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Posterior lunate sulcus in *Australopithecus africanus*: was Dart right?☆

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Abstract

Since Dart's analysis of the Taung skull in 1925 in *Nature*, there has been controversy surrounding the presence of a clearly defined lunate sulcus (LS) in the australopithecines, marking the anterior extent of primary visual cortex (PVC). An anterior position signifies that the LS is in an ape-like position, such as found in *Pan troglodytes*. A posterior position is a more human-like characteristic (autapomorphy). If the latter occurred in *Australopithecus*, then the cerebral cortex underwent some neurological reorganization prior to brain enlargement, thus occurring earlier than the emergence of the genus *Homo*. The endocast of the Stw 505 specimen from Sterkfontein, South Africa, shows an unmistakably posterior placement of the LS. The early hominid brain was reorganized at least by the time of *Australopithecus africanus*, thus vindicating Dart's early assessment.

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Résumé

Sulcus lunatus postérieur chez *Australopithecus africanus* : Dart avait-il raison ? L'analyse du crâne de Taung publiée dans *Nature* par Dart en 1925 a ouvert un débat qui concerne la présence d'un sulcus lunatus (LS) chez les Australopithèques, marquant la limite antérieure du cortex visuel primaire (PVC). Une position antérieure correspond à celle du singe, comme cela est observé sur *Pan troglodytes*. Une position postérieure est caractéristique du genre *Homo* (autaporphie). Si ce dernier schéma est observé sur l'Australopithèque, alors le cortex cérébral doit subir une réorganisation neurologique qui se produit avant l'élargissement du cerveau ; tout ceci ayant lieu avant l'émergence du genre *Homo*. L'endocrâne de l'individu de Sterkfontein Stw 505, d'Afrique du Sud, montre une position postérieure indiscutable du sulcus lunatus. Le cerveau des premiers hominidés était donc déjà réorganisé au plus tard au moment de l'apparition de l'*Australopithecus africanus*, ainsi que l'avançaient les premières affirmations de Dart. **Pour citer cet article :** R.L. Holloway, C. R. Palevol 3 (2004).

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☆ The authors wish to dedicate this paper to the memory of Raymond Dart and Alun Hughes

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1. Introduction

Aside from size, there are few differences in the known neuroanatomical structures of the ape and human brain [23]. The volume of primary visual striate cortex (PVC), Brodmann's area 17, is one of the main neuroanatomical differences between human and ape brains. This cortex in humans is roughly 121% less than expected from an allometric relationship between PVC and brain volumes [24]. It has been recently demonstrated [33, 34] that the frontal lobe, once regarded as the major size difference between apes and humans, is in reality no larger than would be expected for a primate with the size of a human brain. A large reduction in PVC, without a significant increase in frontal lobe volume, signals a relative increase in the size of tissue adjacent to area 17, which would be para- and peri-striate cortex (Brodmann's areas 18 and 19), as well as posterior parietal association cortex, involving regions such as superior and inferior parietal lobules, Brodmann's areas 7, 37, 39, and possibly a relative increase in superior and posterior temporal cortex, including the so-called receptive language area of Wernicke. Indeed, Rilling and Seligman [32] have shown that the temporal cortex in humans is larger than expected on a purely allometric basis. While the precise roles of these tissues and their interactions with the rest of the brain are relatively unknown, the overall general consensus is that they subserve, and are involved in, complex cognitive tasks [39]. Endocasts do not provide enough sulcal details to permit detailed delineation of these cytoarchitectonic regions, but a reduction of PVC most probably means an expansion of posterior association cortex into that region.

The lunate sulcus (LS) is a well-defined sulcus in anthropoid brains (but not in humans) that forms the anterior boundary of PVC [20]. It is a feature readily visible on all ape and cercopithecoid brains, but only occasionally in New World monkeys, i.e., the Anthropoidea. In the chimpanzee brain, the anterior position of this sulcus averages some 30–40 mm arc distance from the occipital pole (OP), i.e., the most posteriorly projecting part of the occipital lobe of the brain, to the

dorsal edge of the LS [26]. The most lateral edge of the LS is about 35 to 40 mm from the OP (see Figs. 1a–3a). When the LS is present in human brains, it is often fragmented, and located much more posteriorly [20, 26, 27]. When a lunate sulcus is not visible in human brains, which is the case in the majority of human brains [3, 31], the PVC is still relatively reduced in

