

Morphology and Histology of Chimpanzee Primary Visual Striate Cortex Indicate That Brain Reorganization Predated Brain Expansion in Early Hominid Evolution

RALPH L. HOLLOWAY,¹ DOUGLAS C. BROADFIELD,^{2,3*} AND
MICHAEL S. YUAN⁴

¹Department of Anthropology, Columbia University, New York, New York

²Department of Anthropology, Florida Atlantic University, Boca Raton, Florida

³Department of Biomedical Science, Florida Atlantic University, Boca Raton, Florida

⁴Department of Anatomy and Cell Biology, School of Dental and Oral Surgery,
Columbia University, New York, New York

ABSTRACT

Human brain evolution is characterized by an overall increase in brain size, cerebral reorganization, and cerebral lateralization. It is generally understood when brain enlargement occurred during human evolution. However, issues concerning cerebral reorganization and hemispheric lateralization are more difficult to determine from brain endocasts, and they are topics of considerable debate. One region of the cerebral cortex that may represent the earliest evidence for brain reorganization is the primary visual cortex (PVC), or area 17 of Brodmann. In nonhuman primates, this region is larger in volume (demarcated anteriorly by the lunate sulcus), and extends further rostrally than it does in modern humans. In early hominid fossil (*Australopithecus*) endocasts, this region appears to occupy a smaller area compared to that in nonhuman primates. Some have argued that the brain first underwent size expansion prior to reorganization, while others maintain that reorganization predated brain expansion. To help resolve this question, we provide a description of two male, common chimpanzee (*Pan troglodytes*) brains, YN77-111 and YN92-115, which clearly display a more posterior lunate sulcal morphology than seen in other chimpanzees. These data show that neurogenetic variability exists in chimpanzees, and that significant differences in organization (e.g., a reduced PVC) can predate brain enlargement. While the human brain has experienced numerous expansion and reorganization events throughout evolution, the data from these two chimpanzees offer significant support for the hypothesis that the neurogenetic basis for brain reorganization was present in our early fossil ancestors (i.e., the australopithecines) prior to brain enlargement. Anat Rec Part A 273A: 594–602, 2003. © 2003 Wiley-Liss, Inc.

Key words: brain evolution; chimpanzee; primary visual cortex; lunate sulcus; human evolution

The evolution of the human brain has encompassed at least three major shifts from a pongid precursor. The first was an increase in overall brain size from roughly 400 ml to about 1400 ml during the past 3–4 million years. The second, and possibly most important, major shift in brain evolution was a reorganization of the brain—particularly of the cerebral cortex, which is associated with complex cognitive behavior (Holloway, 1966, 1995, 1996). The third major shift was an increased degree of cerebral asymmetry, which appears to be most strongly developed in *Homo sapiens*. While there is no disagreement that the brain became reorganized sometime during human evolution, there is controversy over whether this reorganization took

place before or after brain enlargement (Tobias, 1971, 1975; Falk, 1980, 1985, 1991; Holloway, 1985, 1995; Jeri-

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*Correspondence to: Douglas C. Broadfield, Department of Anthropology, Florida Atlantic University, 777 Glades Rd., Boca Raton, FL 33431-0991. Fax: (561) 297-2221. E-mail: broadfie@fau.edu

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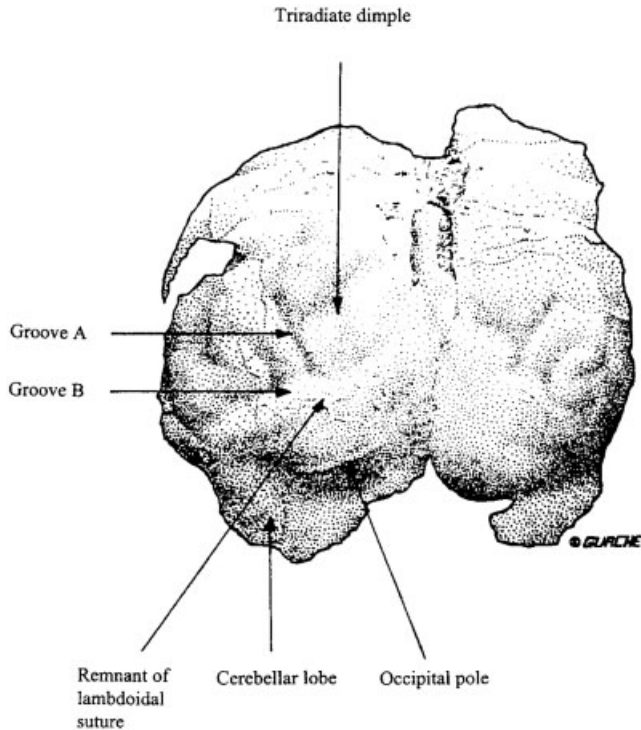


Fig. 1. Occipital view of Hadar AL 162-28 brain endocast of *A. afarensis* showing the proposed gyri and sulcal pattern, which suggests a more posterior, human-like placement of the LS. Groove A is the intraparietal sulcus, and groove B is either the LS or a depression created by the inferior lip of the posterior portion of the parietal bone (see Holloway, 1983a, for discussion).

