Coll. Antropol. **28** Suppl. 2 (2004) 59–65
UCD 572.4:572.72:575.8
Original scientific paper

Hominin Brain Evolution – New Century, New Directions

Dean Falk

Department of Anthropology, Florida State University, Florida, USA

A B S T R A C T

The study of hominin brain evolution focuses on the interiors of fossilized braincases. Applications of recent three-dimensional computed tomography (CT) and magnetic resonance imaging (MRI) techniques for visualizing and measuring »virtual endocasts« from braincases in combination with advances in computer graphics and software for acquiring relevant data are transforming the way in which fossil skulls are analyzed, and improving the quality of paleoneurological investigations. Although CT imaging is preferred for fossil skulls, a novel method that combines high-resolution MRI of physical endocasts, electronic reconstruction of their missing parts, and warping of the resulting virtual endocasts is currently being developed and has great potential for future studies of hominin brain evolution. Applications of CT and MR techniques have already resulted in surprising new findings, which are briefly outlined. Exciting revelations about hominin brain evolution are expected as the 21st century unfolds.

***Key words**: 3D-CT, brain evolution, endocasts, fossils, hominins, MRI*

Introduction

In the summer of 1996, I found myself sitting in a train that was rolling along through the achingly beautiful Austrian Alps. I was surrounded by colleagues who shared an interest in using advanced computer technology to study the fossilized remains of our early ancestors. We were attending a workshop hosted by Professor Horst Seidler, and had just visited the laboratory of Zumtobel in Vorarlberg where we had observed a process in which three-dimensional (3D) computed tomographic (CT) data were used to produce a resin replica of a fossil hominin skull. It was spell-binding to observe the beam from the laser as it cured and shaped a model of a skull that was slowly but surely emerging from a pool of liquid photopolymeric acrylate. The beauty of this process, known as stereolithography, is that it renders models that accurately replicate not only the outer surfaces of fossils, but also most of the features

Received for publication April 6, 2004

within the substance of their bones[1]. Because stereolithographic models are produced in transparent resin, they incorporate some of the benefits of 'virtual' (computer-generated) models of skulls by revealing features of the braincase, cranial sinuses, pathways for nerves, and dentition that are not visible in the opaque fossils themselves. Such melding of virtual and traditional techniques had already been applied successfully to the study of 'Otzi', the famous 5,300-year-old ice mummy (or Tyrolean 'Ice Man') that was housed in a special refrigerator in Innsbruck[2]. That day on the train, we were headed for a special visit with Otzi that Professor Seidler had arranged for us. As we jostled along, there was lively discussion about whether or not the actual fossils might not become somewhat obsolete once (a) they gave up their secrets to 3D computed tomography and (b) scientists began to openly share these data. I argued then, as I will now, that it is still worth keeping good old hard copies of fossils around – no matter how dazzling the applications of yet-to-be-invented medical imaging technology become for the future study of fossil hominins.

Less than a decade after that workshop, we entered a new century in which the field of »virtual anthropology« that Professor Seidler helped to pioneer has evolved from being the »wave of the future« to becoming an important methodological »cutting edge« of contemporary paleoanthropology. Below, I describe recent applications of medical imaging technology to the study of hominin brain evolution, and point out some of their surprising results and theoretical implications.

The study of hominin brain evolution is largely a study of braincases, both fossilized and extant. Braincases provide information about two important parameters: (1) cranial capacity (which approxi- mates brain size), and (2) details about the brain's surface that remain impressed on the interior surfaces of braincases. Traditionally, information about the latter has been obtained from endocranial casts, or endocasts, that may occur naturally, e.g., when a skull fills with fine sediment that fossilizes, or that are prepared in the laboratory with casting materials. Endocasts reproduce details about sulcal pattern, nerves, cranial sutures, blood vessels, venous sinuses, and cerebellar size and shape. Although traditional »hard copies« of endocasts have been studied for well over a century[3], the study of »virtual endocasts« has only recently come into its own.