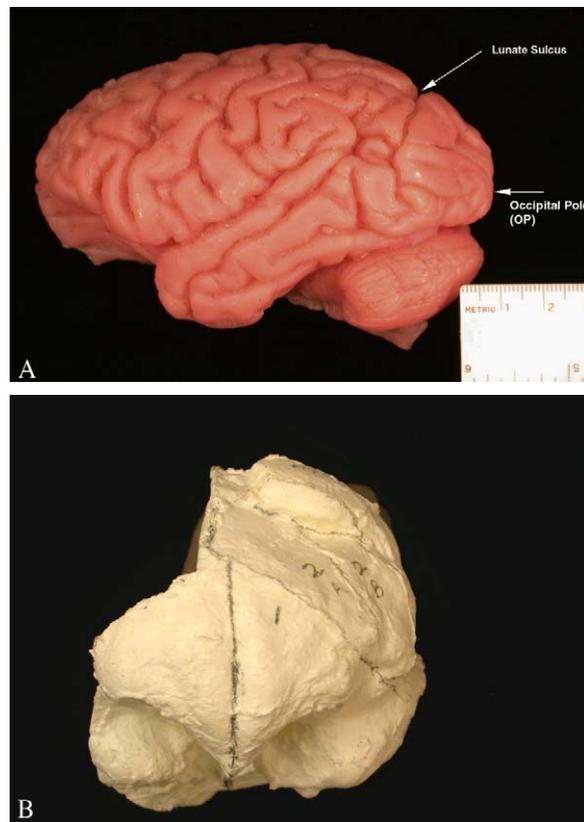


Fig. 1. (A) Left lateral view of a chimpanzee brain cast (ca 400 ml in volume), showing the relatively anterior position of the strong posteriorly concave crescentic lunate sulcus (LS). (B) Frontal view of Stw505 endocast to show that the frontal midline is undistorted and thus available for midsagittal reconstruction.

Fig. 1. (A) Vue latérale gauche d'un moulage du cerveau d'un chimpanzé (environ 400 ml de volume) montrant la position relativement antérieure du sulcus lunatus (LS) en croissant nettement concave postérieurement. (B) Vue frontale du moulage interne Stw505, montrant que la ligne médiane frontale n'est pas tordue et qu'elle est donc disponible pour une reconstitution médio-sagittale.

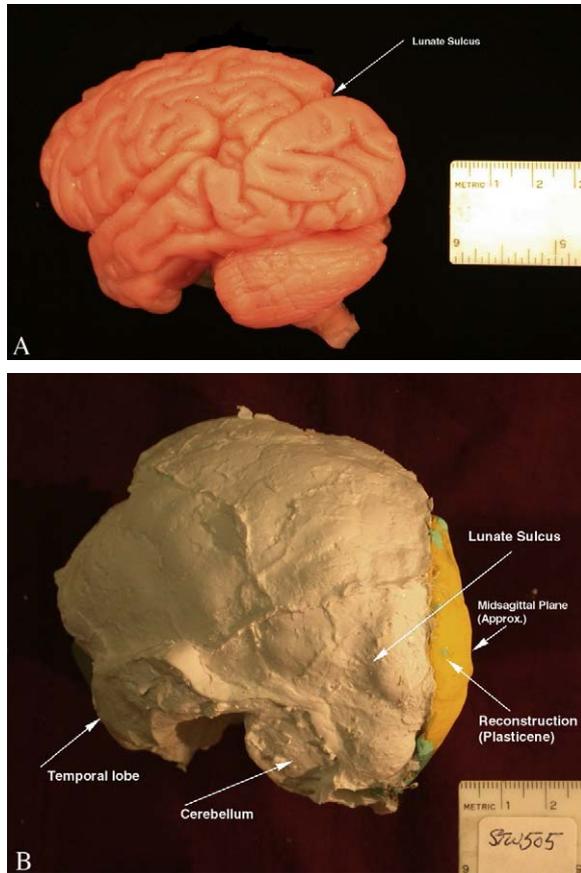


Fig. 2. (A) An oblique view of the same chimpanzee brain cast showing the LS in relation to other cerebral landmarks. (B) An oblique view of the Sw505 partially reconstructed endocast showing the LS and reconstructed midline.

