darwin (1871: p. 133) had stated, "Primeval man, or rather some early progenitor of man, probably first used his voice in producing true musical cadences, that is in singing."

Planum Parietale

The planum parietale is located within the supramarginal gyrus (Brodmann's area 40, or area supramarginalis), a parietal cortex association area that loops around the posterior ascending ramus of the sylvian fissure (parSF). The PP is bounded by the interparietal, inferior postcentral, and posterior subcentral sulci and Wernicke's area (in part, Brodmann's area 22). In general, subcomponents of these regions, perhaps along with components of the angular gyrus, may be involved with down-the-line processing of receptive language functions and the neural substrate of disorders such as dyslexia. Although the supramarginal gyrus is relatively well known, the PP subregion was only recently described and recognized as an independent entity (Jäncke et al., 1994). It was defined as being the "cortex covering the posterior wall of the posterior ascending sylvian ramus." In this *in vivo* magnetic resonance imaging morphometric analysis of 141 mixed-sex and mixed-handedness adults, the PP (as demarcated by the length of the parSF) was shown to be significantly and markedly lateralized anatomically to the right hemisphere with no overt correlation to handedness or sex. However, in combination PP showed a more marked rightward asymmetry in both right-handed males and left-handed females (Jäncke et al., 1994). Interestingly, the nonsignificant correlation between hemispheric asymmetries of the PT (L>R) and PP (R>L) suggested independent involvement of PP with unique cognitive processes that are lateralized both anatomically and functionally to the right hemisphere.

Recently, Lattner et al. (2005) reported a role for the PP region bilaterally (as a distinct functional subunit of receptive language areas), along with the more classic posterior parts of the superior temporal gyrus, that is involved with processing voice spectral information, specifically that of female voices. The finding not only

support a new understanding of right hemisphere regions in language perception dynamics that were not previously recognized but may indicate a comparative behavior approach perhaps related to the tonal nature of primate vocalizations. This finding is also reminiscent of the often forgotten homotype of Broca's language area on the right hemisphere and the importance of its communicative role in prosody and beyond (Friederici and Alter, 2004; Mitchell and Crow, 2005). Like any newly designated brain area, it will take a greater body of evidence for PP to become established, but it is gaining recognition and is being integrated into the literature where it is often referred to as the "so-called planum parietale" (Emmorey et al., 2003).

Dyslexia Within Context of Plana Parietale and Temporale

Many studies in humans have attempted to identify the functional localization of neural substrates that underlie reading and disorders such as dyslexia. It has been considered that hemispheric symmetry of PT and PP may serve as indicators of developmental language and reading disorders. For example, Galaburda et al. (1985) reported an unusual symmetry (vs. the normal L>R asymmetry) of the planum temporale (PT) in four young males with developmental dyslexia. A similar report of 19 teenage dyslexics using MRI demonstrated 70% symmetry of PT in dyslexics vs. 30% in controls (Larsen et al., 1990). In contrast, more recently it was shown that significantly fewer dyslexics showed a rightward asymmetry of the PP while PT L>R asymmetry and dichotic listening parameters were similar (Heiervang et al., 2000).

By use of a comparative approach, it is essential to consider how any morphological similarities between humans and great apes may be interpreted within a functional evolutionary background. This would require that the different counterparts within a complex disorder such as dyslexia be translated within the parlance of behavioral homology. For example, interpretations such as connecting the origins of language (Crow, 1997, 2000), the theory of mind (Brune, 2005), and the mirror system hypothesis (Arbib and Mundhenk, 2005) to schizophrenia and a "symptom-based approach to psychotic disorders in evolutionary perspective" (Brune, 2004) have endeavored to do this. Since the planum parietale may well represent a new component of this ongoing (anatomic vs. functional role/deficits) debate, it may be the right time for a comparative framework to be set in place.

MATERIALS AND METHODS

Morphologic characteristics of the SF, PP, and PT were studied in the left and right cerebral hemispheres of postmortem immersion-fixed brains of chimpanzees, *Pan troglodytes* (n = 23), and orangutans, *Pongo pygmaeus* (n = 4). Specimens were from collections at Columbia University and the Smithsonian Institution and originated from both captive-born and wild-caught individuals. In all cases, postmortem intervals prior to fixation were less than 24 hr with refrigeration. Reliable information about sex and age was not available for approximately half our sample, which precluded statistical correlation of sex or age with interhemispheric expression of SF bifurcation patterns and lengths of SF segments.

Linear measures of SF subcomponents were traced precisely by hand with thick black braided silk suture mate-

rial ("0 Ethicon") as sulcal contours along the external surface of the cerebral cortex. This material allowed for reliable capture of the sulci along a three-dimensional winding course with a minimum of stretching when straightened to obtain a linear measure. The black color also allowed easy identification for reliable alignment with critical landmarks. Three of us (P.J.G., N.M.K., and R.L.H.) were involved with active discussion to determine the validity of gross anatomic landmarks under direct observation. This hands-on observation and measurement approach in intact brains allowed the critical issue of three-dimensional variation (of which there is a considerable degree present in apes as there is in humans) to be taken into account. Similar to that used for our planar area model of the planum temporale (Gannon et al., 1998), in which we utilized a reliable but simple new method that intimately apposed very thin black plastic templates onto the PT and deep into sulci, we were able to achieve reliably a median scientific prediction of anatomical landmarks.

The sylvian point (SyP) located at the most posterior boundary of the horizontal limb of the SF (hlSF) was demarcated by lightly pushing together the superior temporal, inferior parietal (supramarginal), and angular gyri so that the complex became aligned as in life. Although not always necessary, this approach allowed for the realignment of tissues that had undergone some shrinkage due to fixation. The location of the SyP was determined as the midpoint of the fissural/sulcal, offset " $\text{—}<$," formed by the posterior ascending ramus of SF (parSF), posterior descending ramus of SF (pdrSF), and the hlSF. If either parSF or pdrSF was not present, the midpoint of an upright or inverted "L" with the hlSF was used to assign its location (Figs. 1 and 2).

The length along the cortical surface of parSF and pdrSF from the SyP was determined. Since the distal terminations of these rami were often graded and shallow, a new method was used to capture reliably the exact location of these critical endpoints. A focused beam of light, shone at right angles to the ramus and parallel to the cortical surface of the brain, created a sharp dark shadow that clearly indicated a precise repeatable endpoint. After lightly straightening the suture material, linear measures were completed using metric calipers. Two of us (P.J.G. and N.M.K.) conducted this method 10 times, independently and blinded, to arrive at an acceptable margin of error less than 0.5%. Statistical analyses included ANOVA, paired *t*-tests, Pearson product moment correlation, and Fisher's *r*-to-*z* analysis.