In medical CT scanners, an X-ray source and an array of detectors rotate around a specimen and collect data that may be visualized with a gray scale (with white representing highest density and black the lowest density). Because CT is able to resolve small density differences such as those between fossilized bone and attached rock matrix, it is particularly good for investigating fossils[4]. Three-dimensional CT (3D-CT) that is based on a series of contiguous or overlapping scans has therefore become useful as a non-invasive method for visualizing virtual endocasts, e.g., by flood-filling the braincase (ibid). Three-dimensional imaging may also be used to reconstruct missing portions of virtual endocasts by complementing missing parts through mirror imaging[5]. Cranial capacities may also be measured from matrix-filled fossil skulls[6,7]. (It is worth noting, however, that an important first step in developing this technique entailed validation on empty crania for which cranial capacities had already been obtained using the traditional method of packing seeds into the braincase and then measuring their volume in a graduated cylinder. This was carried out by Conroy and Vannier who were among the first to conclude that CT imaging was highly accurate and could have important applications for future paleoanthropological research by allowing anthropologists to visualize and analyze fossil material »in ways never before possible«[7].)

Applying 3D-CT to an australopithecine (*Australopithecus africanus*) partial skull from Makapansgat, South Africa (MLD 37/38) that was filled with solid matrix, Conroy et al. estimated a cranial capacity of 425 cm^3, which was very close to the estimate for that specimen in the contemporary literature[8]. In keeping with its taxonomic attribution, serial scans through the posterior cranial fossa of this specimen revealed an *absence* of grooves for enlarged occipital and marginal (O/M) sinuses that characterize all robust australopithecines and the Hadar specimens attributed to *Australopithecus afarensis*[9]. Along similar lines, Spoor et al. used CT-based 3D reconstruction to 'electronically remove' matrix from the cranial cavity of a robust australopithecine (*Paranthropus robustus*) from Swartkrans, South Africa (SK 47), a procedure that revealed a groove for the right O/M sinus[10]. The observation of an enlarged O/M sinus on SK 47 brings the tally for that feature to 11 out of 11 scorable *Paranthropus* specimens[9].

3D-CT Applied to Stw 505, 'Mr. Ples'

In 1998, two teams, led by Glenn Conroy and Horst Seidler, collaborated to produce an accurate 3D-CT virtual skull and endocast (reconstructed using mirror imaging) of an important australopithecine (*Australopithecus africanus*) cranium from Sterkfontein, South Africa (Stw 505, 'Mr. Ples'). A cranial capacity of 515 cm^3 was determined for the virtual endocast, which turned out to be surprisingly small compared to the over 600 cm^3 that had been expected by experts who had visually inspected the specimen[11]. Conroy and his colleagues suggested that other australopithecines (such as Sts 71) might also be associated with published cranial capacities that were too large and that this could explain why there had been inflated expectations for Stw 505. I, too, had expected the capacity of Stw 505 to be much larger for the simple reason that my hard copies of the specimen and endocast *looked* much larger than those of other australopithecines in my collection. Clearly, something was wrong[12]!

In response to these observations, my team (in collaboration with Seidler's team and Conroy) began to reevaluate the entire record of australopithecine endocasts. The results were, again, surprising and reinforced my conviction that, despite the revolution in virtual anthropology, it is important to keep hard copies of specimens. We found that four *Paranthropus* endocasts needed to be re-reconstructed because, earlier, they had been reconstructed using the endocast of Sts 5 (*Australopithecus africanus*) as a model, which was less than optimal because of shape differences in temporal and frontal lobes reproduced on *Paranthropus* and *Australopithecus* endocasts[13]. John Guyer, from my laboratory, therefore re-reconstructed these four specimens (SK 1585, OH 5, KNM-ER 407, KNM-ER 732) using available *Paranthropus* endocasts from my collection as models (see Appendix of Falk et al. for details[13]). The new endocast reconstructions were water-displaced in order to determine new cranial capacities, and in all four cases the cranial capacities were smaller than earlier estimates (see figure 1) (ibid).

The cranial capacities for Stw 505 and the four *Paranthropus* specimens that were provided (or inspired) by findings from CT analyses by Conroy's and Seidler's teams have far-reaching implications for hominin brain evolution. The four new cranial capacities for *Paranthropus* decrease the mean cranial capacity for that genus (to 450 cm^3, which equals rather than exceeds that for *Australopithecus*) and show that brain size did not increase much over time in that genus (fig. 1). Figure 1 also suggests that it is time to reevaluate the received wisdom that brain size suddenly 'took off' in the genus *Homo* around 2.0 million years