Fig. 2. (A) Vue oblique du moulage de cerveau du même chimpanzé montrant le LS en relation avec les autres zones repères du cerveau. (B) Vue oblique du moulage interne Sw505 partiellement reconstitué, montrant le LS et la ligne médiane reconstituée.

volume and lies in a posterior position around the occipital pole. There is variability in the volume of human PVC as shown by Klekamp et al. [29], Gilissen and Zilles [10, 11], and it has been recently shown to exist also in a very few chimpanzee brains [26, 27, 38]. Since the human and ape lines have separate evolutionary histories for roughly 7 Myr, it is assumed that the primitive ape condition was an anteriorly-placed LS [7], (e.g., *Proconsul africanus*), and that during hominid evolution, the reduction in PVC and perhaps a posteriorly oriented LS would be a derived character state, and thus an autapomorphy, as it appears to be unique to the human lineage.

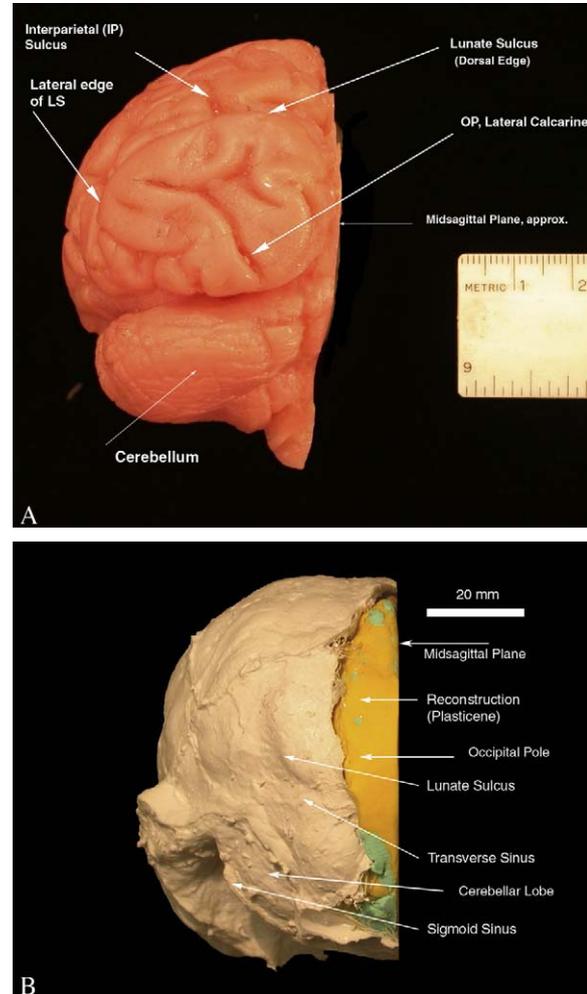


Fig. 3. (A) A full occipital view of the chimpanzee brain cast showing the LS. Note that the LS is ca. 35 mm lateral to the OP (occipital pole) and about 45–50 mm to the midline (midsagittal plane). (B) A full occipital view of the partially reconstructed Stw505 endocast showing the lateral margin of the LS. Note that the distance is about 25–30 mm lateral to the midsagittal plane as currently reconstructed, but that the distance to an expected occipital pole (OP) would be about 10 mm less, since the occipital pole is always located lateral to the midsagittal plane.

Fig. 3. (A) Vue occipitale complète du moulage de cerveau du chimpanzé montrant le LS. À noter que le LS est latéralement à 35 mm environ du pôle occipital (OP) et à environ 45–50 mm de la ligne médiane (plan médio-sagittal). (B) Vue occipitale complète du moulage interne Stw505 partiellement reconstitué, montrant le bord latéral du LS. À noter que la distance est d'environ 25–30 mm latéralement par rapport au plan médio-sagittal tel qu'il est couramment reconstitué, mais que la distance à un pôle occipital attendu (OP) serait d'environ 10 mm de moins, puisque le pôle occipital est toujours situé latéralement par rapport au plan médio-sagittal.

This reorganization has been the object of considerable controversy ever since Dart's [6] description of the Taung child, *Australopithecus africanus*, and has been thoroughly reviewed elsewhere [20, 23]. The problem with the Taung brain endocast, and to a lesser extent, that of the *A. afarensis* AL 162–28 specimen, is that the LS cannot be unambiguously identified on the endocasts, in part because the relevant region is occupied by the lambdoid suture which possibly masks the LS. Rather, one can say only where the LS was *not* located. It has been claimed that the brain had to increase in size before the volume of PVC could reduce, and that a reduced posteriorly placed lunate sulcus could therefore only occur in *Homo* [1, 9, 28]. Others have argued that reorganization occurred before any major increase in brain size beyond known chimpanzee brain volumes, the average of which is roughly 400–420 ml, i.e., the same as in australopithecines of the species *afarensis* and *africanus* [18, 19, 21–25]. The lambdoid suture on the Taung specimen occludes the possible location of a posteriorly located LS, while the typical chimpanzee placement of a lunate on the Taung endocast would violate the parietal sulcal morphology, which courses antero-posteriorly in that region [20]. None of the other published australopithecine brain endocasts have a clearly discernible LS as LeGros Clark [2], and Tobias [35] have maintained, although Falk [8] suggested one appeared on the Sts 60 endocast, but as the occipital lobe is missing on this endocast, the presence is unlikely. The Hadar AL 162–28 endocast remains controversial [9, 18]. Only an unambiguous imprinted LS can settle this controversy.