son, 1991). One area in which reorganization toward the modern human condition may have developed early in hominid evolution is the primary visual striate cortex (PVC) (i.e., area 17 of Brodmann). A reduction in the volume of this primary sensory cortex may have signaled an increase in the adjacent posterior parietal association cortex, which is clearly related to complex cognitive processing (Platt and Glimcher, 1999; Culham and Kanwisher, 2001). For example, one of the present authors previously interpreted (Holloway, 1981, 1983a; Holloway and Kimbel, 1986) the position of the lunate sulcus (LS) in the Taung (*Australopithecus africanus*) and Hadar (*A. afarensis*) endocasts (Fig. 1) as being in a more posterior, human-like position, rather than in the more anterior or pongid (see Fig. 3a) position, as advocated by Falk (1983, 1985, 1986). This discussion concerning possible early cortical reorganization underlines the central question of human brain evolution: When in the course of hominid evolution did reorganization—specifically, a reduction in the amount of PVC relative to other cerebral structures—take place?

The volume of the striate cortex in humans is considerably less than what is expected in other primate groups (Holloway, 1976, 1979). Based on data of Stephan et al. (1981), the volume of the human PVC is roughly 2.28% that of the cerebral cortex, whereas in chimpanzees (5.28%) it is more than double that amount. In primates the correlation between the logs (base 10) of brain volume

and the volume of the striate cortex is very linear, being about 0.98. When the residual of the human value is calculated from a nonhuman primate regression line, the residual is about 121% less than expected. For the lateral geniculate body, the residual is 144% less than expected. From this it is clear that the amount of PVC in the human brain is dramatically less relative to that of its closest relative, the chimpanzee. This distinction between modern humans and nonhuman primates indicates that the general organization of the human brain is unique among the primates. Thus, from current evidence, it would appear that reorganization of the brain occurred exclusively within the hominid clade.

The reduction of the overall cortical area occupied by the visual cortex most likely does not represent a critical event in cognitive evolution on its own, and the reduction of the area occupied by the PVC does not come at the cost of impaired visual function. Indeed, the reduction of the visual cortex may have been due to a relative increase in the parietal cortical association areas of the occipital lobe and/or possible enlargements of the para- and peristriate cortical areas, which have a role in adaptive cognitive behavior (Holloway, 1979, 1983b, 1995). The timing of these events in human brain evolution is unclear, given the controversy over interpretations of fossil australopithecine brain endocasts. Armstrong et al. (1991), Falk (1985), and Jerison (1984, 1991) support the hypothesis that this reorganization of the brain took place after the brain enlarged (and, indeed, that such an enlargement was required), while Holloway (1983a, 1992) believes that the reorganization began within the australopithecine clade prior to the brain expansion that occurred within the genus *Homo*. If it can be demonstrated that modern chimpanzees have the neurogenetic ability to reduce PVC volume without brain enlargement, it would be more likely that similar events could have occurred in *Australopithecus* before brain enlargement. This finding would be compatible with the sulcal morphology found in both the Taung and Hadar 162-28 brain endocasts.

More recently, studies on the brains of our closest living relatives, the chimpanzee, have demonstrated that certain aspects of the cerebral cortex may have originated prior to the ape-human split. For example, it has been reported that the planum temporale (PT) of the common chimpanzee (*Pan troglodytes*) displays human-like leftward asymmetry (Gannon et al., 1998; Hopkins et al., 1998). This is clear evidence of a shared character state in the organization of the brain that must extend back some 5–7 million years. While the PT plays an important role in human language behavior, its role in the chimpanzee is uncertain. One possibility is that gesturo-visual and other nonverbal forms of social communication between chimpanzees are more complex than we thought. More recently, other researchers have reported chimpanzee-human homologues in various brain regions. For example, Nimchinsky et al. (1999) showed that only African apes and humans possess large, spindle-shaped cells in layer Vb of the anterior cingulate cortex. Other studies have demonstrated ape-human homologues in the morphology of the Sylvian fissure (Gannon et al., 2001), the lack of a dense cytochrome oxidase staining layer IVa of the primary visual cortex (Preuss et al., 1999), and asymmetry in the inferior frontal gyrus (Cantalupo and Hopkins, 2001) (however, the latter finding remains controversial, see Sherwood et al., 2003).

