

Looking for the Lunate Sulcus: A Magnetic Resonance Imaging Study in Modern Humans

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ABSTRACT

The position of the lunate sulcus in fossil endocasts (when it can be determined) may serve as a potential marker of cognitive development in extinct hominid species. While the lunate sulcus is reliably present in the brains of great apes and forms the anterolateral boundary of the primary visual cortex, in humans its presentation is much more variable, and even if present, it does not correspond to a functional region. Grafton Elliot Smith, who named the lunate sulcus, claimed that it was homologous in humans and the great apes. Using high-resolution MRI, we assessed the presence/absence and course of the lunate sulcus in 110 adult subjects. We found that in the vast majority of cases, lunate sulci identified on the surface of the occipital lobe are actually composed of smaller sulcal segments that converge into an apparently continuous composite lunate sulcus. We found only 3 examples in 220 hemispheres (1.4%) of continuous lunate sulci that resembled ape lunates in form (albeit in a more posterior position). Composite lunate sulci were found in 32.7% of left hemispheres and 26.4% of right hemispheres. These results, combined with those from histological and functional imaging studies, indicate that human and ape lunate sulci are not homologous structures. We suggest that the extent of functional reorganization of the occipital region during hominid evolution has been underestimated, and that changes in this region were not just passively shaped by expansion of parietal association cortex. *Anat Rec Part 288A: 867–876, 2006.* © 2006 Wiley-Liss, Inc.

Key words: brain; occipital lobe; visual cortex; evolution; endocast

In the early 20th century, anatomist Grafton Elliot Smith (1903, 1904a, 1904b, 1907; see also 1927) published a series of papers in which he attempted to demonstrate that the *Affenspalte*—or “ape sulcus,” located on the posterior lateral surface of the brain and forming the anterior boundary of the occipital lobe—was not unique to apes but could also be found in humans. Obviously, upon demonstration of its existence in humans, “*Affenspalte*” was no longer an appropriate name for the structure, and Elliot Smith renamed it the “lunate sulcus.” In its ideal form, the lunate sulcus forms an arc,

Grant sponsor: National Institute of Neurological Disorders and Stroke; Grant number: Program Project Grant NS 19632; Grant sponsor: the Mathers Foundation.

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Received 6 February 2006; Accepted 4 May 2006

DOI 10.1002/ar.a.20362

Published online 11 July 2006 in Wiley InterScience (www.interscience.wiley.com).

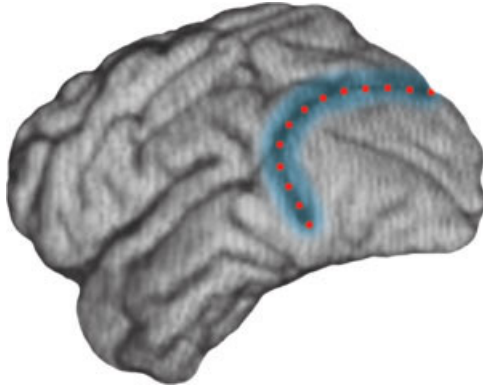


Fig. 1. Three-dimensional MRI reconstruction of the left hemisphere of a chimpanzee brain, with the prominent lunate sulcus highlighted in blue with red dots. (Note that the brain is rotated 45° from a left lateral view towards the occipital pole.)

transversing a large proportion of the lateral surface of the occipital lobe, beginning superiorly close to the medial margin of the hemisphere (Fig. 1). In apes and some monkeys (von Bonin and Bailey, 1947), the lunate sulcus forms the anterior lateral boundary of the primary visual or striate cortex, which is marked histologically by the stripe of Gennari. Using the terminus of the Sylvian fissure as a reference point, the position of the lunate sulcus in humans (when present) is relatively posterior compared to that in nonhuman primates.

In his publications, Elliot Smith provided drawings of a few examples of lunate sulci in modern human brains. He claimed that in a “considerable proportion” of human brains, the stripe of Gennari terminated at the lip of the lunate sulcus, supporting the hypothesis that it was homologous in modern humans and apes (Elliot Smith, 1904a: p. 440). On the other hand, Elliot Smith also observed that it was an extremely variable structure; for example, it was never “exactly symmetrically disposed” in the brain’s two hemispheres and could take a “transverse, oblique, or horizontal” course (Elliot Smith, 1904a: p. 448). Elliot Smith noted that previous researchers had not been able to make much sense of the human lateral occipital sulci, although given the variability in the region, this is not surprising.

In the field of human evolution, the lunate sulcus took on increased importance with the discovery of the Taung child, *Australopithecus africanus*, by Raymond Dart (1925), a former student of Elliot Smith’s. In his evaluation of the Taung natural endocast, Dart identified a lateral occipital groove as the lunate sulcus and argued that its relatively posterior position (compared to a great ape) indicated that there had been expansion in the “parieto-temporo-occipital” association areas, at the expense of the primary visual cortex. Thus, the position of the lunate sulcus was one of several features that led Dart to conclude that the Taung specimen was not simply an extinct ape but an early hominid.