To compare the dimensions of the PT with that of parSF and pdrSF, data that were not used for the original study of PT (Gannon et al., 1998) were used here to correlate expression of these variables. The original PT data used for that study were deep to the brain surface area measures. Here we used linear data collected by a method similar to that used in the first description of PT asymmetry by Geschwind and Levitsky (1968). Our version of this method involved collecting direct linear measures (using metric calipers) of the lateral margin of PT (on the cortical surface), extending from Heschl's sulcus anteriorly and the SyP posteriorly within the anatomical boundaries rules defined in Gannon et al. (1998). To normalize data for one part of correlation analysis, we transformed independent left and right hemisphere values to percent-

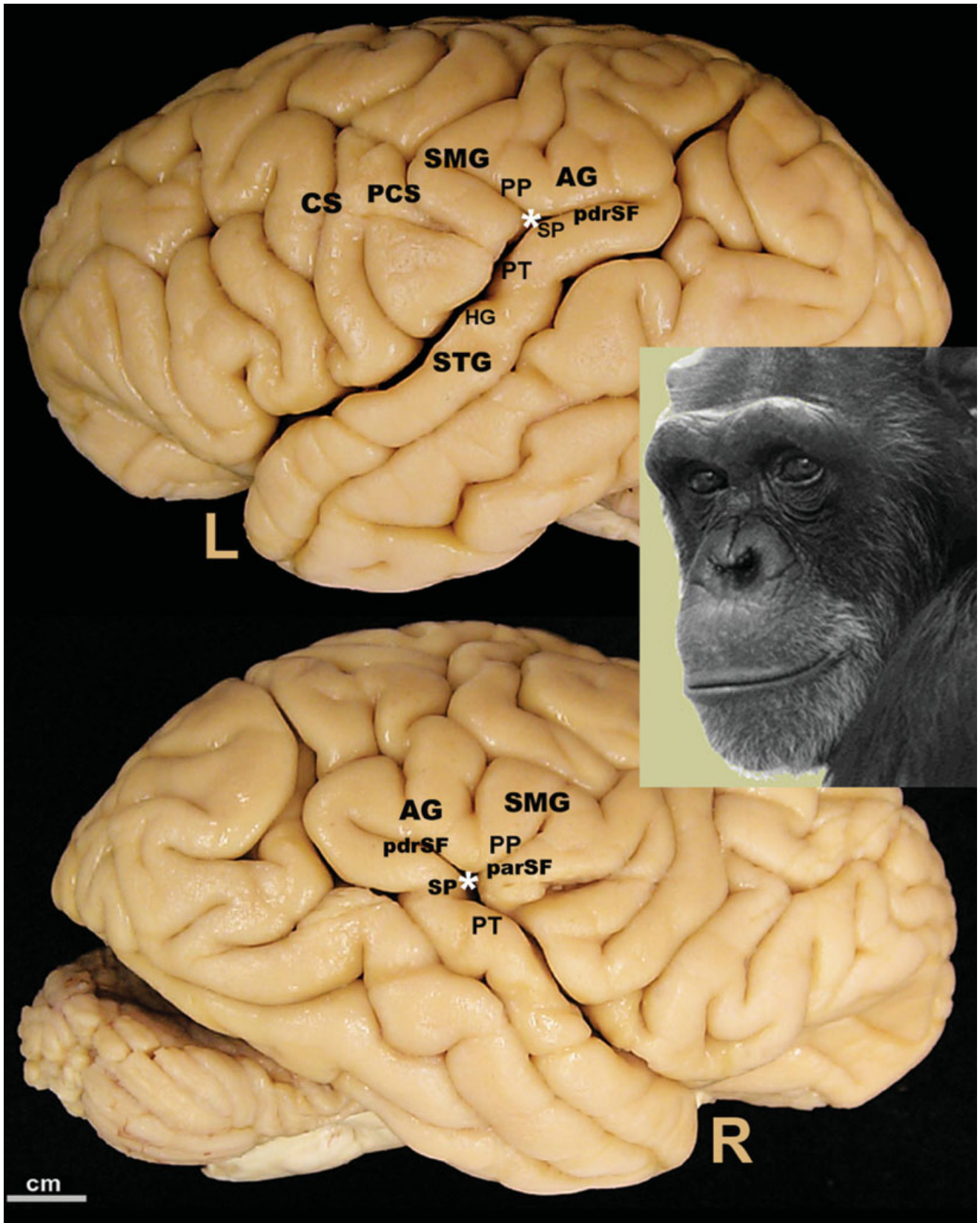


Fig. 1. Left (top) and right (bottom) hemispheres of chimpanzee (*Pan troglodytes*) brain. Although the legendary sign-using chimpanzee Washoe is looking over the figure, this is not her brain. This Grand PanDam is very much alive and well and at age 49 is still teaching Roger and Deborah Fouts at the Central Washington University's Chimpanzee and Human Communication Institute on how to conduct interspecific communication. AG, angular gyrus; CS, central sulcus; cm, centimeters; G-V, gestural-visual communication; HG, Heschl's gyrus; hISF, horizon-

tal limb of the sylvian fissure (lateral fissure); IP, inferior parietal gyrus; L, left hemisphere; PCS, postcentral sulcus; parSF, posterior ascending ramus (limb) of the sylvian fissure; pdrSF, posterior descending ramus (limb) of the sylvian fissure; PP, planum parietale; PT, planum temporale; R, right hemisphere; SF, sylvian fissure (lateral fissure); SMG, supramarginal gyrus; SyP, sylvian point; STG, superior temporal gyrus; V-A, vocal-auditory communication.

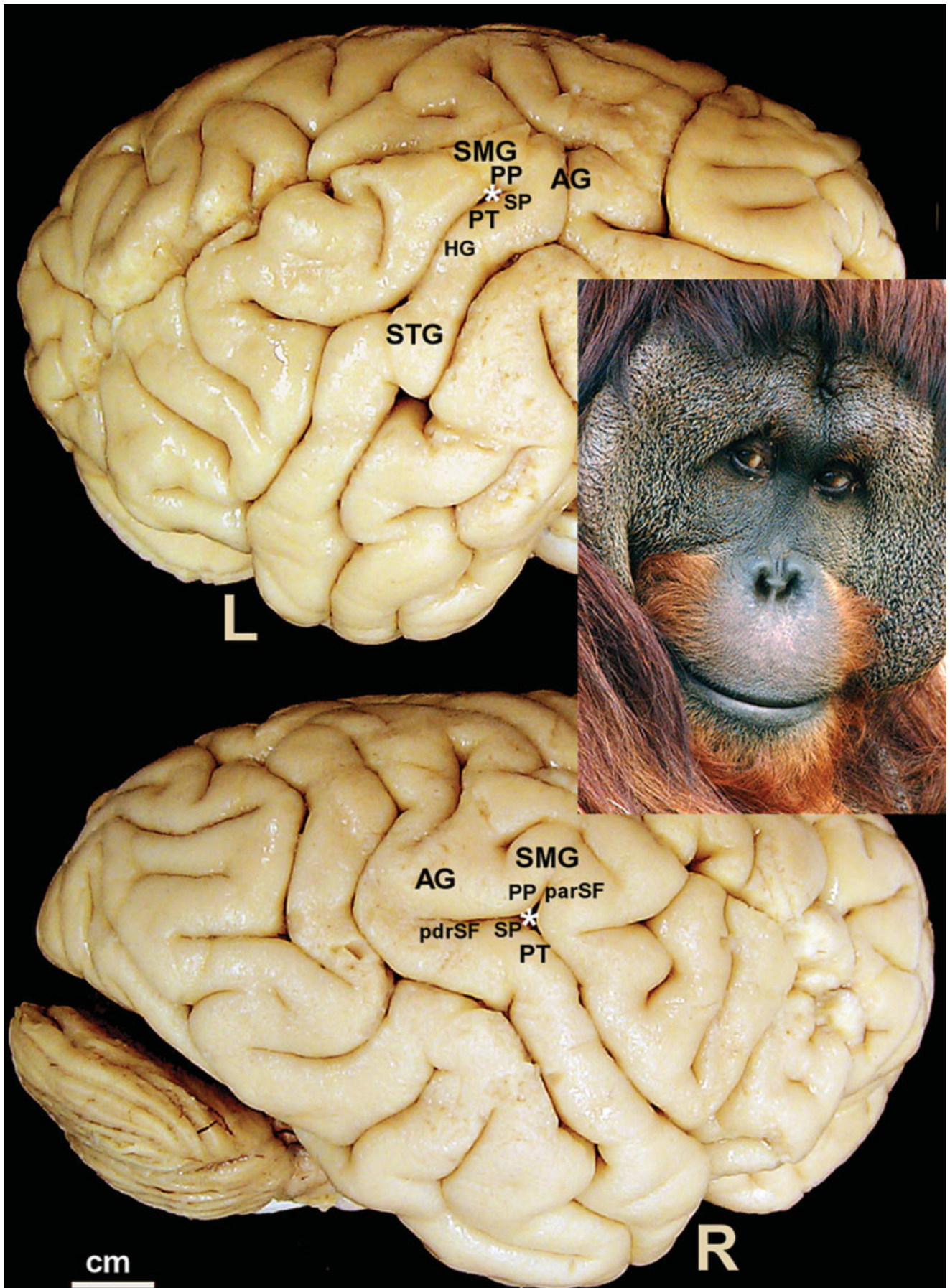


Fig. 2. Left (top) and right (bottom) hemispheres of an orangutan (*Pongo pygmaeus*) brain. The male orangutan Kiko, a celebrity of the Language Project at the Smithsonian National Zoological Park, serves as

an example of a great ape that crossed hominoid species literacy boundaries. He uses keyboard symbols to communicate with humans. This is not his brain.