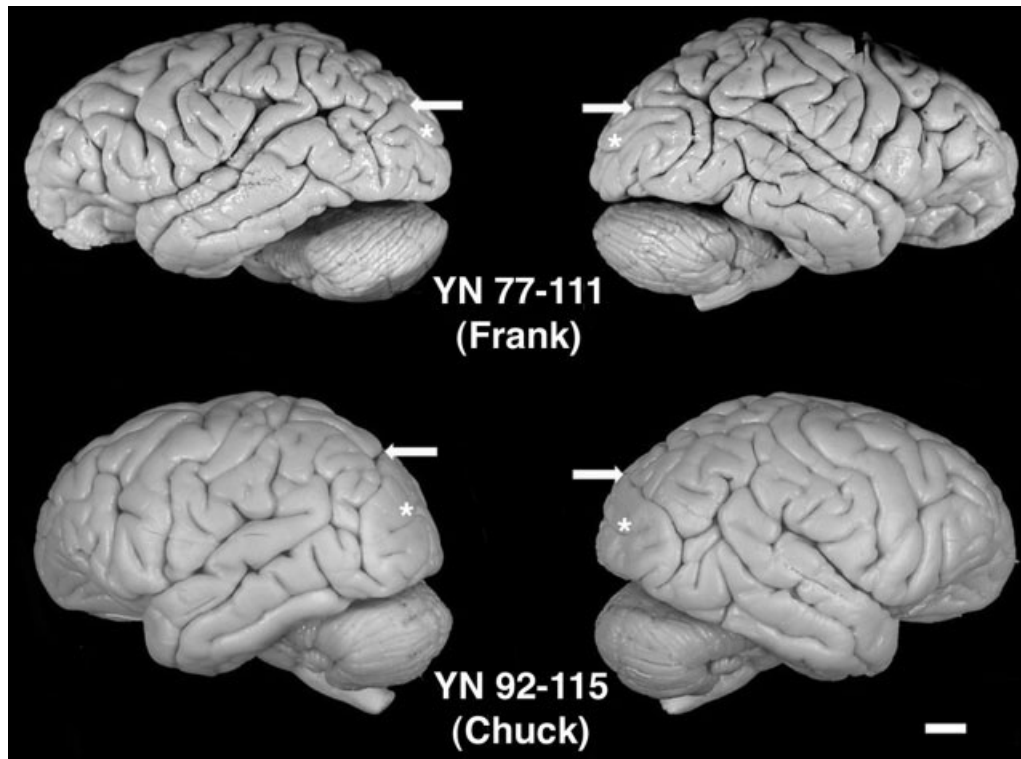


Fig. 2. Lateral views of the left and right hemispheres of YN77-111 (Frank) and YN92-115 (Chuck) with the LS (arrow) and lateral calcarine fissure (*). Bar = 1 cm.

These findings, especially those of Preuss et al. (1999), strongly suggest that certain patterns of cortical organization relating to cognition may have been established prior to the appearance of the genus *Homo*. While it is possible that features such as PT asymmetry are merely examples of parallel evolution in *Pan* and *Homo*, this is highly improbable, since it has been shown that *Pongo* and *Gorilla* also display human-like asymmetry in this region (Gannon et al., 2001). The simplest explanation would be that these are shared characteristics. If so, this would indicate that the earliest hominid ancestor also displayed a similar morphology. More directly, however, it is well appreciated that the amount of PVC found in modern humans is variable (Gilissen et al., 1995; Gilissen and Zilles, 1995, 1996), suggesting that the ontogenetic development of the PVC varies within the human species. In addition, there is strong evidence that the volume of PVC is significantly larger in Australian aborigines than in Europeans (Klemp et al., 1994). These two findings show that there is neurogenetic variability in the amount of PVC that modern humans display, indicating that this feature is an ancient feature of the hominid brain relative to more derived cortical structures.

While the origins of certain human cerebral gyri and sulci may be ancient, it has been assumed that the organization of the human brain (e.g., the amount of PVC) is unique to the genus *Homo* (Jerison, 1984, 1991; Falk, 1985). However, the discovery of two male, common chimpanzee (*Pan troglodytes*) brains has forced us to reconsider the uniqueness and origins of human cerebral organization (Fig. 2). In two earlier papers (Holloway et al., 2001a,

b), we briefly described the morphology of the PVC in gross terms for these chimpanzees. Here, we extend our analyses to show that the histological features of their PVCs clearly show a close correspondence with the gross morphology.

There is an almost invariable relationship between the morphological landmarks that help define the PVC in the great apes (Connolly, 1950; Shantha and Manocha, 1969; Holloway, 1985). The PVC is bounded anteriorly by the LS. Moreover, the position of the LS is usually in a significantly anterior position in pongids as compared to modern humans, in which the LS is seldom recognizable. When it does appear in humans, it is far more posteriorly located than is seen in any nonhuman primate. In both groups, the intraparietal sulcus (IP) separates superior and inferior parietal lobules. The IP in nonhuman primates normally abuts the LS at the most anterodorsal part of its curvature. In addition, the lateral calcarine (LC) fissure often runs diagonally from the occipital pole in a dorsolateral direction toward the LS, but does not reach it. It is this pattern that appears almost invariably in pongid brains (see Fig. 3a). However, two common chimpanzees have been found to display an occipital morphology more reminiscent of hominids than any other pongid heretofore examined.

MATERIALS AND METHODS

Subjects and Tissue Preparation

We received from the Yerkes Regional Primate Center, Emory University, two adult, male common chimpanzee (*Pan troglodytes*) brains with necropsy numbers YN77-111

