Letter to the Editor: Response to Holloway and Broadfield's Critique of Our Reconstruction of the Taung Virtual Endocast

Without providing any support for their claim, Holloway and Broadfield (H&B) assert that "the Falk and Clarke (2007) reconstruction of Taung miscalculates the midsagittal plane, resulting in a significant reduction in cranial capacity that may call into question the taxonomic significance of the fossil" (Holloway and Broadfield, 2011:322). We agree that the 22 cm^3 difference in the capacities of our respective reconstructions of the Taung endocast may be due largely to differences in our reconstructed midsagittal planes; however, we have good reason to reject the assertion that our plane is miscalculated.

The Taung fossil (*Australopithecus africanus*) consists of a natural endocast that reproduces external morphology from most of the right and part of the left hemispheres of the brain, a separate portion of the fossilized face that articulates with the endocast, and a mandible that occludes with the maxillary dentition in the face. The right temporal and both frontal poles are separated from the endocast and embedded in the back of the facial fragment. In 2007, we published a description of a new virtual endocast of Taung in *AJPA* and provided a cranial capacity estimate of 382 cm^3, which is 22 cm^3 smaller than an estimate of 404 cm^3 published by Holloway in 1970. Our reconstruction incorporated, for the first time, *both* frontal lobes, which were extracted manually from the back of the facial fragment, imaged, and attached electronically to the posterior portion of the endocast, which had been reconstructed by mirror imaging the right hemisphere of the separate natural endocast. We, thus, did not mirror image Taung's frontal polar region as H&B claim, and the slight asymmetry (a left frontal petalia) in that part of our reconstruction (Falk and Clarke, 2007: Fig. 2) is not surprising because asymmetries in the frontal polar region occur frequently in apes and more often in humans. More to the point, the slight left frontal petalia reproduced by our reconstruction of Taung's endocast has recently been confirmed independently from a 3D-CT reconstruction of Taung's frontal lobes (Fig. 1).

Taung's natural endocast has a small gap at the midline of the right cerebellar region, which (since it was missing) could not be mirror imaged. A gap was therefore left in this part of the mirrored natural endocast, which was subsequently filled manually (modeled) with Plasticine by DF. This was done by using a mirrored bony fragment of the occipital condyle that was attached to the natural endocast and a trace of an enlarged right marginal sinus as guidelines (see Falk and Clarke, 2007 for details). Because enlarged occipital-marginal (O/M) sinuses of australopithecines are more often present unilaterally than bilaterally, and on the right rather than the left side, DF decided not to mirror the traces of Taung's enlarged right O/M sinus. For our article, we therefore did not calculate a midsagittal plane around which to mirror image either this hand-reconstructed region or the frontal polar region, and thus the asymmetries in these parts of our reconstruction are not attributable to errors in mirror imaging.

Nevertheless, Holloway and Broadfield (H&B) suggest that we 1) mirror imaged Taung's frontal lobes and 2) did so incorrectly because we failed to accurately define the midsagittal plane around which the mirror imaging was supposedly performed: "*A virtual reconstruction of Taung must assume perfect symmetry, a feature called into question here in Taung's most recent reconstruction by Falk and Clarke* (2007)" (H&B, 2011:319). . . ."*The authors rely heavily on mirror imaging to produce the final endocast, but the reconstruction displays a visible lack of symmetry between right and left sides*" (H&B, 2011:319). . . ."*A careful examination of Falk and Clarke's* (2007) *Figure* 2 *(see Fig. 5) indicates that a lack of symmetry exists between left and right cerebral hemispheres. . .. issues of symmetry include. . .a left prefrontal that is not an exact duplicate of the actual right side*" (H&B, 2011:320-322). . . ."*The Falk and Clarke* (2007) *reconstruction of Taung miscalculates the midsagittal plane. . . Again, it is mandatory that the missing left half be exactly the same as the present right half*" (H&B, 2011:322).

