

---

## Revisiting australopithecine visual striate cortex: newer data from chimpanzee and human brains suggest it could have been reduced during australopithecine times

Although this author's (R.L.H.) disagreements with Harry Jerison are legion (e.g. Holloway, 1966, 1974, 1979), I have always found his ideas stimulating and thus of great value to my own work regarding human brain evolution. I believe we best honor Harry Jerison by taking his ideas seriously, whether or not we agree with them.

There do not appear to be any serious disagreements that the brain became reorganized as well as enlarged during hominid evolution, but there is considerable controversy as to when reorganization, particularly that relating to the reduction of primary visual striate cortex, Brodmann's area 17, had taken place. (Reviews of these questions can be found in Holloway, 1995, 1996.) Since the only way we will ever know for absolutely certain when this process occurred requires travel with a time machine and some histological sectioning of australopithecine brains, one might wonder why we are writing this paper. It is already apparent from the literature on early hominid brain evolution that a major controversy exists regarding the fossil australopithecine endocasts and their interpretation regarding that infamous landmark, the lunate sulcus. Falk (1983, 1985, 1986) interprets the paleoneurological evidence from the Taung and Hadar (AL 162-28) endocasts as indicating that the lunate sulcus was in an anterior pongid-like position. Holloway (1981, 1983, 1984) interprets the evidence as suggesting a posterior, more modern-human like position. Basically, the question is when in the course of hominid evolution did reorganization, specifically of the amount of primary visual striate of the cerebral cortex, take place and what is that relationship to the well-documented evidence regarding brain size enlargement during hominid evolution?

Two other views are those of Armstrong *et al.* (1991) and the scientist we now fête, Harry Jerison. Armstrong *et al.* are of the opinion that the hominid brain first had to enlarge before cortical reorganization involving a reduction of area 17 could have occurred, arguing from modern developmental evidence (see Holloway, 1992, for a critique). Jerison, on the other hand, disagrees with an early reorganization of the lateral extent of area 17, because he believes that reducing the lateral extent of area 17 would have involved an addition of area 17 along the calcarine fissure of the midline, which, without overall brain enlargement would have seriously deformed the midline structures such as the corpus callosum. As Jerison notes, since the medial cortex is involved, fossil endocasts will never be of any use in settling this controversy. It is worth quoting him in full here (Jerison, 1984, pp. 288–289).

Holloway believes that the lunate sulcus in *Australopithecus africanus* was displaced posteriorly relative to its position in chimpanzees . . . Language systems homologous to those of living humans could then have appeared in *Australopithecus* anteriorly to the sulcus in the vicinity of the angular gyrus. Falk . . . interprets the “lunate” differently, and would have the hominid and chimpanzee *Affenspalte* in similar positions. I have argued still another position, based not on detailed morphology but rather the morphometric consequences of packing primary visual cortex into a primate brain with a posteriorly displaced lunate . . . The anterior border of area 17 is near the lunate, which limits the extent of visual cortex on the lateral surface of the brain. If Holloway’s interpretation is correct, I argued, and if hominids and chimpanzees required similar amounts of primary visual cortex to process visual information, the representation of vision in *medial* [emphasis Jerison’s] neocortex would have been much greater in early hominids than in living chimpanzees. Packing this additional tissue medially would have required major changes in the medial profile of the brain, especially around the calcarine fissure and the splenium of the corpus callosum, which are among the more major landmarks in mammalian brains.

My argument was uniformitarian . . . : Since the medial callosal region of the brain in placental mammals is similar in appearance in different species, this region in *Australopithecus* should have looked like that of ‘good’ placental mammals, and visual cortex should have been packed normally. Falk’s analysis is consistent with uniformitarianism; Holloway’s is not. But the medial surface of the brain is not visible in endocasts, and this controversy cannot be resolved by the fossil evidence alone.

Here, we must seriously disagree with Jerison, as the fossil evidence can certainly provide some evidence regarding the lateral extent of primary visual cortex, and this datum, whether controversial or not, should not be ignored.