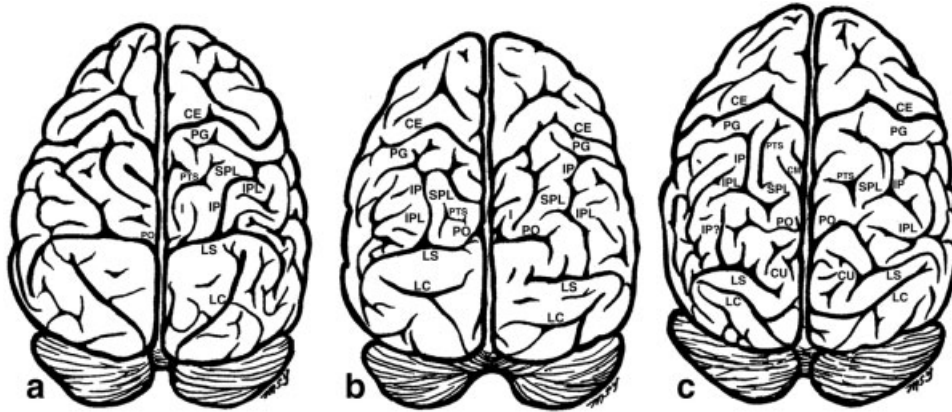


Fig. 3. Dorsal views of a typical chimpanzee brain (a), the brain of Chuck (b), and the brain of Frank (c). CE, central sulcus; CM, sulcus cinguli; CU, cuneus; IP, intraparietal sulcus; IPL, inferior parietal lobule; LS, lunate sulcus; LC, lateral calcarine sulcus; PG, postcentral gyrus; PO, parieto-occipital sulcus; PTS, superior parietal sulcus; SPL, superior parietal lobule.

(Frank) and YN92-115 (Chuck) (Figs. 2 and 3b, c). Each specimen was immersion-fixed in 10% neutral formalin, and examined for visible pathologies. No pathologies were found that would suggest the observed morphology of the brains was due to illness. Moreover, both individuals apparently exhibited normal behaviors, without any recognizable prodigious physical, mental, or visual abilities, while alive (J. Dahl, personal communication). Each brain was weighed using a volume-displacement method (Holloway, 1980). Comparative observations demonstrated that the frontal and temporal morphology, and the position of the central sulcus were consistent with proportions and positions observed in other chimpanzees. Thus, the regions of interest were narrowed to the parietal and occipital lobes. Arc and linear chord measurements were made to determine the length of each hemisphere, the arc length of the LS from the occipital pole, and the width of the occipital lobe. Each brain was then photographed and cast, and compared to other chimpanzee brains ($n = 71$) housed at Columbia University, the Smithsonian Institution (NMNH), and Mount Sinai School of Medicine.

Histology

To determine whether the PVCs in Frank and Chuck were anteriorly demarcated by the LS, the occipital lobes were histologically examined. The occipital lobe was removed by sectioning the cortex just anterior to the parieto-occipital sulcus, thereby including part of the posterior parietal lobe on each hemisphere (Figs. 4 and 5). With the occipital blocks removed, each section was embedded and freeze-sectioned at $40\ \mu\text{m}$ in the sagittal plane from medial to lateral. The subsequent sections were alternately stained using thionine and Weil methods. Each section was examined with a light microscope. The LS of each section was determined as the anterior-most complete gyrus and confirmed by comparisons to photographs and casts of each brain. Confirmation of the PVC was made by identification of the stripe of Gennari (outer band of Bailarger, layer IVb).

RESULTS

Frank

In the brain of Frank, the LS is in a more posterior position than is found in most adult chimpanzees (Connolly, 1950; Shantha and Manocha, 1969) (Figs. 2 (top) and 3c). The arc distance from occipital pole (OP) to LS is usually about 30–35 mm in chimpanzees, but in Frank it is about 20 mm on the right and left sides. On the left side the IP terminates before reaching the LS. In addition, the LS possesses a superior limb, which may be the posterior extension of the interrupted IP. On the right side the IP exhibits a similar morphology, and the IP is noncontinuous as it travels toward the LS. As a result of the tortuous path of the IP, both hemispheres exhibit a gyral morphology unlike that of other chimpanzees. The IP on both sides bifurcates before reaching the LS, and there is a slight extension of the superior parietal sulcus. This suggests a more complicated and highly folded parietal cortex, especially within the inferior parietal lobule.

In other chimpanzee brains, the parieto-occipital sulcus (PO) is continuous with the LS at its medial border as a small superiorly extending branch. In Frank, however, the PO is positioned more anteriorly and is separate from the LS in both hemispheres. Thus, the normal extension of the IP toward the LS is interrupted. This morphology is supported on the right side by the extension of a postero-inferior projection of the PO, connecting it with the LS. On the left side, the PO also projects toward the LS, although the path is more tortuous and incomplete. Based on this morphology, much of the expansion resulting in the more-posterior LS in this individual is due to an expansion of the cuneus and the inferior parietal lobule.