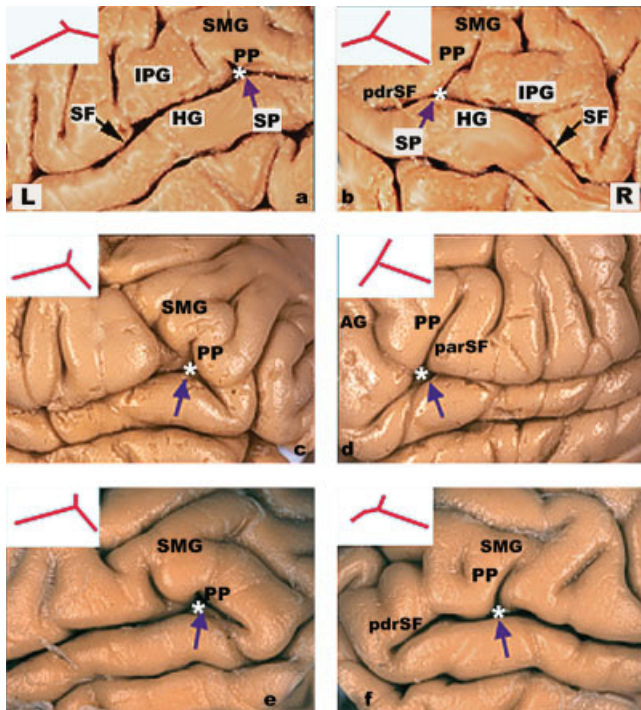


Fig. 3. Examples of variation within the posterior region of the sylvian fissure in six different chimpanzee brains. **a**, **c**, and **e** are left hemispheres; **b**, **d**, and **f** are right hemispheres. The inverted pattern (Ide et al., 1996), in which the parSF is oriented in an anterosuperior direction (**a**, **b**, **d**, and **f**), was the most common. White asterisk shows the position of the sylvian point.

ages of combined left plus right values, e.g., $L\% = L/(L + R)$; $R\% = R/(L + R)$.

RESULTS

We have demonstrated for the first time multifactorial associations between different components of the posterior sylvian fissure that serve as indicators of the PP and PT in both a large sample and a subsample of chimpanzees ($n = 23$ and 11 , respectively) and a representative preliminary sample of orangutans ($n = 4$).

Posterior Rami of Sylvian Fissure

The morphology and the pattern of distribution of the posterior ascending and descending rami of the sylvian fissure (parSF, pdrSF) were similar to patterns described previously for humans. The variant most frequently observed, in 74% of right and left hemispheres of chimpanzee brains, was the inverted pattern (Ide et al., 1996), in which the parSF is oriented in an anterosuperior direction (Fig. 3a, b, d, and f).

Posterior Ascending Ramus of Sylvian Fissure

Chimpanzees. In our assessment of the 23 chimpanzee brains, the length of the parSF (an anatomic indicator of the hemispheric size of the PP) was significantly larger in the right hemisphere ($P = 0.036$; means, left = 5.4 ± 2.9 ; right = 7.3 ± 2.7 mm; Table 1). Considered separately, 14 of 23 chimpanzee brains that had an $R > L$ parSF

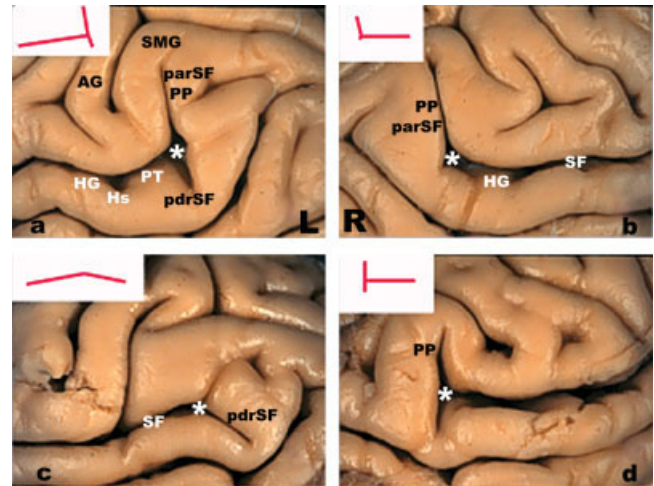


Fig. 4. Examples of variation within the posterior region of the sylvian fissure in orangutan brains. **a** and **c** are left hemispheres; **b** and **d** are right hemispheres. Unlike the chimpanzee, a pronounced inverted pattern of the parSF was not evident and was absent on the left hemisphere of one brain (**c**). White asterisk shows the position of the sylvian point.

showed a mean length of 7.75 ± 12.15 mm, whereas the 9 brains that had an $L > R$ parSF showed a considerably smaller mean length of 3.81 ± 7.45 . Similarly, 3 of the 14 $R > L$ parSF brains were 23.3, 27.8, and 37.5 times $R > L$, whereas only 1 of the 9 $L > R$ parSF brains showed such a large value as 23.7 times $L > R$.

Orangutans. On the four orangutan brains, rami of the posterior sylvian fissure showed more varied bifurcation patterns than that observed in the chimpanzee brains (Fig. 4). However, within this variation, all four of the patterns previously described in humans were observed (Ide et al., 1996) in addition to one in which the left parSF was absent, and although the groove of a cerebral artery branch had the appearance of parSF, it was very shallow and unambiguously not a true sulcus (Fig. 4c).

The length of the parSF was nonsignificantly larger on the right hemisphere of orangutan brains ($P = 0.17$; means, left = 6.5 ± 4.4 ; right = 9.6 ± 3.0 mm; Table 1). This was not surprising since there was considerable variance of parSF on the left (19.7) vs. the right (8.8) hemisphere. For example, on one of the three $R > L$ brains, the left parSF was extremely small, at 0.15 mm, with the right side being 6.9 mm. Conversely, the parSF of one brain was 20% $L > R$.

Posterior Descending Ramus of Sylvian Fissure

This region of the temporoparietal junction served as an objective control since in humans it is not directly related to lateralized language functions like PT and PP and is dissimilar in cytoarchitecture.

Chimpanzees. The pdrSF was not significantly larger on the left or right hemisphere of the 23 chimpanzee brains ($P = 0.55$; means, left = 9.02 ± 4.24 ; right = 9.44 ± 2.94 mm). However, a subjective trend toward rightward asymmetry was evident since 11 brains that showed an $R > L$ pdrSF were 7.26 ± 13.8 times larger vs. 11 $L > R$ pdrSF brains that were 1.3 ± 0.26 times larger.