The matter of how much striate cortex is (or was) needed to process visual information is unanswerable, and in fact there is considerable variation in amounts of primary visual striate cortex, both in humans and chimpanzees, with no apparent indication of any causal relationship to variation in visual acuity, or processing of visual information. If it can be shown that such morphometric variation of primary visual striate cortex does exist currently in extant species, it certainly allows for the possibility that it existed in the past using the same uniformitarian framework that Jerison championed above. In other words, the neurogenetic bases for expanded and reduced volumes of primary visual striate cortex may be very similar (if not totally homologous) between chimpanzee and modern human. Given a pongid–hominid split of perhaps 5–7 million years ago, such a neurogenetic basis could have been operating in *Australopithecus*, and other early hominids. From the data of Stephan *et al.* (1981), it is clear that the volume of primary visual striate cortex is some 121% less than would be expected for a primate of our brain size, corroborated by the additional fact that our lateral geniculate nucleus is about 140% less than expected (Holloway, 1995, 1996). Passingham & Ettlinger (1973) had shown such a diminution back in 1969, but chose not to stress it (see Holloway, 1979, for a review). We mention this because at least the comparative evidence is unambiguous on whether or not human primary visual striate cortex is less than expected when allometry is considered.

We will show here that indeed, both in modern humans and chimpanzees, there is considerable variability regarding volume of primary visual striate cortex, and that the brain endocasts of the Hadar 162-28 specimen, using Falk's (1983) placement of the lunate, shows a reduction toward the human case.

## **Newer observations**

### **Variation of primary visual striate cortex in modern humans**

Gilissen & Zilles (1995, 1996) and Gilissen *et al.* (1995) have studied the relationships between the following variables: striate cortex volume, depth and area of the calcarine fissure. These variables can be quantified using

MRI scans. Their findings suggest a very high degree of variability of striate cortical volume with coefficients of variation (CV) twice that associated with total brain volume. Striate cortex showed CVs of 18.7 and 19.3%, while total brain volume CV was 9.0–10.6 %, based on two human samples of  $N=20$  and  $N=9$ . In the Gilissen *et al.* (1995) paper, they found that the projection area of the medial surface (as measured by calcarine length and depth) had CVs of 20–23%, and occipital surface area had a CV of 18.4 %, while cortical surface area (total and non-occipital) had CVs around 9.5%. They conclude that occipital surface area correlates significantly with calcarine length, while the calcarine surface varies independently from the rest of the variables (p. 454). There is no evidence of deformation of the medial surface, splenium of the corpus callosum, or poor visual information processing in these healthy modern humans. (There is a large literature on this question of variation of volume of striate area 17 cortex, and the reader is advised to peruse the references in these authors' papers, as well as the various chapters in Peters & Rockland (eds.), 1994.)

An additional interesting indication of a neurogenetic basis for considerable variability in striate cortical volume comes from the work of Klekamp and his colleagues. Klekamp *et al.* (1994) have shown that the Australian Aborigine's visual striate cortical volume is significantly larger (both absolutely and relatively) than in the German Caucasian sample they measured. There is no evidence of any environmental factors affecting this size difference, and the authors' conclude that some neurogenetic factor in ontogenetic development is most likely the explanation for this difference.

### **Variation in visual striate cortical volume in chimpanzee brains**

That the lunate sulcus in chimpanzee is placed well anterior to where it occasionally exists in modern humans has long been appreciated (see Holloway, 1985, for a review). We know that the lunate is roughly the anterior boundary of primary visual cortex, and this anterior placement is the usual configuration of all apes, and indeed the Old World monkeys as well.

Recently, two very interesting departures from the normal morphometric position of the lunate sulcus have appeared in two common chimpanzees (*Pan troglodytes*) whose brains have been sent to my laboratory for study from Yerkes. 'Frank' and 'Chuck', two male chimpanzees from Yerkes show a fascinating composite of features of the lunate sulcus.

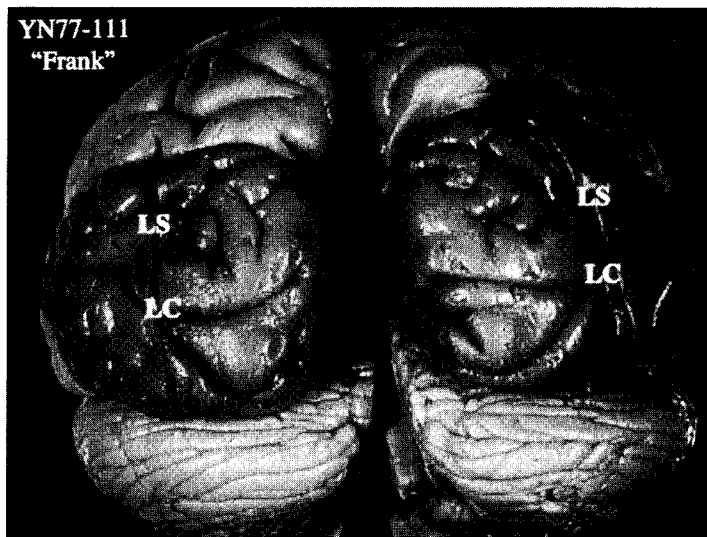


Fig. 9.1. An occipital view of the brain of 'Frank'. LS is the lunate sulcus, and LC is the lateral calcarine fissure. The darker shading is the result of preliminary staining, and the most anterior part of the staining is approximately where the lunate sulcus is usually found in *Pan troglodytes*. These sulci on 'Frank' are in the same position as on the right hemisphere of 'Chuck' in Fig. 9.2.