Unlike several of his contemporaries, Elliot Smith (1925) was quite willing to accept Dart’s interpretation of Taung, initially citing the position of the lunate sulcus as one of the key features suggestive of its human affinities. Interestingly, in a subsequent and reasonably complete appraisal of Taung, Elliot Smith (1927) pointed to

overall brain size (large for a juvenile) and expansion of the prefrontal region as the characteristics visible in the Taung endocast that indicated it was a hominid. He did not mention the lunate sulcus in Taung, nor did he label it in a drawing of the endocast. Much later, the position of the lunate sulcus in Taung became the subject of intense debate (Falk, 1980, 1983, 1985, 1989, 1991; Holloway, 1981, 1984, 1985, 1991). Recently, it has been claimed that Dart’s assessment of the position of the lunate in Taung has been reaffirmed (Broadfield et al., 2005), and the proposed identification of a lunate in a posterior position in the endocast of another *A. africanus* specimen (Stw 505) indicates that brain reorganization in a “human-like” direction may have occurred by this juncture in hominid evolution (Holloway et al., 2004a). The lunate sulcus has also been used as a marker of cognitive ability in other extinct hominid species. Falk et al. (2005) have identified a posteriorly placed lunate sulcus in the endocast of *Homo floresiensis* specimen LB1 and argued that, despite its small overall brain size, this specimen may have had the capacity for “higher cognitive processing.”

In order to assess realistically the evolutionary significance of the position of the lunate sulcus in fossil forms, it is necessary to develop an accurate picture of its presentation in contemporary species. In chimpanzees, the lunate sulcus is reliably found as a deep sulcus in a fairly localized region (relative to other sulci), marking the anterior limit of the occipital lobe. However, the recent discovery of two chimpanzees who have lunate sulci in a markedly posterior position provides new insights into evolution in this brain region (Holloway et al., 2001, 2003). Holloway et al. suggest that the presence of these posteriorly placed lunates in modern chimpanzees indicates that the human-chimpanzee common ancestor possessed the neurogenetic variability underlying functional reorganization in this brain region; furthermore, such reorganization could have occurred in the absence of significant cerebral expansion.

Despite Elliot Smith’s confident appraisal of the lunate sulcus in humans, variability in the lateral occipital region is extensive. This is evident when comparing different anatomical texts. Holloway et al. (2004b) point out that in humans the lunate sulcus is frequently “fragmented.” Duvernoy (1999: p. 7) shows the lunate as a minor sulcus forming a T-terminal at the end of the lateral occipital sulcus (although see p. 205 for a more prominent example). Such terminal endings are also commonly found in the occipital region at the posterior ends of the intraparietal and inferior temporal sulci, so identifying any one of these minor sulci as the “lunate sulcus” would be an arbitrary decision. Ono et al. (1990: p. 74) provide two photographic examples of lunate sulci. Both are minor sulci, with somewhat different forms; both transverse a substantial portion of the posterior lateral surface of the occipital lobe. Ono et al. (1990) reported that no lunate could be found in 40% of the right hemispheres and 36% of the left hemispheres. In an advanced teaching brain atlas (Nolte and Angevine, 2000), no lateral occipital sulci are named, likely a reflection of the variability in this region.

In his extensive analysis of the lunate in human brains, Connolly (1950) divided the lunate sulcus into five different forms (including absent or fragmentary). His meticulous drawings demonstrate that such a classi-

ficatory scheme is itself evidence of the high variability in the region. The assignment of different sulcal segments or fragments to the lunate seems somewhat arbitrary and based on an a priori assumption that a lunate sulcus in the posterior lateral occipital lobe should typically be present. Based on his own studies and those of earlier researchers (for references, see Connolly, 1950), Connolly believed that a lunate sulcus in some sense homologous to that seen in apes could be found with reasonable frequency in modern humans. However, he acknowledged that there were some problems in interpreting the literature, especially in terms of detecting the frequency of its appearance (Connolly, 1950: p. 234): "Obviously the criterion for judging the presence of a sulcus lunatus differs among the authors, some recording perhaps only the primitive type (i.e., a strong ape-like lunate sulcus). The form and position of the s. lunatus differ so markedly in different specimens that unless these are accurately described or illustrated, the percentages recorded do not give the desired information."

In this study, we report on the presence/absence and form of the lunate sulcus in modern humans *in vivo* as assessed by high-resolution magnetic resonance imaging. MRI scans were obtained from a total of 110 subjects. One of the advantages of MRI compared to autopsy studies (aside from avoiding postmortem changes in the brain) is that features identified on the surface of the brain can also be analyzed in their depth from multiple 2D slice orientations. In looking for the lunate sulcus, we find that in the majority of cases, when a lunate can be identified on the brain's surface, it is typically composed of multiple sulcal segments, which are visible on contiguous axial slices through the occipital region of the brain. We will argue, therefore, that modern humans do not typically possess a lunate sulcus homologous to those seen in great apes; furthermore, if modern humans do not possess a strong lunate sulcus, the phylogenetic significance of a posteriorly placed lunate in some extinct hominids needs to be reassessed.