2. Newer evidence

The recently described [30] *A. africanus* specimen from Sterkfontein, South Africa, Stw 505, with a currently calculated cranial capacity of 515 ml ([4] provides the required evidence (see Figs. 1B–3B and *Nota Bene* below).

Here, we wish to concentrate on the question of reorganization. A silastic rubber endocast was made from the original cranial portion by Dr. R. Clarke, and sent to RLH. Figs. 1B, 2B, and 3B show that the occipital lobe possesses a strongly curving crescentic sulcus just superior to where the transverse sinus is located. The crescent is strongly concave posteriorly

and medially, and is situated some 20–25 mm posterior to the sigmoid sinus. In chimpanzee brains (see Figs. 1A, 2A, and 3A), the LS is normally flush or only slightly posterior to the sigmoid sinus, and the lateral arc distance from the occipital pole (OP) to the LS is on average 35–40 mm [26]. It is important to note that the OP is always lateral to the midsagittal plane, so that the distance from the LS to the midsagittal plane is clearly greater than the 35–40 mm average in chimpanzees. On the Stw 505 specimen, the distance to where the occipital pole would be if the occipital bone were complete is less than 20 mm. **No other sulcus normally found in the occipital lobe, including the lateral calcarine, inferior and lateral occipital sulci, matches the position or strong posterior crescentic concavity of this sulcus on the Stw 505 brain endocast, either in chimpanzee or *Homo*.** The dorsal extension of the LS is only visibly present for a short distance, and yields an approximate dorsal arc significantly smaller than on chimpanzee brains of lesser volume. This value is between 30–35 mm on most chimpanzee brains, with volumes usually around 350 ml, which is very significantly less than the 515-ml volume of the Stw 505 endocast. The best estimate we have of this possible distance on the Stw 505 endocast is a maximum of 25 to 30 mm (see scales in Figs. 1–3), and that distance is from the concavity to the midsagittal plane, not the OP, which would be significantly less, that is, approximately 20 mm. It should be noted that the midsagittal plane reconstructed in Figs. 1–3 is clearly medial to where the expected occipital pole on the endocast would be, a distance which in chimpanzees is between 5–10 mm. This means that the distances suggested for the lunate sulcus are maximal since the occipital pole is not available on Stw 505. However, on the Taung endocast the OP to midsagittal plane distance is about 10 mm, and the same would be anticipated for Stw 505. It is important to note that the midline (midsagittal) morphology is present and undistorted on both dorsal and ventral portions of the frontal lobe, extending from the rostral bec for a distance of roughly 65 mm on the dorsal surface. This morphology permits a reasonably accurate midline to be extended posteriorly.

Based on a sample of 78 chimpanzee brain hemispheres (this is a recently increased sample from that reported in [26]), the correlation between the logs (base 10) of brain volume and distance from the OP to

the LS is 0.678, with a slope of 0.375, indicating a normal within-species allometric relationship. This r is statistically significant at the 0.001 level. With a cranial capacity of Stw 505 thought to be about 575 ml from our first reconstruction (in prep.), the predicted OP–LS distance is calculated to be 41 mm, if there is an allometric relationship between these two variables in *Pan*. This is nearly double the actual distance seen on the endocranial cast of Stw 505, and visible in Figs. 1B, 2B, and 3B. The point we wish to make here is that the large size of the Stw 505 endocast would demand a larger distance of the LS to the OP if the endocast followed a *Pan* pattern. Clearly, the opposite is the case.