A histological analysis of Frank revealed that the area identified as the LS was indeed the anterior border of the PVC (Fig. 4). Through all sections, the stripe of Gennari was observed to end at or just posterior to the LS. There was no continuation of the stripe of Gennari anteriorly within the region bounded by the LS and PO. Moreover, the stripe of Gennari was not observed in the region just medio-superior to its termination. Thus, in Frank, the

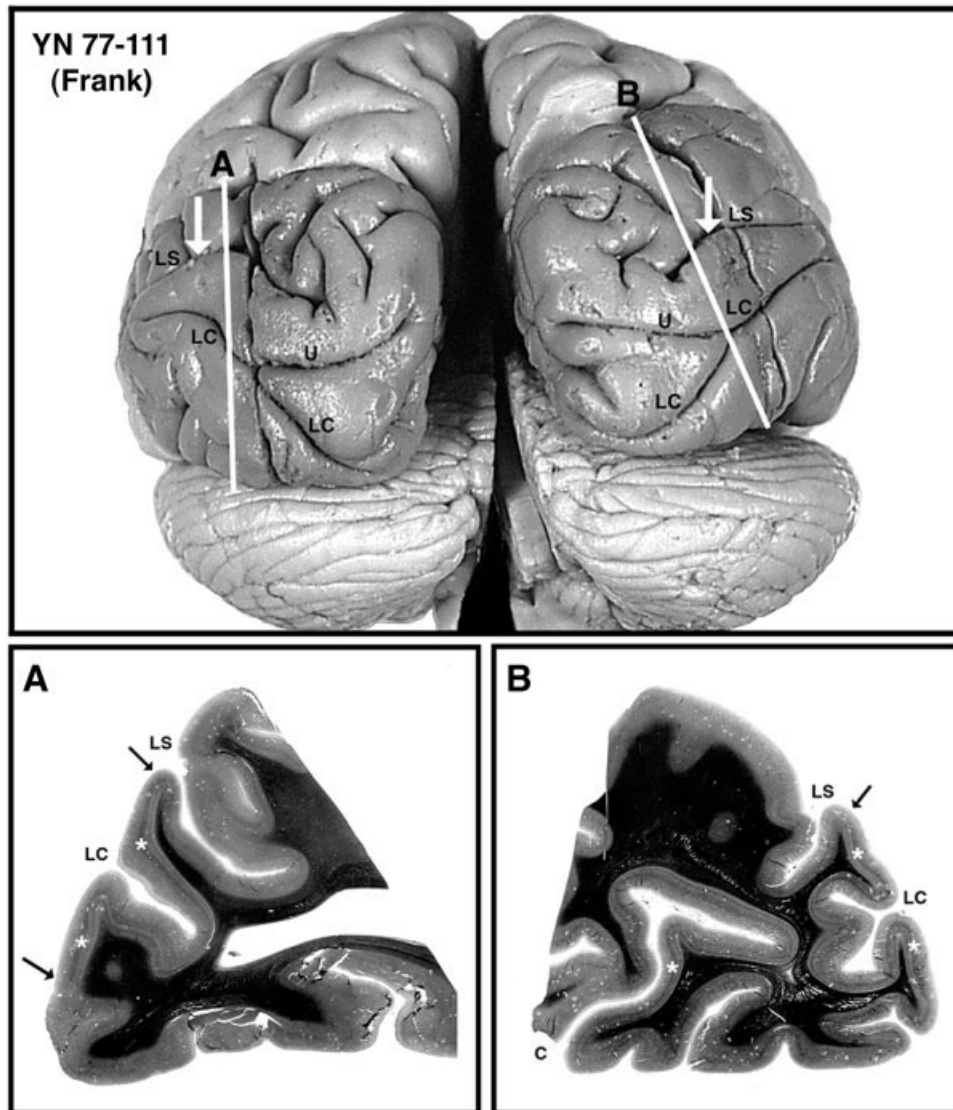


Fig. 4. Occipital views of the brain from Frank (YN77-111) with sample Weil stain histological sections. The region of interest is indicated by the dark shaded regions on the posterior cerebrum. Histological section **A**: Left side, corresponding to the highlighted area on the left

occipital lobe. Histological section **B**: Right side, corresponding to the highlighted area on the right occipital lobe. LC, lateral calcarine; LS, lunate sulcus; U, superior ramus LC; *, stripe of Gennari; white arrow, LS; black arrow, anterior and posterior boundaries of PVC.

area occupied by the PVC is smaller than that observed in other chimpanzees.

Chuck

Chuck differs from Frank in that the left hemisphere shows the typical anteriorly-placed LS, while the right hemisphere shows a posterior placement of the LS (Figs. 2 (bottom) and 3b). In the left hemisphere the IP extends from just posterior to the central sulcus and intersects with the LS. In addition, the LS extends from its medial connection with the short PO laterally to the lateral-most edge of the occipital lobe, a pattern consistently seen in other chimpanzees. The right hemisphere, however, exhibits a morphology more similar to that seen in Frank. On this side the IP extends further posteriorly than the

left side. However, unlike in Frank, the IP clearly terminates at the LS, resulting in a less tortuous superior parietal lobule.

The PO of the right hemisphere in Chuck is at the same position as the LS on the left, and approximately 11 mm superior to the right LS. The right PO extends laterally approximately 17 mm before bifurcating into anterior and posterior rami. In Chuck, the PO is situated closer to the LS than it is in Frank. Moreover, the extension of the IP to the LS in Chuck, as opposed to the interrupted IP in Frank, indicates that there is expansion in three separate areas of the right posterior cerebral hemisphere. First, there is a slight expansion of the cuneus to occupy the area between the PO and LS. Second, there is a posterior expansion of the superior