Although we did not compute a midsagittal plane for Taung's frontal polar region, we did compute one for the separate natural endocast so that we could mirror image its nearly complete right hemisphere. As H&B note, the reconstruction of the midsagittal plane is critical for obtaining an accurate cranial capacity. This is true because the position of the midsagittal plane of an object limits its volume on one side of that plane and therefore constrains the mirrored (doubled) volume. Our procedures for mirror imaging the right hemisphere of Taung's natural endocast were described in detail, and were performed with advanced computer technology and software (Falk and Clarke, 2007). After an automated digitization process that captured 3D data from all surfaces of the Taung natural endocast, we sequentially digitized all of the points on the obvious midline (Fig. 1) that courses along the endocast's dorsal surface (including the sagittal suture, SS) and continues ventrally midway between the orbits and medial to the frag-

*Correspondence to: Dean Falk, School for Advanced Research, Santa Fe, New Mexico 87505 and Department of Anthropology, Florida State University, Tallahassee, FL 32306-7772.
E-mail: dfalk@fsu.edu

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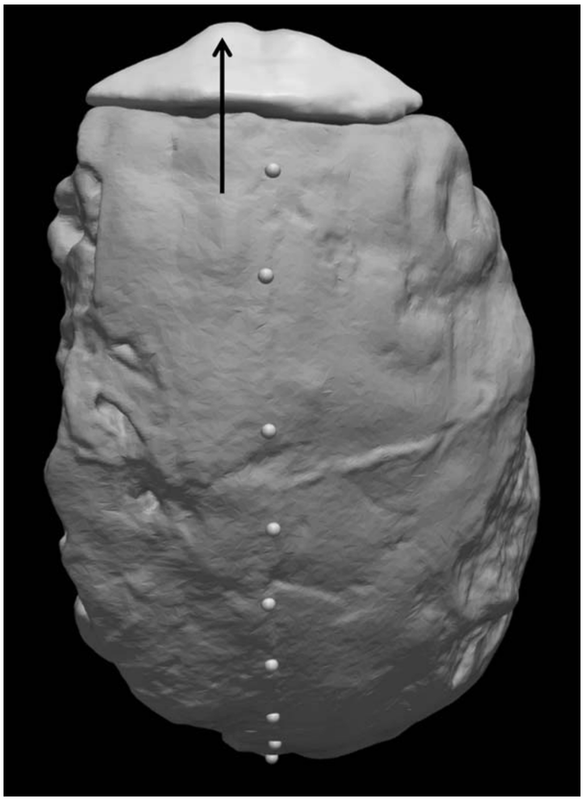

Fig. 1. Virtual reconstruction of Taung's natural endocast and its frontal polar region, which was segmented and smoothed by Sylvain Prima, Benoit Combès, José Braga and Gérard Subsol from 3D-CT data from the archives of the University of Vienna. The posterior (natural) endocast was registered automatically to the back of Taung's facial fragment, and JB identified points along the obvious sagittal midline. This midsagittal line is the same as that determined independently by the authors (see Falk and Clarke, 2007: Fig. 2). The arrow indicates (and confirms) Taung's slight left frontal petalia. Image courtesy of Sylvain Prima, Benoit Combès, José Braga, and Gérard Subsol.

Fig. 2. Holloway's (1970) reconstruction of the Taung hemiendocast (left) and a Wenner Gren cast of the original endocast (right). Photograph reproduced from Holloway and Broadfield (2011, Fig. 4), with labels FL (flash line from casting process) and sagittal suture (SS) added here. Holloway sanded the plaster copy of Taung's endocast (occipital lobe at bottom) to a midsagittal plane that was estimated from three visually selected points (indicated by the three black dots on the image). These two images are aligned differently. The sanded plane on the left of the hemicast appears convex rather than flat which could be due to one or more factors including a misaligned (tilted) dorsal view, imprecise sanding of the sagittal plane, or a camera that was focused between the two specimens rather than on the dorsal surface of the hemicast. The cast on the right is aligned with the flash line from the casting process approximately vertical and the midsagittal line rotated clockwise (similar to two dorsal photographs of the Wenner Gren endocast in Holloway et al., 2004, 100–101). Although we know it is not intentional, the misorientation of the Wenner Gren cast gives the impression that the frontal lobe is wider than it actually is.