'Frank' (see Fig. 9.1), shows a pattern that departs significantly from all the other chimpanzee brains these authors have ever seen. The lunate sulcus is clearly in a more posterior position than found in most other chimpanzee hemispheres that we have measured.

'Chuck' is even more surprising, in that the left hemisphere shows a typical anterior pongid position for the lunate sulcus, while the right hemisphere shows a more posterior position (see Fig. 9.2). The medial surface surrounding the calcarine fissure is normal in both brains, and there are no behavioral observations that would indicate that these two chimpanzees had anything but normal vision and information processing. The histological staining we have done thus far indicates that the stripe of Gennari (layer 4c) is visible up to the limit of the lunate sulcus in both chimpanzees, and particularly so in the case of 'Chuck'. Clearly, the neurogenetic bases for variability regarding reduction in the posterior placement of the lunate sulcus is present in modern chimpanzee and modern human. Applying Jerison's penchant for 'uniformitarianism', these observations suggest that similar, if not identical neurogenetic processes obtain in the ontogenetic development of primary visual striate

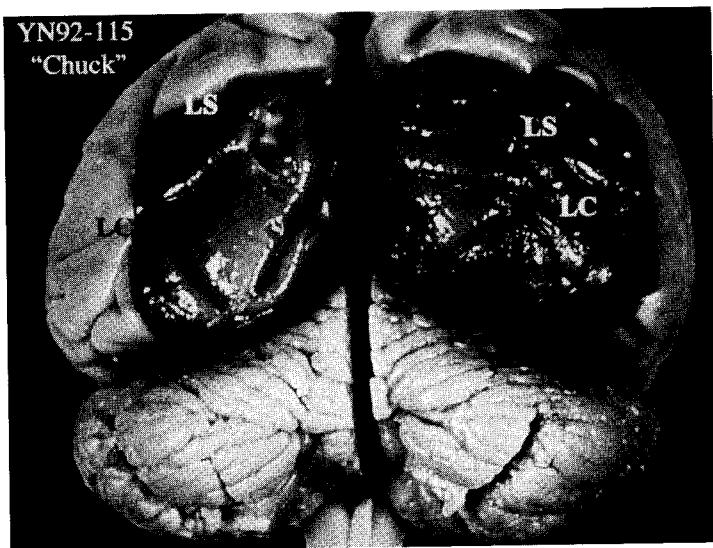


Fig. 9.2. An occipital view of the brain of 'Chuck'. Notice that the left hemispheric position of the lunate is considerably more anterior than on the right side.

cortex. Why should these processes have skipped the *Australopithecines*? We don't believe they have.

#### **Statistical analysis of the position of the lunate sulcus in *Pan* and *Australopithecus***

Published measurements in Holloway (1983, 1988, 1995) and Holloway & Kimbel (1986) which showed that if Holloway and Falk (1986) do agree on the position of the intraparietal sulcus on the Hadar 162-28 *Australopithecus afarensis* specimen, the modern chimpanzee position of the lunate sulcus is roughly twice as great as the distance for the Hadar specimen, even though many of the chimpanzee hemispheres measured were of smaller brain size than that of the Hadar specimen (i.e. 385–400 cm<sup>3</sup>).

Our mixed-sex sample of chimpanzee hemispheres has now increased to 39 without 'Frank' and 'Chuck', and measurements of the distance from occipital pole (OP) to lunate sulcus (LS) provide a mean OP–LS distance of 31.55 mm, and a standard deviation (SD) of 4.6 mm, and an average brain weight of 137.8 g for each hemisphere, SD = 32.3 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 on chimpanzee brains. If ‘Frank’ and ‘Chuck’ are included, the mean OP–LS distance is 30.87 mm, and the SD is 5.24 mm. The mean brain weight is 141.3 g,  $SD = 32.7$  g.