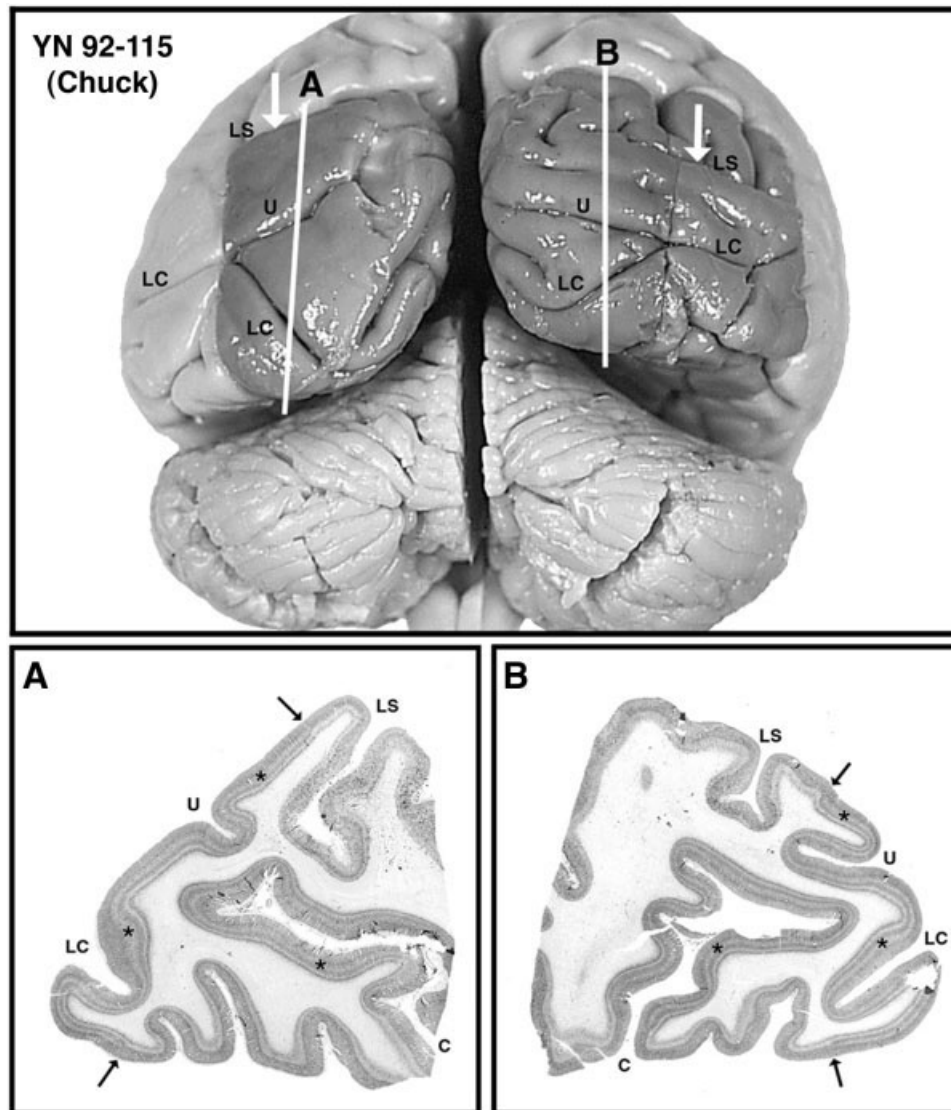


Fig. 5. Occipital view of the brain from Chuck (YN92-115) with sample thionine stain histological sections. The region of interest is indicated by the dark shaded regions on the posterior cerebrum. Histological section **A**: Left side, corresponding to the highlighted area on the left

occipital lobe. Histological section **B**: Right side, corresponding to the highlighted area on the right occipital lobe. LC, lateral calcarine; LS, lunate sulcus; U, superior ramus LC; *, stripe of Gennari; white arrow, LS; black arrow, anterior and posterior boundaries of PVC.

parietal lobule. Finally, there is a posterior expansion of the inferior parietal lobule.

The histology of the region confirms these observations (Figs. 5 and 6). The stripe of Gennari on the right and left sides is observed to end at the base of the LS. Moreover, the stripe does not continue into the region occupied by the cuneus or superior parietal lobule. Thus, the histological extent of the stripe of Gennari in Chuck clearly shows that the extent of PVC is neurogenetically variable in chimpanzees (and even varies between hemispheres), and thus is similar, if not homologous, to the variability seen in modern humans. This suggests to us that since humans and chimpanzees (*Pan*) shared a common ancestry some 5–7 million years ago, it is likely that some of the earliest hominids, such as *Australopithecus afarensis*, displayed left–right variation in this region.