MATERIALS AND METHODS

Subjects

Subjects included 87 right-handed and 23 left-handed individuals (assessed by the Oldfield-Geschwind Hand-Edness Inventory; right-handers had a mean score of 95 ± 11 ; left-handers had a mean score of -97 ± 4.4). The right-handed subjects included 43 men (mean age, 49.4 ± 20.8 years; range, 22–88) and 44 women (mean age, 47.0 ± 16.7 years; range, 23–74). The left-handed subjects included 15 women (mean age, 37.7 ± 12.9 years; range, 18–55) and 8 men (mean age, 34.6 ± 9.3 years; range, 23–47). All subjects were healthy and with no history of neurological or psychiatric illness. The vast majority of our subjects (108 of 110) were of European or European-American descent; 2 were of Asian ancestry. Older subjects (greater than 60 years) were assessed by interview on a case-by-case basis for general health status and medication usage. None had a clinical history of heart disease, hypertension, diabetes, or any other common age-associated disease. All brain MRIs were screened for the presence of visible pathology. All subjects gave informed consent in accordance with institutional and federal rules.

Image Acquisition

Thin-cut T1-weighted MR images were obtained in a GE Signa scanner operating at 1.5 Tesla using the following protocol: SPGR/50, TR 24, TE 7, NEX 1, matrix 256×192 , FOV 24 cm. We obtained 124 contiguous coronal slices, 1.5 or 1.6 mm thick and interpixel distance 0.94 mm. The slice thickness was adjusted to the size of the brain so as to sample the entire brain while avoiding wrap artifacts. Three individual data sets were obtained for each brain during each imaging session. These were coregistered and averaged posthoc using Automated Image Registration (AIR 3.03; UCLA) (Woods et al., 1992; Holmes et al., 1998) to produce a single data set of enhanced quality with pixel dimensions of 0.7 mm in plane and interslice spacing of 1.5–1.7 mm between planes. All brains were reconstructed in three dimensions using Brainvox (Frank et al., 1997), an interactive family of programs designed to reconstruct, segment, and measure brains from MR-acquired images.

Anatomical Analysis

Using 3D MRI reconstructions of each hemisphere, the lateral surface of the occipital lobe was assessed for the presence or absence of a lunate sulcus. As discussed above, the lunate sulcus is clearly highly variable in modern humans. We identified a lunate as any continuous sulcus that transversed (i.e., followed an superior-to-inferior course) a substantial portion of the posterior lateral surface of the occipital lobe (for information on the parcellation of the major lobes, see Allen et al., 2002, 2003; Damasio, 2005). Ideally, this would correspond to a deep sulcus that would be similar to the lunate as seen in a nonhuman primate (albeit in a more posterior position); such a sulcus was found infrequently in our subject group. In most cases, the sulcus we identified as a lunate was relatively small and shallow, similar to those pictured in Ono et al. (1990: p. 74) and to the continuous forms of the lunate recognized by Connolly (1950).

Once identified, the course of the lunate sulcus was marked on the lateral surface of the occipital lobe. Although a sulcus may appear to be continuous on the surface, in many cases a "continuous" sulcus may in fact be composed of several independent segments; these segments align with one another to give the appearance of being a single sulcus (Fig. 2). In order to determine if the lunate sulcus was composed of a single or multiple sulcal segments, the sulcus was marked in contiguous 2D axial slices (0.7 mm slice thickness) through its entire course. Different colors were used to mark different sulcal segments (Fig. 2). We refer to a lunate sulcus that appears to be composed of two or more sulcal segments as a "composite lunate sulcus." Our criteria for classification of the lunate sulcus are summarized in Table 1. Statistical analyses were performed using SPSS for Windows version 11.0.1 (SPSS, Chicago, IL).

RESULTS

In Table 2, frequencies for the presence or absence of the lunate sulcus in each hemisphere, by sex and handedness, are presented. Pearson chi-square tests (for left and right hemispheres separately) indicate that there are no significant differences among the groups (left-