TABLE 1. Length of posterior ascending and descending rami of sylvian fissure in chimpanzees and orangutans

	CHIMPANZEES							
	Posterior ascending ramus SF, mm				Posterior descending ramus SF, mm			
	LEFT	RIGHT	L > R	R > L	LEFT	RIGHT	L > R	R > L
JH1	9.8	8.5	1.15		0.2	4.6		23.00
JH4	6.2	10.1		1.63	4.7	7.8		1.66
YN88-256	6.6	10.2		1.55	10.1	12.1		1.20
YN97-139	8.3	6.3	1.32		12.5	8.8	1.42	
YN95-60	8.1	8.5		1.05	7.2	11.3		1.57
BOD-25	0.4	11.1		27.75	9	4.6	1.96	
YN92-111	3.5	9.1		2.60	6.7	11.5		1.72
JH-5	3.1	8.2		2.65	7.7	8.6		1.12
YN95-4	6.1	2.8	2.18		10.3	8.4	1.23	
JH6	5.4	4.8	1.13		10.8	7	1.54	
JH7	2.9	4.6		1.59	0.15	6.6		44.00
JH8	9.1	7.5	1.21		13.8	13.8		
YN92-115	2.8	6.8		2.43	8.8	6.6	1.33	
YN92-264	7.1	0.3	23.67		7	9.1		1.30
J961	4.9	7.9		1.61	6	9.4		1.57
YN80-7	6	4.5	1.33		9.1	8.5	1.07	
YN94-225	3.4	5		1.47	6.9	6.1	1.13	
F610[JH2]	8.1	7	1.16		11	9.1	1.21	
PTT-0[95-9]	8.9	7.9	1.13		7.1	10.3		1.45
PTT-1	0.3	7		23.33	17.1	14.9	1.15	
PTT-7	0.2	7.5		37.50	16.1	10.9	1.48	
PTT-12	6.7	11.3		1.69	13.5	12.1	1.12	
PTT-16	6.2	10.2		1.65	11.8	15		1.27
Average	5.40	7.27	3.81	7.75	9.02	9.44	1.33	7.26
StDev	2.87	2.70	7.45	12.15	4.24	2.94	0.26	13.80
n =	23		9	14	23		11	11
	ORANGUTANS							
YN93-312	9.5	7.9	1.20		7.90	5.70	1.39	
YN93-345	9.6	13.6		1.42	4.90	2.40	2.04	
YN93-216	0.15	6.9		46.00	7.50	4.50	1.67	
YN89-200	6.7	10.1		1.51	10.20	6.00	1.70	
Average	6.49	9.63		16.31	7.63	4.65	1.70	
StDev	4.43	2.97		25.71	2.17	1.63	0.27	
n =	4		1	3	4		4	0

Linear measurements in chimpanzee (n = 23) and orangutan (n = 4) brains of the length of the posterior ascending rami (an indicator of the planum parietale - PP) and posterior descending rami of the sylvian fissure (parSF, pdrSAF). Descriptive statistics show R > L versus L > R hemispheric size distribution of measures. See key for legend and figures 5 and 6.

Orangutans. The length of the pdrSF was significantly larger on the left hemisphere of orangutan brains ($P = 0.007$; means, left = 7.6 ± 2.2 ; right = 4.7 ± 1.6 mm; Table 1). There was similar but overall low levels of variance in the size of the left and right pdrSF (VAR left = 4.7; right = 2.7; = 1.8 times L>R) compared to the parSF (VAR left = 19.7; right = 8.8; = 2.2 times L>R). Although compelling, the small sample size can only serve as an indicator.

In order to determine any leveling effect or independence of the ascending and descending rami in chimpanzees, a hemispheric summation analysis was conducted (where left summed rami of SF is $L \text{ arSF} + L \text{ drSF} = L \text{ srSF}$, and right summed rami of SF is $R \text{ arSF} + R \text{ drSF} = R \text{ srSF}$). Results showed a significant rightward asymmetry of srSF ($P = 0.03$) by use of a paired two-sample for means t -test, and a strong trend to rightward asymmetry of srSF ($P = 0.09$) by use of a two-sample assuming equal variances t -test. See below for correlation analysis.

Planum Temporale in Chimpanzees

A complementary subsample (n = 11) of the chimpanzee brains used in a previous study (Gannon et al., 1998) was aligned with current data. However, instead of using the area measures of PT that were generated for the previous study (which would have been statistically inappropriate), new linear measures of the PT were gathered in order to compare these statistically with the new linear measures of the parSF (PP indicator).

The new linear values for the hemispheric dimensions of the PT showed a significant left hemisphere predominant size (length) asymmetry ($P = 0.2^{-5}$; means, left = 6.43 ± 1.6 ; right = 3.28 ± 1.6 mm; Table 2).

In order to determine whether a combination of the separate asymmetries gives rise to a leveling effect in chimpanzees similar to that reported for humans, we compared these via the total planar area (TPA) summing approach ($L\text{-PT} + L\text{-PP} = L\text{TPA}$ vs. $R\text{-PT} + R\text{-PP} = R\text{TPA}$) used by Heiervang et al. (2000). We demonstrated

Hemispheric Differences in Size of Chimpanzee Planum Parietale

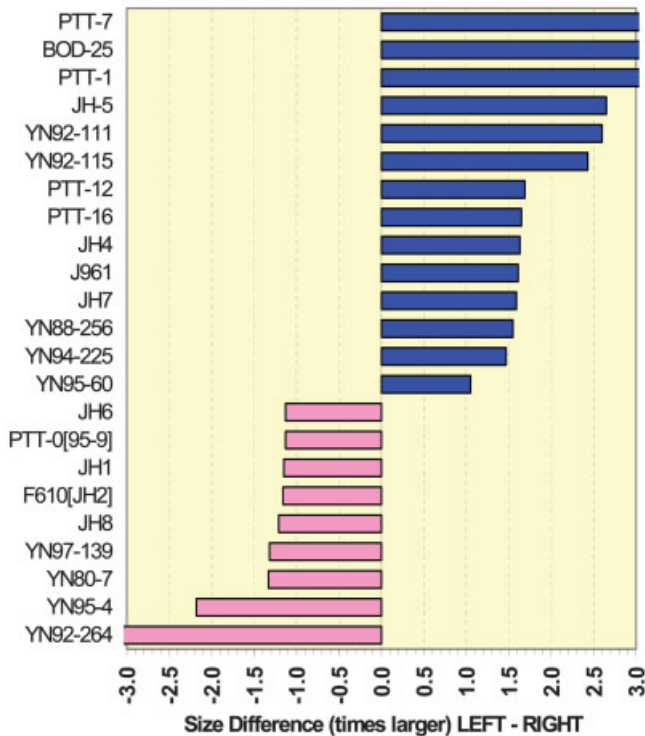


Fig. 5. Chart shows in chimpanzee brains ($n = 23$) the distribution of left (upper right bars; $n = 14$) vs. right (lower left bars; $n = 9$) relative lengths of the posterior ascending rami of the sylvian fissure (parSF), which serve as an indicator of the size of the PP. Largest L>R (YN92-264; off-scale lower left) is 23.7 times larger, whereas the three R>L (PTT-1, BOD-25, and PTT-7; off-scale upper right) are 37.5, 27.8, and 23.3 times larger. See Table 1 for data.

a nonsignificant but strong trend towards an L>R asymmetry of the TPA measure ($P = 0.06$) with left TPA sum of 137.3 mm and mean of 12.5 ± 2.9 mm, with right TPA sum of 113 mm and mean of 10.3 ± 2.2 mm. This finding was similar to the significant leftward asymmetry of TPA shown in both dyslexic and control children (Heiervang et al., 2000).

We also conducted an interhemispheric analysis of differences of an intrahemispheric summation of the parSF and pdrSF (left arSF + drSF vs. right arSF + drSF) to determine if there was any indication of an anatomic dominance effect. There was a significant rightward asymmetry of this compounded measure ($P = 0.03$; means, left = 14.4 mm, SE = 0.96; right = 16.7 mm, SE = 0.93).