Morphometric Analysis of the LS

Measurements on the position of the LS in Frank and Chuck were compared to a sample of 71 chimpanzee hemispheres that displayed the lunate in the more common anterior position. In the sample of normal chimpanzee brains, the mean distance from the occipital pole to the LS is 33 mm, with a standard deviation (S.D.) of 4.6 mm, and an average brain weight of 153.36 g for each hemisphere (S.D. = 34.5 g). The OP–LS distance in Frank is 22 mm (left) and 20 mm (right). In the case of Chuck, the right OP–LS distance is 20 mm, while the left OP–LS distance is 35 mm, a value most often seen in other chimpanzee brains (Table 1). There is a statistically significant difference in the OP–LS distance measurements for the right hemispheres of Frank and

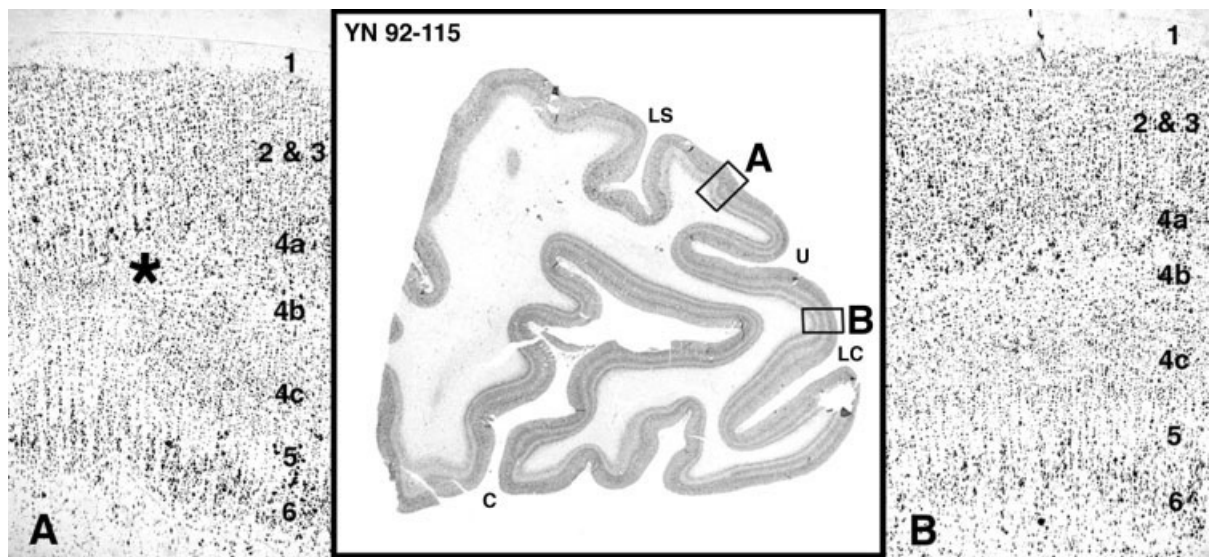


Fig. 6. Thionine section from Chuck (Fig. 5B), demonstrating the layers of the PVC. Note the stripe of Gennari (layer 4b). * indicates the end point of the stripe of Gennari and PVC.

TABLE 1. Arc measurements on chimpanzee and Hadar cast

Specimen	Brain weight (ml)	Right side		Left side
		OP-LS	SD	OP-LS
Chimpanzee (N = 71 ^a)	153.36 ± 34.5 ^b	33 ^c	4.6 ^c	
Frank (YN77-111)	388.96	20		22
Chuck (YN92-115)	364.8	35		20
Hadar AL 162-28	385-400			15.5

^aHemispheres.

^bGrams.

^cAverage for left and right hemispheres.

Chuck from the average chimpanzee at the 0.001 level, using one-sample t-tests (SPSS). In addition, the average chimpanzee OP-LS distance is statistically significantly different from the Hadar AL 162-28 endocast, and from modern *Homo sapiens*. Indeed, the endocast of the newly discovered Stw 505 A. *africanus* from Sterkfontein, South Africa, shows an LS distance from a presumed OP that is within the range of both Frank and Chuck's reduced measurements. If these findings are confirmed (Holloway et al., unpublished results), they should lay to rest the controversy concerning the position of the LS in *A. africanus* (see below).

DISCUSSION

While the position of the LS observed in Frank and Chuck may be rare, it does indicate that the neurogenetic basis for reduction in volume of PVC is not exclusive to modern humans. Furthermore, study of histological sections of these two chimpanzee brains confirms that the stripe of Gennari (layer IVb), which helps define the cytoarchitecture of the PVC, is bounded by the LS in both chimpanzees, and in both individuals it appears that the visual cortex extends, in part, to its normal sulcal boundaries. While the morphology of the anatomical boundaries of the PVC is consistent with that of other primates, the area occupied by the visual cortex in Frank and Chuck is

certainly significantly smaller than what is normally observed.

In other chimpanzees, the PO and LS are assumed to be portions of the same general sulcus demarcating the anterior border of the PVC and occipital lobe. In Frank and Chuck, however, only the PO occupies the normal anterior position of the occipital lobe, and the area occupied by the PVC is reduced. Thus, the area occupied in other chimpanzees by the PVC is instead occupied by various extensions of the superior and inferior parietal lobules in these two individuals. In this way, Frank and Chuck approximate the condition seen in humans, even though the observed morphology is not synonymous with the human condition.

In humans, the parietal lobe is expanded more posteriorly than is observed in the extant great apes. The area occupied by the PVC in humans is reduced, and the cuneus is observable often only on the medial border of the occipital lobe. In addition, the position of the cuneus in humans is similar to that observed in chimpanzees. However, both Frank and Chuck appear to possess an expanded cuneus. What this condition may have meant for these two individuals is difficult to discern, since neither animal was tested in a manner that would assess their individual visual skills. Moreover, it is also difficult to

understand what role parietal expansion played in these two individuals.