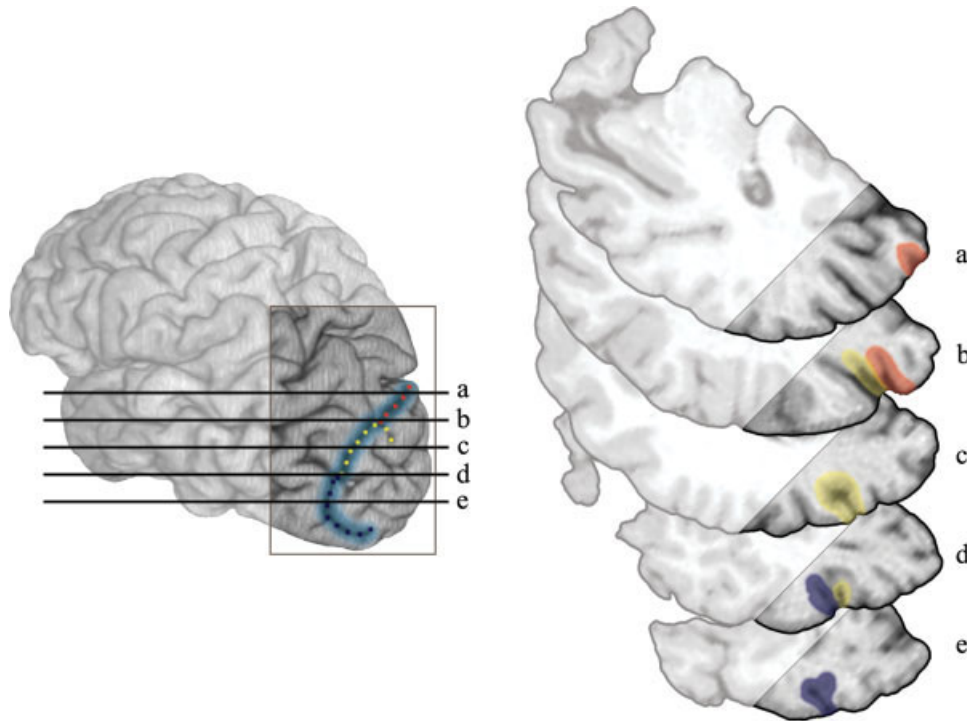


Fig. 2. **Left:** the lateral occipital surface of the left hemisphere of subject 2156 is highlighted. The composite lunate sulcus is shadowed in blue, and the different colored dots indicate the different sulcal segments that comprise the sulcus in this particular example (note that the hemisphere is rotated 45° from a left lateral view toward the occi-

pital pole). **Right:** in the axial slices (a–e), the different sulcal segments are colored in, demonstrating that although a continuous sulcus can be traced on the surface of the brain, it is in fact composed of three separate segments.

TABLE 1. Classification of lunate sulci used in this study

Category	Criteria
<i>Lunate Sulcus</i>	A continuous sulcus that transverses a substantial portion of the lateral surface of the posterior portion of the occipital lobe. When examined in contiguous axial slices, it is clearly composed of a single, continuous sulcus. Corresponds approximately to Connolly (1950) groups 1 and 2, although development of an opercular lip is not necessary (<i>contra</i> Connolly's group 1).
<i>Composite Lunate Sulcus</i>	A continuous sulcus that transverses a substantial portion of the lateral surface of the posterior portion of the occipital lobe. However, when examined in contiguous axial slices, it is clearly composed of portions of two or more separate sulci that converge to form a continuous but irregular sulcus on the surface of the brain. Corresponds approximately to Connolly (1950) group 3.
<i>No Lunate Sulcus</i>	No single or composite continuous sulcus visible that transverses the posterior portion of the occipital lobe. Corresponds approximately to Connolly's groups 4 and 5.

and right-handed, male and female) in lunate or composite lunate sulcus frequencies (chi-square = 5.288; 6 df; $P = 0.507$). When combining all subjects, the frequencies for the left hemisphere are 65.5% no lunate, 32.7% composite lunate, and 1.8% lunate. For the right hemisphere, the frequencies are 72.7% no lunate, 26.4% composite lunate, and 0.9% lunate.

In Table 3, group differences in lunate sulcus asymmetries are presented. Although there is some variation, a Pearson chi-square test indicates that there are no significant differences between the groups for the presence or absence of the lunate in either hemisphere (chi-square = 10.603; 9 df; $P = 0.304$). In all subjects combined, 48.2% do not have a lunate or composite lunate in

either hemisphere, while 10.0% have one in both hemispheres. It is somewhat more common (24.5%) to have a lunate in the left hemisphere alone rather than the right hemisphere alone (17.3%).

Figure 3 presents 3D MRI reconstructions of the posterior lateral occipital surfaces of all subjects possessing a lunate or composite lunate sulcus. In the top row, the three subjects who possess "true" lunate sulci, i.e., those that are composed of a single sulcal segment, are shown. Although the three sulci are quite different from one another, none of them are direct extensions of the intraparietal sulcus or form a T-termination with that sulcus. Many anatomists (e.g., Elliot Smith, 1903; Duvernoy, 1999) refer to the sulcus that forms a T-termination with

TABLE 2. Lunate and composite lunate sulcus frequencies¹

Group (n)/ <i>Hemisphere</i>	No Lunate Sulcus (%)		Composite Lunate Sulcus (%)		Lunate Sulcus (%)	
	<i>Left</i>	<i>Right</i>	<i>Left</i>	<i>Right</i>	<i>Left</i>	<i>Right</i>
RH Female (44)	68.2	72.7	31.8	25.0	0	2.3
RH Male (43)	62.8	69.8	34.9	30.2	2.3	0
LH Female (15)	53.3	73.3	40.0	26.7	6.7	0
LH Male (8)	87.5	87.5	12.5	12.5	0	0

¹RH, right-handed; LH, left-handed.

TABLE 3. Lunate and composite lunate sulcus frequency by hemisphere¹

Group (n)	No lunate in either hemisphere (%)	Lunate or composite lunate in left only (%)	Lunate or composite lunate in right only (%)	Lunate or composite lunate in both hemispheres (%)
RH Female (44)	52.3	20.5	15.9	11.4
RH Male (43)	46.5	23.3	16.3	14.0
LH Female (15)	26.7	46.7	26.7	0
LH Male (8)	75.0	12.5	12.5	0

¹RH, right-handed; LH, left-handed.

the intraparietal sulcus as the “transverse occipital sulcus”; it is clear that these lunate sulci are distinct from a transverse occipital sulcus. In each case, the lunate sulcus is posterior to the preoccipital notch, which is consistent with the common observation in humans that the lunate sulcus is found much more posteriorly than in the great apes.