ment of the left pterygoid process that adheres to the endocast's ventral surface (compare midline in Fig. 2 of Falk and Clarke, 2007 with the independently identified midline in Fig. 1). The software automatically increased tension on the digitized midline creating a best-fit midsagittal line (plane) along which the right hemisphere was electronically mirrored (much like a linear regression reduces the cumulative residuals for the sample on which it is based). For an illustration, see Falk and Clarke (2007:Fig. 2).The reason for this step is because endocasts are never perfectly symmetrical and the SS and other midline features meander a bit due to well-known natural asymmetries or torques in brains/endocasts. For example, if one were to place a shoelace on a surface in a line that is relatively but not perfectly straight, one could straighten it into a perfect line by pulling on both ends, i.e., by increasing tension along its length. In the case of our reconstruction, the software automatically increased the tension along the digitized midline in such a way that it achieved the "best fit" midline (and plane, since it curved over the surface of the endocast) around which to mirror the right half of the natural endocast. The advantage of this method is that it takes into account all of the points approximating the visible midline of the endocast and automatically computes the best-fit midsagittal plane around which to mirror image morphology that is available only on one side.

We think this method for establishing a midsagittal plane is preferable to the method used by Holloway in 1970 (and still preferred by H&B). The 1970-method involves visually selecting just three of the thousands of points that meander along the external midsagittal surface of a plaster copy of the Taung endocast and sanding the left side down to a plane that contains those three points (Fig. 2). Manually sanded planes vary depending on the three selected points, whereas an automatically computed plane determined from all of the visible points that approximate the midline is the best-fit plane, which increases the probability that any three of these points are actually located on it.

Although we believe that different methods for computing the midsagittal plane is the main reason why H&B's 404 cm^3 estimate for Taung's cranial capacity is 22 cm^3 larger than our estimate of 382 cm^3, it should be noted that if Taung shared the typical human pattern of greater right than left volume for the frontal lobes, doubling the volume of the right frontal lobe as H&B did would also have contributed to the inflated volume.

To summarize, Holloway and Broadfield's assertion that we mirror imaged the two parts of our virtual reconstruction of Taung's endocast that are asymmetrical is incorrect. Our reconstruction is an improvement over earlier ones because we included both of Taung's frontal poles (rather than replace the left one with a mirror image of the right one), thereby revealing a previously unrecognized asymmetry in the shape of the frontal polar region that has since been independently confirmed in a 3D-CT virtual endocast of Taung's frontal polar region (Fig. 1). Rather than calculating the midplane of Taung's natural endocast based on a few visually selected points, we used state-of-the-art computer technology that incorporated all of the available midline information to reconstruct a best-fit midsagittal plane around which to mirror unilaterally present morphology. That said, Holloway and Broadfield's general point that a suitable reconstruction of the midsagittal plane is crucial for obtaining an accurate endocast volume is well taken. There can be no doubt that high-tech methods for modeling and reconstructing missing parts of endocasts are advancing the field. However, if reconstructions incorporate parts that have been mirrored from one side to the other (which most of them do), computation of the midsagittal plane around which the mirroring is performed constrains the estimates for endocast volume. In other words, the accuracy of estimated volumes for reconstructed endocasts depends significantly on that of their reconstructed midsagittal planes.

DEAN FALK[1] AND RON CLARKE[2]
[1]*School for Advanced Research, Santa Fe; and, Department of Anthropology, Florida State University*
[2]*Institute for Human Evolution Palaeosciences Centre, University of the Witwatersrand*

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