Correlation Analyses in Chimpanzees

It has been considered by some that PP and PT are analogous functional/anatomic units across the left and right hemispheres of humans (Witelson and Kigar, 1992), although a correlative analysis by other workers showed a different trend (Jäncke et al., 1994). The first position might render hemispheric asymmetry of the PT and PP a potentially redundant issue since their separate but pur-

portedly combined hemispheric asymmetries would result in combinatorial hemispheric symmetry. As such, it is necessary to determine whether this might be the case in apes since, not surprisingly, indicators of a similar human-like pattern of asymmetries of PT (L>R) and PP (R>L) are emerging within our study. All correlations were conducted on data modified to percentages of relative hemispheric size. Due to the small sample size, correlation analyses were not conducted in orangutans.

Correlation of parSF and pdrSF

Correlation analyses of the two posterior rami of the sylvian fissure were conducted in chimpanzees within the large sample size ($n = 23$). A similar analysis of these was made within a smaller sample size ($n = 11$) of chimpanzees that also included the PT.

There was a nonsignificant negative correlation between the size of the left and right parSF ($CC = -0.04$; $P = 0.84$), which complemented results of the t -test that indicated a significant rightward asymmetry of the parSF ($P = 0.036$). There was a significant positive association ($CC = 0.63$; $P = 0.001$) between the right and left pdrSF. This correlate complemented the t -test that indicated hemispheric symmetry of the pdrSF ($P = 0.55$).

Correlation of parSF and PT

Correlation analyses of linear measures of the left and right posterior ascending rami of the sylvian fissure (parSF-L and parSF-R) and lateral linear measures of the left and right planum temporale (PT-L/R) were conducted in the smaller subsample of chimpanzee brains that were used for a previous study of PT ($n = 11$; Table 3) (Gannon et al., 1998).

There was a nonsignificant negative association ($CC = -0.3$; $P = 0.4$) between the left PT and the right parSF. Interestingly, there was also a similar level of nonsignificant negative association ($CC = -0.3$; $P = 0.4$) between the right PT and the left parSF.

There was a nonsignificant positive association between the left and right PT ($CC = 0.3$; $P = 0.4$), which supported the t -test that indicated this relationship to be significantly leftward asymmetric ($P = 0.2^{-5}$).

An unexpected and interesting correlation was that of the left PT vs. the left parSF and the right PT vs. the right parSF. Both hemispheres showed a highly significant association ($P < 0.001$, both), the left being negative at -1.0 and the right being positive at 1.0 .

DISCUSSION

Our new findings reported here persuasively support a contention for the incorporation of a new component to balance the comparative neuroanatomic complex that defines brain language areas. PP contributes to strengthening the evolutionary links that living great apes may offer to better understand the origins of these highly progressive parts of the brain. A similar recent report by Sherwood et al. (2003), which studied variation and expression of asymmetry in the homolog of Broca's area in chimpanzees and gorillas, concluded that "gross morphologic patterns do not offer substantive landmarks for the measurement of Brodmann's area 44 in great apes. Whether or not Broca's area homologue of great apes exhibits human-like asymmetry can only be resolved through further analyses of microstructural components."

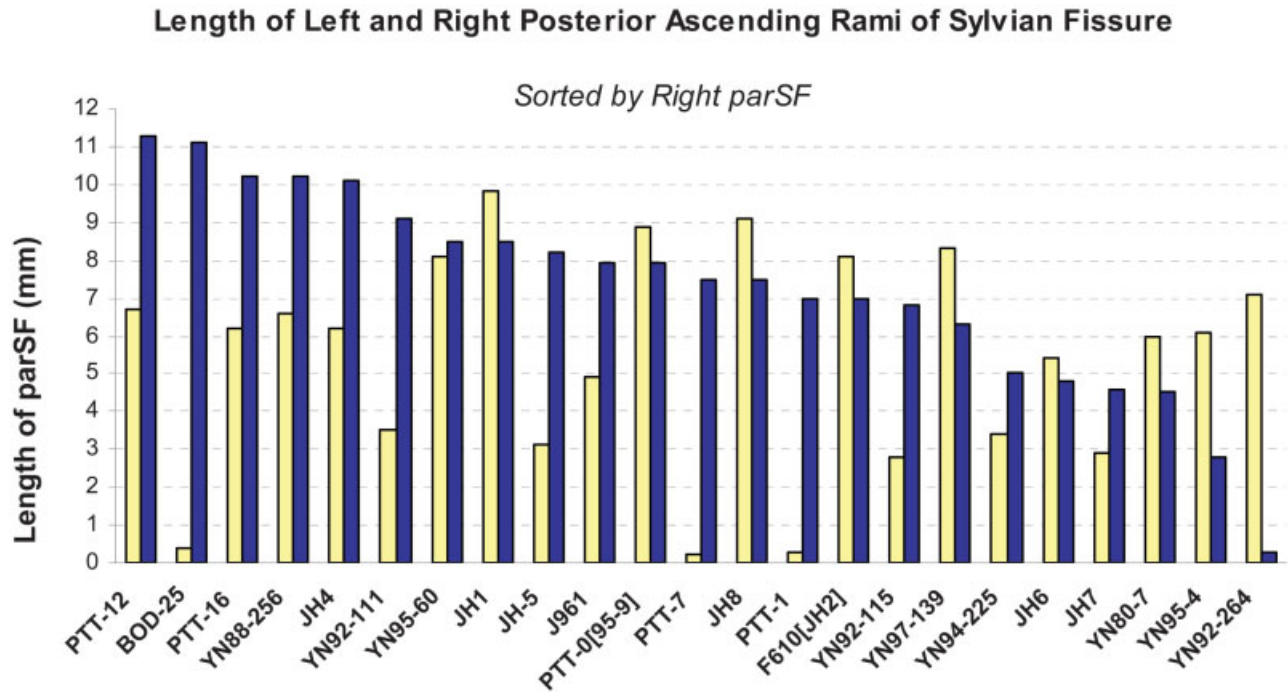


Fig. 6. Chart shows in chimpanzee brains ($n = 23$) the distribution of, on the left (light bars) vs. right (dark bars) hemispheres, absolute lengths (mm) of the posterior ascending rami of the Sylvian fissure (parSF) sorted by lengths of the right parSF.

TABLE 2. Measures (mm) of length of chimpanzee planum temporale and posterior Sylvian fissure rami

Specimen	PT-L	parSF-L	pdrSF-L	PT-R	parSF-R	pdrSF-R
YN97-139	8.06	9.80	0.20	1.50	8.50	4.60
JH5	9.13	3.10	7.70	2.47	8.20	8.60
JH-1	5.19	9.80	0.20	2.08	8.50	4.60
YN92-115	5.65	2.80	8.80	2.62	6.80	6.60
YN88-256	7.63	6.60	10.10	3.56	10.20	12.10
JH-8	5.53	9.10	13.80	2.58	7.50	13.80
J961	8.01	4.90	6.00	4.02	7.90	9.40
F6-10	5.27	8.10	11.00	2.72	7.00	9.10
YN95-4	4.00	6.10	10.30	2.34	2.80	8.40
JH7	6.22	2.90	0.15	4.87	4.60	6.60
YN94-225	6.03	3.40	6.90	7.27	5.00	6.10
Mean	6.43	6.05	6.83	3.28	7.00	8.17
Stdev	1.56	2.82	4.76	1.63	2.11	2.91

Linear measurements in chimpanzee brains ($n = 11$) of the length of the lateral border of the planum temporale, the parSF and the pdrSF on the left and right hemispheres.

This does not appear to be the case for comparative consideration of R>L hemispheric asymmetry of the PP, a newly described human language area (Jäncke et al., 1994). Similar to our report of human-like anatomy of the planum temporale (PT) in living chimpanzees (Gannon et al., 1998), there are numerous overtly human-like anatomic features that clearly delineate the PP and its magnitude of rightward asymmetry in chimpanzees and orangutans (see Figures 5 and 6).