The remaining lunate sulci pictured in Figure 3 are all composite lunate sulci: although forming an apparently continuous sulcus on the surface of the brain, they are each actually composed of more than one sulcus when examined below the cortical surface (as shown in the example in Fig. 2). By inspection, it is apparent that the occipital sulci are highly variable, even when it is possible to identify a lunate sulcus among the posterior extensions of the intraparietal and superior temporal sulci and the various irregular minor sulci of the occipital lobe. If a typical pattern can be discerned among these composite lunates, it is one in which the superior portion is formed by the extension of intraparietal sulcus (i.e., the transverse occipital sulcus), which then extends downward to form a junction with another occipital sulcus (e.g., the lateral occipital sulcus or occipitopolar sulcus, *sensu* Duvernoy, 1999). Examples of this pattern can be seen in the left hemispheres of 2166 and 2177 and in the right hemispheres of 2230 and 2675 (Fig. 3). In general, Elliot Smith’s observation that the sulci of the two hemispheres are rarely symmetrical in the region of the brain is supported, although a few of the subjects that have composite lunates in both hemispheres do display some symmetry (e.g., 2156, 2176).

In the great apes, the lunate sulcus may be deep enough to form an occipital operculum, a “semilunar fold of cortex which extends forward so as to overlap” a portion of the cortex anterior to the lunate sulcus itself (Elliot Smith, 1903: p. 76). In none of our subjects do we find the development of an ape-like occipital operculum, even in cases where a continuous lunate is relatively strongly marked. The sulci of the lateral occipital lobe

are in general shallow, with the exception of the intraparietal/transverse occipital sulcus.

DISCUSSION

Frequency of Lunate Sulcus in Modern Humans

Our results indicate that a “true” lunate sulcus is quite rare in modern humans; we found only three examples in 220 hemispheres (1.4%). We defined a “true” lunate sulcus as one that is formed from a single continuous sulcus, in contrast to a composite lunate sulcus, which is composed of two or more sulcal segments that can be traced as a continuous sulcus on the surface of the occipital lobe. Composite lunate sulci are much more common (32.7% in the left and 26.4% in the right hemisphere). Overall, about half (51.8%) of the subjects possessed a lunate or composite lunate sulcus in at least one hemisphere.

The lunate sulcus percentages we report here are somewhat lower than those found by earlier investigators. Ono et al. (1990) report that the lunate sulcus was present in 60% of right and 64% of left hemispheres ($n = 25$). It is difficult to compare our results with theirs, since they show only two examples of the lunate and do not provide any explanation of how they defined the sulcus. We agree that the two lunate sulcus examples they show are lunates or composite lunates.

Connolly (1950) provides a more complete account of his classification of the lunate sulcus in 30 “White” and 30 “Negro” brains (we will combine the results for the two groups). He placed the lunates into five different groups: (1) crescentic in form with an opercular lip covering at least part of the transverse occipital sulcus; (2) crescentic in form and wholly separated from the transverse occipital; (3) irregular in form but continuous; (4) interrupted by a “translunate” gyrus; and (5) fragmentary or not identifiable. The percentages for categories 4 and 5 together are 41.6% on the left and 41.7% on the right; these are effectively the percentages for which no