Nota Bene. A new volume estimate for the endocranial capacity of the Stw505 *A. africanus* hominid is being prepared. The volume estimate of 515 ml, based on CT scanning, is too small, at least in the opinion of the first author. Indeed, Hawks and Wolpoff [13] calculated a larger volume of about 575 ml. The Stw505 endocast shows some plastic deformation, as well as several cranial breaks that must be corrected. However, the base and anterior dorsal region of the frontal lobe are undistorted and provide midline landmarks that can be extended posteriorly to the occipital lobe to provide an accurate midsagittal plane to within ± 5 mm. The actual distance that should be compared with chimpanzee measurements are from the occipital pole and not the midsagittal plane. Thus the distance from most probable OP on Stw 505 to the crescentic furrow would be less than the 20–25 mm suggested in Figs. 1–3, based on the midsagittal plane. While this part of the occipital lobe bearing the OP is missing, it would certainly have been lateral to the present midsagittal plane, thereby increasing the contrast with the measurement in chimpanzees. On chimpanzee brains, the OP is usually 5–10 mm lateral to the midsagittal plane. The first author's preliminary reconstruction with these corrections yields a volume of roughly 575 ml. The first author believes this to be accurate to within 20 ml. If the original volume of 515 ml is used, the predicted OP to lunate sulcus distance is around 39–40 mm, still considerably larger than found on the Stw505 endocast.

3. Discussion

Clearly, this Stw 505 specimen of *A. africanus* has an indisputable crescentic, concave-posterior, lunate

sulcus as seen in Fig. 3B and it is in a posterior, non-*Pan* position, indicating that at least one member of the species had undergone some cortical reorganization toward a more human-like condition. If there is some other sulcal element that has caused this strong crescentic sulcus we have not been able to identify it. No other known sulcal morphology appears in this position. We think it is now perhaps more parsimonious to regard the older specimens, such as Taung, and the *A. (Paranthropus) robustus* SK 1585 as having LS's in posterior positions rather than in the typical ape anterior position, because a chimpanzee-like anterior position violates the sulcal morphology available, a conclusion that applies to the Hadar AL 162–28 *A. afarensis* specimen as well as Taung and SK 1585. Indeed, the 15.5 mm distance between OP and LS on the Hadar specimen is some 4 SDs posterior to where the LS would lie on an average chimpanzee brain [26]. If one looks down the axis of the lambdoid suture on the Taung endocast, there does appear to be a groove that might be ascribed to the lunate sulcus, although we prefer to believe that the posterior inferior lip of the parietal bone is responsible for the groove, the puckering of the occipital lobe notwithstanding. The SK 1585 endocast shows a more pronounced puckering in this region and a complete smoothness of the endocast anterior to where the lambdoid suture is present. The Stw 505 specimen indicates that at least this early hominid brain was indeed reorganized toward a more human-like pattern despite its small brain volume, and prior to any significant cortical enlargement as seen in the genus *Homo*. In sum, this endocast strongly suggests that cortical reorganization preceded brain enlargement in hominid evolution as argued elsewhere [14–17]. We repeat, that in brains with strongly developed lunate sulci, the sulci are the anterior limit to PVC. We have not found evidence that this finding is violated in either humans or apes (please refer the literature discussed in [26]).

It is tempting to speculate about what selection pressures may have played a role in the evolution of this derived neural condition. Relative to the earliest hominids [37], the associated faunal and geological evidence from the later *Australopithecus*-bearing sites suggest more open habitats and an expansion of niches with food resources separated by increased distances. Stone tools, while showing minimal standardization but primitive patterns exist as early as 2.6 Myr [5, 12],

a date not at odds with that of Member 4 of Sterkfontein [36]. Elsewhere [14–17, 23], RLH has speculated that reorganization of the *Australopithecus* brain indicates an expanded posterior parietal cerebral cortex, and was most likely associated with enhanced social behavior including communication: [1] this region involves multimodal processing involving visual, auditory, and sensorimotor integration; [2] visuospatial integration related to tool use and making, throwing objects with force and accuracy, as well as more sophisticated longer-term memory of spatial locations and qualities of self, others (i.e., facial recognition), prey and predators, including objects and resources (stone, digging sticks, trees, waterholes, etc.). All of these were possibly adding to a more advanced cognitive adaptation within a changing and expanding ecological zone, and formed the basis for additional cognitive changes, such as patterned tool-making, and possibly more advanced communicative skills that accompanied the evolution of the genus *Homo*. We are cautioned, of course, to realize that one endocast with this unambiguous sulcal location might not be representative of the entire species, but thus far, we have seen no alternative strong evidence that there were *A. africanus* (or *A. afarensis*) individuals with lunate sulci in ape positions.

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