The exact nature of a functional homolog of the PT, regardless of how well the anatomy or role of this brain language area may be understood in humans, offers a challenge due to the dearth of comparative and functional information. Consideration of a functional homolog of PP

is even more difficult despite the compelling evidence for its role as part of a broad neural complex that subserves language functions in humans and its robust, rightward lateralized presence in great apes.

The vanguard of the PP, Jäncke (2005) offered these personal communication comments to our study. "The planum parietale is a tricky anatomical region. In most subjects it covers the supramarginal gyrus; thus, classical functions associated with that region may be related to the PP. For example, the ventral part of the left PP might house neural assemblies processing higher auditory functions (maybe for language issues). It may also project into other parts of the parietal cortex to subservise spatial functions as part of the dorsal stream in the auditory system.

TABLE 3. Correlation matrix of chimpanzee planum temporale and posterior sylvian fissure rami

	PT-L	parSF-L	pdrSF-L	rSFtot-L	PT-R	parSF-R	pdrSF-R	rSFtot-R
PT-L	1.00							
parSF-L	-0.27	1.00						
pdrSF-L	0.04	0.29	1.00					
rSFtot-L	0.32	0.83	0.31	1.00				
PT-R	0.00	-0.55	-0.34	-0.54	1.00			
parSF-R	0.52	0.29	0.04	0.59	-0.24	1.00		
pdrSF-R	0.22	0.32	0.72	0.44	-0.22	0.35	1.00	
rSFtot-R	0.47	-0.13	-0.20	0.15	0.49	0.73	0.16	1.00

Maybe on the right there are more spatial functions in the PP. The more dorsal parts of the PP are clearly associated with several spatial functions. For example, the most dorsal part of the PP borders the intraparietal sulcus, which is strongly involved in visuomotor transformations. Although one can discuss a lot about the putative functions of the PP, a lot is fragmentary." Clearly, much research needs to be conducted on this new entity to characterize its role within the broad functional mosaic of human and great ape language. However, due to the nature of the anatomic and functional information that has already been published, a potential role of the PP in the human disorders of developmental dyslexia, language development, and visual attention, a plausible and cohesive characterization of this complex region is slowly emerging. Collectively, these results warrant inclusion of PP into the complex mosaic of lateralized language areas and thus provide a basis for studying these areas within a comparative evolutionary context.

DATA AND RESULTS: ENIGMAS AND CHALLENGES

A previous comparative anatomy report of the planum temporale in the great and lesser apes showed a progressive trend (meaning "human-like" here) of anatomic characteristics and leftward asymmetry in tandem with divergence from common ancestors (Gannon et al., 2001a). Lesser apes, particularly siamangs, showed a PT that was indistinguishable anatomically from the condition seen in Old World monkeys. Here we focused on representatives of the two ends of the great ape spectrum (meaning the period of evolutionary divergence from shared common ancestors with humans), chimpanzees and orangutans. Preliminary results in orangutans serve here as an indicator of the evolutionary depth of PP expression since it appears that its comparative anatomic expression may follow an evolutionary trajectory that is similar to that we described for the PT.

Chimpanzee Planum Temporale

For this study, we made new linear cortical surface measures of the PT in order to correlate interhemispheric expression with those of the PP. Although this approach was similar to the earliest report of PT leftward asymmetry in humans (Geschwind and Levitsky, 1968), our previous approach used a planar template approach to capture the total surface of the PT.

These new linear measures of the PT arrived at a significance value of hemispheric asymmetry two levels of magnitude beyond that provided by the area values (Gannon et al., 1998) previously captured in the same speci-

mens ($P = 2.3 \times 10^{-5}$ for linear vs. 1.0×10^{-3} for area measures), even though the sample size was smaller ($n = 11$ vs. 15). Further, many of the individual hemispheric difference values were markedly distinct. For example, for specimen YN97-139, the PT area measure indicated a 2.5 times L>R value, whereas the PT linear measure of this specimen indicated more than double this L>R value at 5.4 times. Similarly, in specimen JH5, the PT area measure indicated an L>R value of 1.6 times, whereas the PT linear measure indicated more than double at 3.8 times. This higher level of magnitude for differences in hemispheric asymmetry was unexpected; however, since the original area measures could not be used to correlate with linear measures of parSF (PP), the method was standardized for this study.

In light of these new data, perhaps Crow (2004) might consider modification of his widely discussed, Web-published lecture (<http://www.ling.ed.ac.uk/evolang/2004/AB-STRACKS/TALKS/crow.doc>) in which he states that "in one study (Gannon et al., 1998) lateralization of the planum temporale was reported in 17 out of 18 chimpanzees by a method (inserting cardboard triangles into the lateral sulcus) that clearly was not blind and is unlikely to have detected the asymmetry rediscovered by Geschwind and Levitsky in 1968. Yet chimpanzees were found to be more lateralized than Man!" First, we never used the crude method of cardboard triangles that Crow (2004) reported. Second, it would be nice to hear from Crow (2004) how blinding could be put into place for studies such as these where difficult decisions regarding expression and variation of the structures involved need to be made by open pragmatic discussion during measurement; blinded individual/s could not realize this critical step (see paragraph 2, Materials and Methods section). Furthermore, the classic study by Geschwind and Levitsky (1968) was certainly not blinded. Third, we have now shown that the lateral linear measure of PT method, used by Geschwind and Levitsky (1968), showed an even greater magnitude of L>R asymmetry of the PT when used in our chimpanzee sample. Perhaps a more plausible conclusion would be that PT asymmetry was reduced by neurological modification in line with a common theme of selective pruning and refinement of neural circuits as an evolutionary mechanism similar to normal development (Chechik et al., 1998).

For the area and linear measure comparisons, the conditions of scientific and statistical significance were met independently. However, a lesson to be learned from these findings is that a multiplicity of methods, measures, and landmarks used to describe and interpret the expression of anatomic variation and hemispheric asymmetry for

structures such as the PT and PP must account for confounding variables. Critical issues such as these were discussed in a recent review of the PT (Shapleske et al., 1999). We dealt with these important issues upfront by alignment of our approaches with well-accepted previous reports.

Bifurcation of the posterior part of the hLSF at the SyP is unique to the great apes, whereas the hLSF of all other primates terminates posteriorly at the sylvian point (SyP). For humans, it was considered that only the parSF was continuous with the hLSF, not the pdrSF (Witelson and Kigar, 1992; Witelson et al., 1995). This was based in part on identification of a contiguous cytoarchitecture between PT and PP. Since the cytoarchitectonic homolog of PT and PP in those primates without a posterior bifurcation of the SF is a single continuous site, area Tpt is always located anterior to the SyP on the lateral part of the superior temporal gyrus (Galaburda et al., 1978a; Habib and Galaburda, 1986). It would be interesting to consider why the appearance of the pdrSF involved anatomical separation of selected components of the original temporoparietal auditory area (area Tpt) during the evolutionary neural adaptation in the hominoid ancestor. Perhaps this could be interpreted as selection for a specific posterior component of area Tpt that may have already been functionally multifactorial as indicated by both intra- and interhemispheric microanatomic segmentation throughout this and related sites (Gannon et al., 1999; Kheck et al., 2000; Lewis and Van Essen, 2000). If so, the presence of this new pattern in great apes alone might qualify as a neural anatomic indicator of one of the many major adaptive shifts that occurred during hominoid evolutionary transitions (Goodenough, 2002).