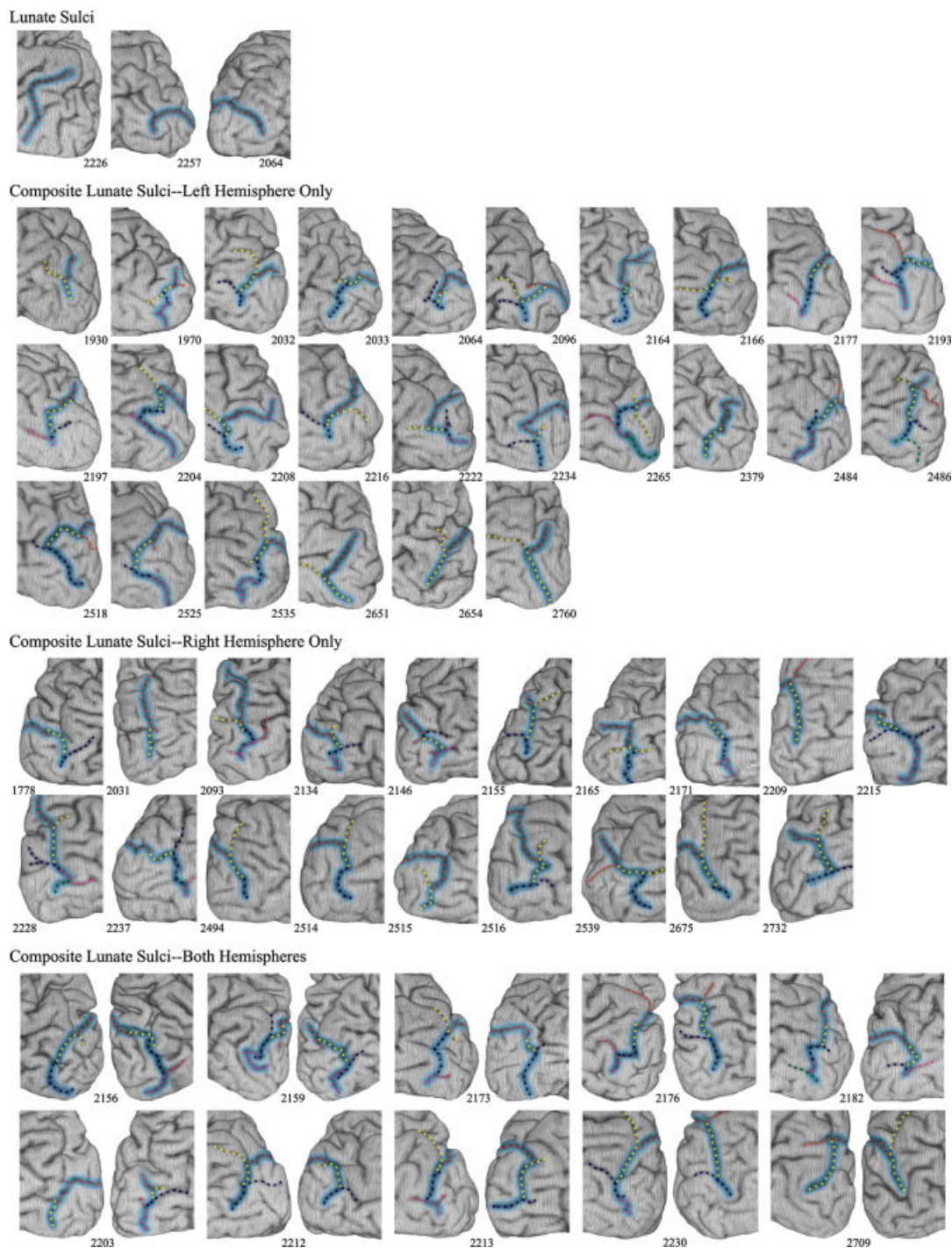


Fig. 3. Views of the occipital lobes of all 68 hemispheres in which a lunate or composite lunate sulcus was identified. Hemispheres are rotated 45° from a lateral view toward the occipital pole. Composite lunate sulci are marked as described for Figure 2A and B. Numbers below each brain are subject IDs.

lunate sulcus could be identified. The percentages for categories 1 and 2 combined are 24.9% on the right and 28.3% on the left; these are the best examples of lunate sulci he identified. Category 3 percentages were 33.3% on the right and 30.0% on the left. Again, these numbers

indicate a higher lunate frequency than we report. In looking at Connolly's illustrations, we note that there are several lunates that he identifies that would not have been labeled as such by us. For example, there are some that take a largely horizontal course, while we

counted as lunate sulci only those that transversed a significant portion of the surface of the occipital lobe. Connolly also identifies some relatively short and minor sulci as lunates; these would not have satisfied our criteria for being identified as lunates. Connolly places seven subjects in category 1, for which there was some degree of opercularization present. As we reported, we saw no evidence of an occipital operculum in any of our subjects. We note that more pronounced atrophy in brain regions anterior to the occipital lobe (due to age or pathology), combined with the effects of fixation, could create an operculum-like artifact in the occipital lobe (Connolly 1950: Fig. 273, p. 247).

Given the great degree of variability in the sulci of the lateral occipital lobe, and the absence of a structural or functional constraint on the potential form of the lunate sulcus, we conclude that measuring the frequency of the lunate sulcus in modern humans is a somewhat arbitrary undertaking. A limitation of this or any other study of the lunate sulcus in humans is that the structure itself defies the development of hard measures. The criteria we developed to classify the lunate (Table 1) are somewhat different from those of Connolly (1950), but we found a three-part scheme was sufficient to describe the potential forms a lunate or lunate-like sulcus could take in the human brain.

It is safe to say that in at least 40% of hemispheres, nothing like the lunate sulcus can be identified (a result similar to that found in Ono et al., 1990). In Figure 3, we show all of the lunate and composite lunate sulci we could identify. If we relaxed our criteria somewhat, by identifying shorter or more horizontal sulci as lunates, we could increase our percentages; conversely, we could tighten our criteria by identifying only those lunates that consist of a prominent single sulcus. Our designation of the vast majority of our putative lunate sulci as composite lunate sulci is in recognition of the fact that these do not really seem to be very much like the *Affenspalte* of the great apes. Rather, we used the *Affenspalte* as a guide for pattern recognition among the relatively disorganized sulci of the human lateral occipital lobe. That said, we did find three examples (Fig. 3) of “true” lunate sulci in modern humans that are in a relatively posterior position compared to those found in other primates. Should these be considered homologous to the lunate sulcus of the great apes?

Is Human Lunate Sulcus Homologous With *Affenspalte*?