Given an OP–LS distance of 15.5 on the Hadar 162-28 *A. afarensis* endocast, this is 3.49 SD posterior to the mean chimpanzee value. When the two unusual chimpanzees are included, the Hadar specimen’s OP–LS distance is 2.93 SD posterior to the chimpanzee mean. Earlier and smaller samples were indicating SDs of approximately 5. As the sample increases so does the variability, and the SD also becomes lower. Such SDs as currently available from these samples indicate a very statistically significant difference between the chimpanzee and *A. afarensis* positioning of the lunate sulcus, if indeed the lunate can be unambiguously determined on the australopithecine brain endocasts.

### Summary

Our studies on the variability of morphogenetic characters in both modern humans’ and chimpanzees’ brains suggest that neurogenetic processes underlying reduction of the volume of primary visual striate cortex, area 17 of Brodmann, are both expressed in these two species. Given that this variability is shared between *Homo* and *Pan*, it would appear possible that some of the australopithecine ancestors of *Homo* could have expressed these variations also, given a pongid–hominid divergence of 5–7 MYA. While the data on these variations cannot prove such a contention, they are supportive of our claims, and the paleoneurological evidence, despite its controversial nature, supports our claims of a diminution of the lateral extent of primary visual cortex by *A. afarensis* times.

### Hopes and predictions on the state of brain studies in the year 2010

Hopes are surely easy to pronounce; predictions are another matter, but here goes, anyway. We would hope for far more quantitative information about primate brains, much of it along the lines provided by Stephan and his associates, but which would include within-species variation. That is, we would have the most accurate volumetric data for all neural nuclei as well as fiber tracts for each species of primate with a sample of at least 10

each. We would hope that the scientific community could begin to show a strong interest in within-species variation of brain structure and behavior, so that we might have a better understanding of what are the units of structure and behavior that become targeted by evolutionary processes, and of course, their neurogenetic underpinnings and ontogenetic development. We would hope that scientists interested in human brain evolution (or any other creature's) would finally come to realize that size alone, whether allometrically scaled or not, will not be sufficient to inform us about brain evolution, as the brain's organization must be a critical component of species-specific behavior and evolutionary processes. Of course, this includes the hope that all of these species will still be around in a non-endangered state by 2010. We would also hope that neuroimaging techniques (noninvasive) develop rapidly to permit accurate assessments of cognitive capacities in other animals (particularly *Pan*), such as are becoming available through fMRI and PET on humans. Next, a cure for Alzheimer's so that we can all read about it by 2010!

Needless to say, paleoneurologists can only hope and pray that we will find *the* perfect australopithecine brain endocast, lunate sulcus unambiguously in place, either anterior or posterior, or for that matter completely lacking. We would also keep our hopes high for a frozen complete Neandertal brain, fully intact within its brow-ridged cranium.

We predict that none of the above will come to pass by 2010. Instead, we expect a dozen or so more fossil hominid partial crania to be discovered which will provide limitless opportunities for controversy regarding their brain sizes and organizations. If the frontal lobe is the issue, the requisite fossils will only have the posterior part of the brain present, while if the lunate sulcus is what matters, only the frontal portions of the crania will be preserved. We predict that cranial capacities will continue to be determined using a multitude of techniques, including seed, shot, water displacement, computer imaging and CT-scanning, water dowsers, Tarot Cards, not to forget crystal balls. We finally predict that Harry Jerison's 1973 book will still be a classic in the field, and required reading for all evolutionary neuropaleontologists.

### Acknowledgments

The authors are grateful to the editors for including us in the opportunity to fête Harry Jerison. We would like to thank Harold McClure, Dan Anderson, Tom Insel, Jeremy Dahl and Jim Rilling of Yerkes Regional



Primate Center for their cooperation in allowing us access to these many chimpanzee brains, and to Patrick Gannon, Nancy Kheck, and Star Gabriel of Mount Sinai School of Medicine, for their advice and help with sectioning some of the brain tissue. We also wish to thank Sam Marquez, Jill Shapiro, and Chet Sherwood for their comments and suggestions.