COMPARATIVE AND INTERPRETATIVE ISSUES

A number of reports have linked the PP and PT to human behaviors, variation, and disorders such as musical skill, sex, handedness, dyslexia, language impairment, and schizophrenia (Steinmetz et al., 1991; Steinmetz, 1996; Heiervang et al., 2000; Foundas et al., 2002; Leonard et al., 2002; Eckert, 2004; Mitchell and Crow, 2005).

One prominent example of PP functions to consider within a comparative framework requires that it is necessary to recognize upfront that reading may not be a species-specific adaptive trait that is unique to humans. Simply stated, outside of the elevated intellectual milieu of humans, not enough (evolutionary) time has passed to merit the inclusion of reading as a species-specific trait or adaptation that was directly selected for during recent evolution. Reading and writing (defined here as symbols written or imprinted on a surface to represent the sounds or words of a language) have been in common usage for less than 150 years. As well noted in a recent review by Gayán (2001), it must be remembered that reading and writing are very recent augments to the polymodal communicative repertoire of humans. Even though the first writing systems were initiated by classic cultures such as the Babylonians and Greeks, they were reserved for the cultural elite and all publications were hand written by specialists, the scribes. It was only recently, in the 19th century, that educational reforms allowed widespread public reading to occur and thus facilitated the recognition of dyslexia as a disorder. What was it before?

In light of this, it may be possible to consider the potential for living comparative examples that may provide the root of a prelinguistic communicative venue. One example to consider may be the extraordinary cross-specific capacity of the bonobo Kanzi, a great ape prodigy who communicates so effectively within the language platform of another species (humans) by use of abstract lexigrams (Savage-Rumbaugh et al., 1986; Savage-Rumbaugh and Lewin, 1994). If this comparative extension was valid, Kanzi may serve as a comparative behavioral model of the true evolutionary depth for the neural origins of reading within an integrated lexivisual modality. Likewise, could the use and self-directed teaching of sign language (gestural-visual communication) to other apes by the chimpanzee Washoe (Fig. 1) (Gardner and Gardner, 1969; Fouts and Waters, 2001) also be considered a behavioral homolog to writing and reading, which is known to utilize human brain language areas? Both of these great apes and others such as the orangutan Kiko (Fig. 2) of the Language Project at the Smithsonian National Zoological Park, who uses keyboard symbols, have served as pioneers of the interspecific communication arena. With regards to language and literacy in humans, our preliminary work (Gannon et al., 2002) and that of Varney (2002) support the hypothesis that stand-alone gestural-visual communication, which now serves as an augment of spoken and signed languages, may have served as a neural substrate and the baseline primary modality (Hewes, 1973; Corballis, 1992, 1999; Iverson and Goldin-Meadow, 1998; Gannon et al., 2002). This logical sequence may also contribute to an explanation of why visual attention deficits occur more commonly in dyslexics (Heiervang and Hugdahl, 2003).

Until we are able to communicate freely both within and between human communication systems and those that are unique to the great apes, perhaps an open-minded and extended comparative approach will allow us to identify the neural substrates that provided early humans with the ability to develop a unique cognitive and communicative package in such a relatively short time. The communicative flexibility that this package allowed for, as evidenced by the onset of literacy with the ability to read, write, and comprehend over an even shorter period of time, indicates the presence of a broadly accessible neural mosaic with far-reaching interactive components. To end with a broad comparative message to try and capture language evolution, the brain does not discriminate communication channels, just their intraspecific intelligibility quotient.

ACKNOWLEDGMENTS

The authors thank Dr. Mark Weiss of the National Science Foundation for his good advise; Dr. Lutz Jäncke, Institute of General Psychology, Heinrich Heine University, Düsseldorf, Germany, who published the original description of and named the planum parietale, for his comments and an update on its role; Dr. Roger S. Fouts, Chimpanzee and Human Communication Institute, Central Washington University, for letting them use the picture of Washoe and providing them with her magic on Figure 1; and the Smithsonian's National Zoological Park through the Office of Public Affairs, particularly Carolyn Martin and Ann Batdorf, for letting them use the photograph of their wonderful male orangutan Kiko for Figure