At the heart of Elliot Smith’s argument to rename the *Affenspalte* as the lunate sulcus was the claim that in at least some human cases, the lunate sulcus formed the lateral anterior boundary of the primary visual cortex, and therefore it was directly homologous in humans and other primates. In his study of a large series of Egyptian brains, Elliot Smith (1903) reported that in at least half of the cases, the primary visual cortex (as indicated by the stripe of Gennari) extended to the lateral surface, and “in some cases quite” as far forward as the lunate sulcus. This finding became the basis of his later statement (Elliot Smith, 1904: p. 448) that “the evidence afforded by the distribution of the stria Gennari absolutely demonstrates the correctness of the homology

which in my former note I instituted between the sulcus lunatus in the human brain and the so-called ‘*Affenspalte*’ of the Apes.” Although in these initial papers on the lunate, Elliot Smith balanced his strong claims for homology with an acknowledgment that the lateral occipital region is highly variable, in Figure 38 of his 1927 book, the normative human visual pathway is shown as beginning with the eyes and ending at the posterior bank of the lunate sulcus. This is despite the fact that even by Elliot Smith’s own reckoning, such a configuration could be found in only a minority of modern human brains.

Over the past few decades, an extraordinary amount of research has been devoted to mapping the visual areas of the brains of humans and other primates (Allman and McGuinness, 1988; Dougherty et al., 2003; Grill-Spector and Malach, 2004). In general, recent mapping efforts are wholly in agreement with the classical studies of Brodmann (1999 [1909]) and von Economo and Koskinas (1925), which show that the primary visual cortex (V1) is located primarily around the calcarine sulcus, extending to the occipital pole, with a minimal representation on the lateral surface of the occipital lobe. As a rule, then, the human primary visual cortex does not extend to the lunate sulcus, even if one is present. An example of this can be seen in a series of coronal slices from Duvernoy (1999: p. 200–213), in which the relative positions of a prominent lunate sulcus and the striate cortex are clearly represented.

A refinement of classical cytoarchitectonic studies was provided by Amunts et al. (2000) in their mapping of Brodmann’s areas 17 (primary visual cortex) and 18. They conducted MR scans of 10 fixed whole brains recovered from autopsy, which were subsequently embedded in paraffin and sectioned coronally. Histological analysis of the occipital lobe sections was then conducted to determine the size and extents of areas 17 and 18. The ROIs defined histologically were subsequently rendered on the surface of 3D MRI reconstructions of the brains. The maps make clear that area 17 is highly variable, although it is centered around the calcarine sulcus. The caudal extent of area 17 on the surface of the occipital lobe in particular is highly variable. Amunts et al. (2000: p. 77) conclude that “variability can be interpreted as variability into the kind that is not predicted from visual landmarks and the kind that can be related to sulcal patterns. . . . The variable positions of area 17 on the free surface of the occipital pole and its border to area 18 . . . belong to the first kind.” Rademacher et al. (1993) showed that in only 35% of cases was there an extension of area 17 to the lateral surface of the occipital pole, an area substantially posterior to the position of the typical lunate sulcus in humans.

It is important to note that there is some evidence of population-level variation in the size and distribution of the primary visual cortex. Klekamp et al. (1994) found that the PVC was significantly larger in Australian aborigines compared to Caucasians, and differences in the distribution of area 17 have been noted between Caucasian and Chinese subjects (Filiminov (1932) in Uylings et al., 2005). Connolly (1950: p. 234) emphasized that the lunate sulcus itself “is not a racial character,” although he did show that there was some variation in the distribution of lunate form between American whites and Negroes. Unfortunately, since our population was

very homogeneous, we could not address the issue of population-level variation in lunate form.

The fact that the lunate sulcus is irregularly present in modern humans, and when present has no structural or functional relationship to the primary visual cortex (except perhaps in rare cases), supports the supposition that the human lunate sulcus is not homologous with the lunate sulcus of great apes, such as the chimpanzee. Further evidence for this comes from a study by Holloway et al. (2003) of two chimpanzee brains, in which the lunate sulcus was present in an anomalous, posterior, "human-like" position (in both hemispheres in one of them and in only one hemisphere of the other). Holloway et al. (2003) found that the primary visual striate cortex in the chimpanzees was still bounded by the anomalous lunate sulci, despite their posterior placement. They interpreted this as providing evidence for the hypothesis that neurogenetic variability underlying selection for primary visual cortex reduction in hominids was likely present in the common ancestor of humans and chimpanzees. Holloway et al. (2003: p. 600) point out that even though these chimpanzees approximate the human pattern in some ways, "the observed morphology is not synonymous with the human condition." In chimpanzees, no matter what the position of the lunate sulcus, it still maintains a structural-functional relationship with the primary visual cortex; in humans, as has been demonstrated many times over the years, there is no such relationship.

Evolutionary Significance of Lunate Sulcus

As reviewed above, the primary evolutionary debate concerning the lunate sulcus has been focused on whether or not its position in various extinct hominids reflects a more ape-like or human-like form. The essential compendium of hominid endocasts of Holloway et al. (2004b) makes clear that a posteriorly placed lunate sulcus probably was the norm in *Australopithecus afarensis* and *afrikanus*, dating to as early as 3.5 million years ago. This pattern indicates that relative reduction of the primary visual cortex preceded significant expansion in brain size in hominid evolution; this conclusion is consistent with the association of a posterior lunate sulcus with reduced striate cortex size in the occasional chimpanzee brain (Holloway et al., 2003). It is important to keep in mind, however, that these posteriorly placed lunate sulci are human-like only in terms of position, and that they may still reflect an ape-like histological or functional organization in some regards. Rather than thinking of the functional organization of the australopithecine occipital lobe as either ape- or human-like, it may be more productive to start thinking of it as a unique, albeit clearly intermediate, feature. Obviously, such an inference depends on accepting the relatively posterior placement of the lunate sulcus in australopithecines as advocated by Holloway and colleagues for specimens such as Stw 505 and others; we recognize that these attributions, and the identification of sulci on endocasts in general, is not without controversy (Falk, 1992).