## References

- Armstrong, E., Zilles, K., Curtis, M. & Schleicher, A. (1991). Cortical folding, the lunate sulcus and the evolution of the human brain. *Journal of Human Evolution*, **20**, 341–348.
- Falk, D. (1983). The Taung endocast. A reply to Holloway. *American Journal of Physical Anthropology*, **53**, 525–539.
- Falk, D. (1985). Hadar AL 162-28 endocast as evidence that brain enlargement preceded cortical reorganization in hominid evolution. *Nature*, **313**, 45–47.
- Falk, D. (1986). Reply to Holloway and Kimbel. *Nature*, **321**, 536–537.
- Gilissen, E. & Zilles, K. (1995). The relative volume of primary visual cortex and its intersubject variability among humans: a new morphometric study. *Comptes Rendus Academie des Sciences (Paris) serie II*, **t.320**, 897–902.
- Gilissen, E. & Zilles, K. (1996). The calcarine sulcus as an estimate of the total volume of the human striate cortex: a morphometric study of reliability and intersubject variability. *Journal of Brain Research*, **37**, 57–66.
- Gilissen, E., Iba-Zizen, T., Stievenart, J.-L., Lopez, A., Trad, M., Cabanis, E. A. & Zilles, K. (1995). Is the length of the calcarine sulcus associated with the size of the human visual cortex? A morphometric study with magnetic resonance tomography. *Journal of Brain Research*, **36**, 451–459.
- Holloway, R. L. (1966). Cranial capacity and neuron number: critique and proposal. *American Journal of Physical Anthropology*, **52**, 305–314.
- Holloway, R. L. (1974). On the meaning of brain size. A review of H. J. Jerison's 1973 *Evolution of the Brain and Intelligence*. *Science*, **184**, 677–679.
- Holloway, R. L. (1979). Brain size, allometry, and reorganization: toward a synthesis. In *Development and Evolution of Brain Size: Behavioral Implications*, eds. M. E. Hahn, G. Jensen & B. C. Dudek, pp. 59–88. New York: Academic Press.
- Holloway, R. L. (1981). Revisiting the S. African Australopithecine endocasts: results of stereoplotting the lunate sulcus. *American Journal of Physical Anthropology*, **56**, 43–58.
- Holloway, R. L. (1983). Cerebral brain endocast pattern of *A. afarensis* hominid. *Nature*, **303**, 420–422.
- Holloway, R. L. (1984). The Taung endocast and the lunate sulcus: a rejection of the hypothesis of its anterior placement. *American Journal of Physical Anthropology*, **64**, 285–288.
- Holloway, R. L. (1985). The past, present, and future significance of the lunate sulcus in early hominid evolution. In *Hominid Evolution: Past, Present, and Future*, ed. P. V. Tobias, pp. 47–62. New York: A. R. Liss.
- Holloway, R. L. (1988). 'Robust' Australopithecine brain endocasts: some preliminary observations. In *Evolutionary History of the 'robust' Australopithecines*, ed. F. E. Grine, pp. 97–105. New York: Aldine-deGruyter.

- Holloway, R.L. (1992). The failure of the gyrification index (GI) to account for volumetric reorganization in the evolution of the human brain. *Journal of Human Evolution*, **22**, 163–170.
- Holloway, R.L. (1995). Toward a synthetic theory of human brain evolution. In *Origins of the Human Brain*, eds. J.P. Changeaux & J. Chavaillon, pp. 42–55. Oxford: Clarendon Press.
- Holloway, R.L. (1996). Evolution of the human brain. Chapter 4 in *Handbook of Human Symbolic Evolution*, eds. A. Lock & C. Peters, pp. 74–116. Oxford: Clarendon Press.
- Holloway, R.L. & Kimbel, W.H. (1986). Endocast morphology of Hadar AL 162-28. *Nature*, **321**, 538.
- Jerison, H.J. (1973). *Evolution of the Brain and Intelligence*. New York: Academic Press.
- Jerison, H.J. (1984). Fossil evidence on the evolution of the neocortex. In *Cerebral Cortex. Vol. 8A. Comparative Structure and Evolution of Cerebral Cortex, part I*, eds. E. Jones & A. Peters, pp. 285–309. New York: Plenum.
- Klekamp, J., Reidel, A., Harper, C. & Kretschmann, H. J. (1994). Morphometric study on the postnatal growth of the visual cortex of Australian Aborigines and Caucasians. *Journal of Brain Research*, **35**, 541–548.
- Passingham, R. & Ettlinger, G. (1973). A comparison of cortical functions in man and other primates. *International Review of Neurobiology*, **16**, 233–299.
- Peters, A. & Rockland, K.S. (eds.) (1994). *Cerebral Cortex. Vol. 10. Primary Visual Cortex in Primates*. New York: Plenum.
- Stephan, H., Frahm, H. & Baron, G. (1981). New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologia*, **35**, 1–29.