The discovery of the morphology observed in Frank and Chuck represents an important step in understanding human brain evolution, because it demonstrates that the neurogenetic basis for parietal expansion is not unique to the modern human genome. Furthermore, if the same neurogenetic bases for variability in reduction of the PVC are present in *Pan* and *Homo*, why would the australopithecines necessarily be without such variability? We cannot speak with great confidence about lunate sulcal variability, because unfortunately there are not enough well-preserved australopithecine brain endocasts to examine. On the other hand, several other specimens—the Stw 505 (Holloway et al., unpublished results), and particularly the Taung and Hadar AL 162-28 endocasts—tend to show morphological features. This indicates that if an LS did exist in this genus, it was in a non-pongoid, in a more posteriorly located position than is observed in the brains of today's pongids (particularly the chimpanzee) (Holloway, 1983a, 1985; Falk, 1985, 1986, 1991).

With an OP-LS distance of 15.5 mm, the Hadar 162-28 *A. afarensis* endocast is 3.49 S.D.s posterior to the mean chimpanzee value (Table 1). When the measurements for Frank and Chuck are included, the Hadar specimen's OP-LS distance is still 2.93 S.D.s posterior to the chimpanzee mean. Such an S.D., as currently available from these samples, indicates a very statistically significant difference between the chimpanzee and *A. afarensis* positioning of the LS, if indeed the lunate can be unambiguously determined on the australopithecine brain endocasts. The morphometric features of the two chimpanzee brains discussed here provide relevant evidence of early hominid brain evolution. For example, the distance from the OP to the proposed posterior part of IP on the Hadar endocast approximates the position of these features in Frank and Chuck, if one considers the effect of fixation artifact (i.e., shrinkage from years of fixation in formalin). This is demonstrated by the overall reduction in the volume of chimpanzee hemispheric volumes over time, which is often less than the volume calculated for the Hadar specimen of 385–400 ml. We believe this is strong evidence that if the posterior part of the IP is correctly identified on the Hadar specimen, and Falk's (1985, 1986) assertion that the LS is underneath the remnant of the lambdoid suture is correct, the LS is in a more human than pongid position. Furthermore, the obverse part of our argument must also apply to australopithecines. That is, if there were some common form of neurogenetic basis for these morphological variations, we would expect the LS to be in a more anterior position in some of the australopithecines, as it is in most *Pan* brains. To date, none have appeared.

The human characteristics of the PVC apparently began to develop before the ape–human split. For example, Preuss et al. (1999) found that apes and humans lack a cytochrome oxidase, dark-staining layer 4A band in area V1. In the light of the current data from Frank and Chuck, it appears that other aspects related to the organization of the PVC also may have arisen before the advent of the hominid clade. The posterior advancement of the parietal lobe into that area occupied by the PVC in apes does not appear to require any significant genetic shift. In part, this expansion of the parietal may be the result of general ontogenetic events in the brain. It has been shown in

humans that the brain grows in a posterior direction, with frontal development occurring before occipital development (Sowell et al., 2001; Thompson et al., 2001). Thus, the development of more anterior structures can affect the position of more posterior elements. Although it is uncertain whether the same scenario takes place in apes, it is possible that this growth pattern is relevant to that group. For example, Semendeferi et al. (2002) demonstrated that the percentage of the cortex occupied by the frontal lobe in great apes is similar to that in humans. This implies that the general growth of the cerebrum in apes and humans is similar. One possible reason for the unique presentation of the LS in Frank and Chuck is that there was additional development of the inferior parietal lobule and a portion of the superior parietal lobule that permitted asymmetric development of the occipital lobe, such that the LS was more posteriorly positioned, and the PO and cuneus were more pronounced and laterally placed.

The condition seen in Frank and Chuck provides evidence for the early evolution of hominid brain reorganization.¹ The observed morphology in these individuals supports the argument made earlier by Holloway (1975, 1981, 1983a, b, 1984, 1995, 1996) that the LS was more posteriorly placed by at least the time of *A. afarensis*. This would indicate that some cortical reorganization occurred some 3–4 million years ago, such that there was a relative increase in posterior cortical association areas. Most importantly, Frank and Chuck clearly demonstrate that a posteriorly placed LS does *not* require any increase in brain size. If these assumptions are correct, it would likely mean that natural selection had operated on aspects of cortically-mediated adaptive behavior well before cortical brain tissue expanded to any *Homo* level. However, we caution that Frank and Chuck do not provide any evidence for the existence of the ontogenetic conditions necessary to provide for the cognitive morphology seen in hominids. What they demonstrate is that while cortical reorganization may have been a feature associated with early hominid brains, some critical aspects of human behavior (perhaps language, perhaps tool-making—indeed, the prerequisites of a cultural adaptation) may have come somewhat later, as populations accumulated other mutations that resulted in further differential development of cortical areas relevant to human cognition. Nevertheless, it can be postulated from these data that many of the cortical and cognitive features that are assumed to be unique to humans are older than many paleoanthropologists believe.

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¹A third, newly uncovered chimpanzee brain (Sellers) has been found to have an expanded parietal cortex and cuneus, and a posteriorly positioned LS. However, unlike the PVCs in Frank and Chuck, the PVC in Sellers does not appear to be reduced in volume.

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