2. Supported by the National Science Foundation (SBR 9617262 and IBN 9905402 to P.J.G.).

LITERATURE CITED

- Anderson SR, Lightfoot DW. 2000. The human language faculty as an organ. *Ann Rev Physiol* 62:697–722.
- Arbib MA, Mundhenk TN. 2005. Schizophrenia and the mirror system: an essay. *Neuropsychologia* 43:268–280.
- Brune M. 2004. Schizophrenia—an evolutionary enigma? *Neurosci Biobehav Rev* 28:41–53.
- Brune M. 2005. “Theory of mind” in schizophrenia: a review of the literature. *Schizophr Bull* 31:21–42.
- Chechik G, Meilijson I, Ruppin E. 1998. Synaptic pruning in development: a computational account. *Neural Comput* 10:1759–1777.
- Chomsky N. 1975. *Reflections on language*. New York: Pantheon.
- Corballis MC. 1992. On the evolution of language and generativity. *Cognition* 44:197–126.
- Corballis MC. 1999. The gestural origins of language. *Am Scientist* 87:138–145.
- Crow TJ. 1997. Is schizophrenia the price that *Homo sapiens* pays for language? *Schizophr Res* 28:127–141.
- Crow TJ. 2000. Schizophrenia as the price that *Homo sapiens* pays for language: a resolution of the central paradox in the origin of the species. *Brain Res Brain Res Rev* 31:118–129.
- Crow TJ. 2004. Who forgot Paul Broca? Evolution of Language Fifth International Conference. Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
- Cunningham DJ. 1892. *Contributions to the surface anatomy of the cerebral hemispheres*. Dublin: Academy House.
- Darwin C. 1871. *The descent of man and selection in relation to sex*. London: John Murray.
- Eckert MA. 2004. Neuroanatomical markers for dyslexia: a review of dyslexia structural imaging studies. *Neuroscientist* 10:362–371.
- Emmorey K, Allen JS, Bruss J, Schenker N, Damasio H. 2003. A morphometric analysis of auditory brain regions in congenitally deaf adults. *Proc Natl Acad Sci USA* 100:10049–10054.
- Foundas AL, Leonard CM, Hanna-Pladdy B. 2002. Variability in the anatomy of the planum temporale and posterior ascending ramus: do right and left handers differ? *Brain Lang* 83:403–424.
- Fouts RS, Waters GS. 2001. Chimpanzee sign language and Darwinian continuity: evidence for a neurological continuity for language. *Neurol Res* 23:787–794.
- Friederici AD, Alter K. 2004. Lateralization of auditory language functions: a dynamic dual pathway model. *Brain Lang* 89:267–276.
- Galaburda AM, Sanides F, Geschwind N. 1978a. Human brain: cytoarchitectonic left-right asymmetries in the temporal speech region. *Arch Neurol* 35:812–817.
- Galaburda AM, LeMay M, Kemper TL, Geschwind N. 1978b. Right-left asymmetries in the brain. *Science* 199:852–856.
- Galaburda AM, Sanides F. 1980. Cytoarchitectonic organization of the human auditory cortex. *J Comp Neurol* 190:597–610.
- Galaburda AM, Sherman GF, Rosen GD, Aboitiz F, Geschwind N. 1985. Developmental dyslexia: four consecutive patients with cortical anomalies. *Ann Neurol* 18:222–233.
- Gannon PJ, Holloway RL, Broadfield DC, Braun AR. 1998. Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke’s brain language area homolog. *Science* 279:220–222.
- Gannon PJ, Kheck NM, Hof PR. 1999. Brain language area evolution: III, left hemisphere predominant asymmetry of cytoarchitectonic, but not gross anatomic, planum temporale homolog in Old World monkeys. *Soc Neurosci Abstr* 47:17.
- Gannon PJ, Kheck NM, Hof PR. 2001a. Language areas of the hominoid brain: a dynamic communicative shift on the upper east side planum. In: Falk D, Gibson KR, editors. *Evolutionary anatomy of the primate cerebral cortex*. Cambridge: Cambridge University Press. p 216–240.
- Gannon PJ, Valachovic AM, Hof PR, Kheck NM, Erwin JM. 2001b. Evolution of primate brain receptive language area homologs: interhemispheric symmetry of sylvian fissure length in *Erythrocebus patas* with operculum of sylvian point by right middle temporal gyrus. *Soc Neurosci Abstr* 822:1.
- Gannon PJ, Kheck N, Goldin-Meadow S, Valachovic AM, Braun A. 2002. Everyday US sign language: a new look at Hewes’ hypothesis for a gestural origin of spoken language. *Am J Phys Anthropol* 71:29.
- Gardner RA, Gardner BT. 1969. Teaching sign language to a chimpanzee. *Science* 165:664–672.
- Gayán J. 2001. The evolution of research on dyslexia. *Anuario Psicología* 32:3–30.
- Geschwind N, Levitsky W. 1968. Human brain: left-right asymmetries in temporal speech region. *Science* 161:186–187.
- Goodenough WH. 2002. Anthropology in the 20th century and beyond. *Am Anthropol* 104:423–440.
- Hauser MD, Chomsky N, Fitch WT. 2002. The faculty of language: what is it, who has it, and how did it evolve? *Science* 298:1569–1579.
- Habib M, Galaburda AM. 1986. Biological determinants of cerebral dominance. *Rev Neurol (Paris)* 142:869–894.
- Heiervang E, Hugdahl K, Steinmetz H, Inge Smievoll A, Stevenson J, Lund A, Erslund L, Lundervold A. 2000. Planum temporale, planum parietale and dichotic listening in dyslexia. *Neuropsychologia* 38:1704–1713.
- Heiervang E, Hugdahl K. 2003. Impaired visual attention in children with dyslexia. *J Learn Disabil* 36:68–73.
- Hewes GW. 1973. Primate communication and the gestural origin of language. *Curr Anthropol* 14:5–24.
- Holloway RL. 1976. Paleoneurological evidence for language origins. *Ann NY Acad Sci* 280:330–348.
- Holloway RL. 1983. Human paleontological evidence relevant to language behavior. *Hum Neurobiol* 2:105–114.
- Hopkins WD, Marino L, Rilling JK, MacGregor LA. 1998. Planum temporale asymmetries in great apes as revealed by magnetic resonance imaging (MRI). *Neuroreport* 24:2913–2918.
- Ide A, Rodriguez E, Zaidel E, Aboitiz F. 1996. Bifurcation patterns in the human sylvian fissure: hemispheric and sex differences. *Cereb Cortex* 6:717–725.
- Iverson JM, Goldin-Meadow S. 1998. Why people gesture when they speak. *Nature* 396:228.
- Jäncke L, Schlaug G, Huang Y, Steinmetz H. 1994. Asymmetry of the planum parietale. *Neuroreport* 5:1161–1163.
- Josse G, Tzourio-Mazoyer N. 2004. Hemispheric specialization for language. *Brain Res Brain Res Rev* 44:1–12.
- Kheck NM, Gannon PJ, DeFereos M, Hof PR. 2000. Cytoarchitectonic heterogeneity within the lateralized profile of area Tpt in *Macaca fascicularis*. *Soc Neurosci Abstr* 71:8.
- Larsen JP, Høien T, Lundberg I, Odegaard H. 1990. MRI evaluation of the size and symmetry of the planum temporale in adolescents with developmental dyslexia. *Brain Lang* 39:289–301.
- Lattner S, Meyer ME, Friederici AD. 2005. Voice perception: sex, pitch, and the right hemisphere. *Hum Brain Mapp* 24:11–20.
- LeMay M. 1976. Morphological cerebral asymmetries of modern man, fossil man, and nonhuman primate. *Ann NY Acad Sci* 280:349–366.
- Leonard CM, Lombardino LJ, Walsh K, Eckert MA, Mockler JL, Rowe LA, Williams S, DeBose CB. 2002. Anatomical risk factors that distinguish dyslexia from SLI predict reading skill in normal children. *J Commun Disord* 35:501–531.
- Lewis JW, Van Essen DC. 2000. Mapping of architectonic subdivisions in the macaque monkey, with emphasis on parieto-occipital cortex. *J Comp Neurol* 428:79–111.
- Mitchell RL, Crow TJ. 2005. Right hemisphere language functions and schizophrenia: the forgotten hemisphere? *Brain* 128(Pt 5):963–978.
- Pinker S, Jackendoff R. 2005. The faculty of language: what’s special about it? *Cognition* 95:201–236.
- Rubens AB, Mahowald MW, Hutton JT. 1976. Asymmetry of the lateral (sylvian) fissures in man. *Neurology* 26:620–624.
- Savage-Rumbaugh S, McDonald K, Sevcik RA, Hopkins WD, Rubert E. 1986. Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *J Exp Psychol Gen* 115:211–235.

- Savage-Rumbaugh S, Lewin R. 1994. *Kanzi: The ape at the brink of the human mind*. New York: John Wiley and Sons, Inc.
- Shapleske J, Rossell SL, Woodruff PW, David AS. 1999. The planum temporale: a systematic, quantitative review of its structural, functional and clinical significance. *Brain Res Brain Res Rev* 29:26–49.
- Sherwood CC, Broadfield DC, Holloway RL, Gannon PJ, Hof PR. 2003. Variability of Broca's area homologue in African great apes: implications for language evolution. *Anat Rec A Discov Mol Cell Evol Biol* 271:276–285.
- Sowell ER, Thompson PM, Rex D, Kornsand D, Tessner KD, Jernigan TL, Toga AW. 2002. Mapping sulcal pattern asymmetry and local cortical surface gray matter distribution in vivo: maturation in perisylvian cortices. *Cereb Cortex* 12:17–26.
- Steinmetz H, Ebeling U, Huang YX, Kahn T. 1990. Sulcus topography of the parietal opercular region: an anatomic and MR study. *Brain Lang* 38:515–533.
- Steinmetz H, Volkman J, Jäncke L, Freund HJ. 1991. Anatomical left-right asymmetry of language-related temporal cortex is different in left- and right-handers. *Ann Neurol* 29:315–319.
- Steinmetz H. 1996. Structure, functional and cerebral asymmetry: in vivo morphometry of the planum temporale. *Neurosci Biobehav Rev* 20:587–591.
- Tattersall I. 2004. The dual origin of modern humanity. *Coll Antropol* 28(Suppl 2):77–85.
- Tobias PV. 1987. The brain of *Homo habilis*: a new level of organization in cerebral evolution. *J Hum Evol* 16:741–761.
- Varney NR. 2002. How reading works: considerations from prehistory to the present. *Appl Neuropsychol* 9:3–12.
- von Bonin G. 1962. Anatomical asymmetries of the cerebral hemispheres. In: Mountcastle V, editor. *Interhemispheric relations and cerebral dominance*. Baltimore, MD: John Hopkins University Press. p 1–6.
- Witelson SF, Pallie W. 1973. Left hemisphere specialization for language in the newborn: neuroanatomical evidence of asymmetry. *Brain* 96:641–646.
- Witelson SF, Kigar DL. 1992. Sylvian fissure morphology and asymmetry in men and women: bilateral differences in relation to handedness in men. *J Comp Neurol* 323:326–340.
- Witelson SF, Glezer II, Kigar DL. 1995. Women have greater density of neurons in posterior temporal cortex. *J Neurosci* 15:3418–3428.
- Yeni-Komshian GH, Benson DA. 1976. Anatomical study of cerebral asymmetry in the temporal lobe of humans, chimpanzees, and rhesus monkeys. *Science* 192:387–389.