Several lines of evidence suggest that structural and functional reorganization of the occipital lobe during human brain evolution has been extensive. These include loss of a "true" lunate sulcus, or if present, found

in a position posterior to that observed in the great apes; dissociation between the lunate sulcus and the primary visual cortex; loss of representation of the primary visual cortex in the lateral occipital region, which is in turn replaced by visual association cortices (for example, functional imaging studies have shown that the lateral occipital cortex is involved in the visual processing of human bodies and parts thereof: the extrastriate body area) (Downing et al., 2001; Astafiev et al., 2004); relative reduction in size of the primary visual cortex compared to either whole brain volume (Stephan et al., 1981; Holloway, 2000; but see also Kaskan et al., 2005) or the size of the parieto-occipital sector, which occupies a similar proportion of the brain volume in the great apes and humans (Semendeferi and Damasio, 2000); and evolution of a unique cortical anatomy in layer 4A of the primary visual cortex in humans compared to other primates (Preuss et al., 1999; Preuss and Coleman, 2002). The human primary visual cortex in particular and the occipital lobe as a whole may also have a unique minicolumn anatomy (Buxhoeveden et al., 2001; Buxhoeveden and Casanova, 2002) and gene expression profile (Cáceres et al., 2003). The sum total of these changes suggests that the reorganization of the occipital lobe, including the primary visual cortex, was not simply a passive process resulting from the expansion of the parietal association cortices (Elliot Smith, 1904a, 1925), although this likely played a role. Rather, changes in the occipital lobe may have been directly selected for in the context of cerebral expansion and cognitive elaboration during hominid evolution.

Unfortunately, many of these features cannot be assessed in endocasts, and determining the presence or absence of the lunate sulci is especially difficult in larger-brained forms (Holloway et al., 2004b). The human form of the lunate (as opposed to position) is typically without opercularization: the lunate sulcus is relatively small and shallow if present. It may be that the definitive retention of the lunate, albeit in a more posterior position than found in apes, in various australopithecines reflects the first phase in occipital reorganization. In these forms, the association between the lunate and the primary visual cortex may have been maintained, along with the formation of an occipital operculum, which increased the likelihood that an impression of the sulcus was preserved on the interior of the neurocranium of the skull.

We believe that our results show that the presence of a "true" lunate sulcus in modern humans is quite rare, although a composite lunate sulcus can be identified in about half of the hemispheres. Based on appraisal of current knowledge on the human visual cortex, we suggest that Elliot Smith's claim that the lunate sulcus in humans is homologous with the lunate sulcus (*Affenspalte*) of other primates is overstated. Biological homology is a loaded concept, which may be applied and interpreted in many different ways (Kauffman, 1973–1974). For assessing homologous areas in the primate visual cortex, Orban et al. (2004) suggest the use of four criteria: cyto- and myeloarchitecture, connectivity, retinotopic organization, and function. Since the lunate sulcus in humans is not typically structurally associated with the primary visual cortex (a region that can, based on other criteria, be demonstrated as homologous to that seen in other primates), it seems misleading to suggest that the

human lunate is itself a homologous structure. In the rare cases in which the striate cortex may extend to a sulcus identified as a lunate, this may best be considered a convergence on the form found in other primates.

The interpretation of the evolutionary significance of the surface anatomy of the sulci and gyri of the human brain has had a somewhat checkered history (Weiss and Aldridge, 2003). Elliot Smith was fully aware of the great degree of variability found in the lateral occipital sulci, which he himself alluded to repeatedly in his publications on the topic. However, despite this, he emphasized the relatively few human specimens that showed a "primitive" form of the lunate sulcus and used these to bolster his argument for homology. It is important to remember that the argument for homology was tendered against the observations of earlier anatomists who had failed, in Elliot Smith's view, to make sense of this part of the human brain. His emphasis on the putative homology of the human lunate sulcus served to differentiate his view of the lateral occipital lobe from those of his predecessors.

We do not mean to denigrate Elliot Smith's achievements: the lunate sulcus is a critical structure for understanding hominid brain evolution. In fact, we argue that the view that the human lunate sulcus is simply homologous with that seen in other primates has led us to underestimate the extent and importance of occipital reorganization that has occurred in hominid evolution. The challenge now is to understand why such reorganization has occurred, especially in the context of the evolution of human behavioral complexity and plasticity.

ACKNOWLEDGMENTS

The authors thank the reviewers of this paper for their extensive comments, which helped to improve the paper markedly. They also thank Jocelyn Cole for technical assistance and Tony Waldron for providing material about Elliot Smith.

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