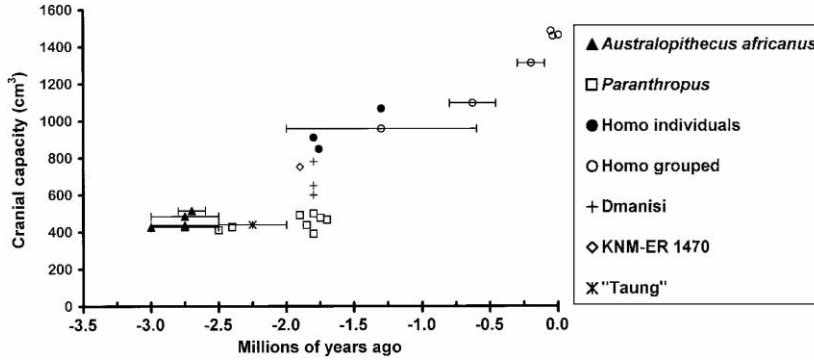

Fig. 1. Cranial capacities for Australopithecus africanus, Paranthropus, and a number of key representatives of Homo (both individuals and group means) plotted against time; see reference 13 for details. Error bars pertain to estimated dates for specimens. Specimens that share features with both Australopithecus and Homo include KNM-ER 1470 and three skulls from Dmanisi. Taung represents the projected adult cranial capacity for the only hominid from that site and, although it is the type specimen for A. africanus, it manifests a number of Paranthropus-like features in its skull, teeth, and endocast[9]. Brain size remained relatively conservative in Paranthropus. Contrary to the traditional view that brain size did not »take off« until 2.0 mya in Homo, these data suggest that it may have begun to increase considerably earlier in the Australopithecus ancestors of Homo.

ago[14]. Rather than there being a sudden jump in cranial capacity at the base of the known record for *Homo*, the trend toward increased brain size may have begun in the *Australopithecus* ancestors of *Homo* one million years earlier[15]. New specimens from a 1.75-million-year-old Eurasian site in Georgia (known as Dmanisi) also lend credence to a more gradual transition (including in brain size) from australopithecines through early *Homo*[16,17]. Thus, several skulls from Dmanisi share features with both *Australopithecus* and African early *Homo erectus*, and are associated with Oldowan-like stone tools that have been found with the former. Notably, 3D-CT analysis of one skull (D2700) reveals features that appear transitional between the two genera including a cranial capacity of about 600 cm^3. If confirmed, the hypothesis (brought to you courtesy of research inspired by 3D-CT) that brain size did not suddenly begin to increase around two million years ago in early *Homo* would represent a paradigm shift for paleoanthropology.

Magnetic Resonance Imaging (MRI)

Similar to CT imaging, magnetic resonance imaging (MRI) interprets signals from scanned data to produce visual images based on densities that are translated according to a gray scale (black represents the lowest, white the highest intensity). Instead of using an X-ray source, however, MRI uses pulses of radiofrequency energy to map specimens that have been subjected to a strong magnetic field. Whereas CT is ideal for imaging fossil material, MRI is most suitable for imaging soft-tissue structures[10]. For example, Falk et al. used 3D-MR to identify new asymmetries in lengths and positions of certain sulci in the human cerebral cortex[18]. Exciting recent MRI work by Katerina Semendeferi and colleagues is challenging another received wisdom in paleoanthropology – namely the hypothesis that humans evolved relatively larger frontal lobes compared to the great apes. When one controls for overall brain size, however, the relative size of the frontal lobes is, in fact, the same in the two

groups. What gives humans the edge in certain cognitive abilities appears to be due, in part, to differences in the relative sizes of subregions within the frontal lobe[19].

I am currently collaborating with Karl Zilles and his colleagues from the Research Center Julich, Germany and the Vogt Brain Research Institute at the University of Dusseldorf in applying a novel approach to studying the hominin endocasts in my collection. This approach entails a combination of high-resolution MRI of endocasts, 3D electronic reconstruction, and subsequent application of a multigrid elastic transformation algorithm to the resulting data. I took thirteen fossil endocasts to Germany for MR scanning (with specimens submerged in water for contrast). The endocasts included four *Paranthropus*, three *Australopithecus*, three *Homo erectus*, one archaic *Homo*, and two Neanderthal specimens. After scaling of the resulting virtual endocasts to adjust for size differences, each endocast was warped to match precisely the shape of a mean human endocast using an elastic transformation. Finally, the 3D deformation fields that describe quantitatively the regional distribution of the forces effecting the warping were visualized as color-coded maps on the mean human endocast, with warmer colors (yellows, reds) indicating areas that required local expansion, and cooler colors (greens, blues) showing regions that were compressed to match the shape of the human endocast[20]. An advantage of this technique is that it permits visualization of changes that occurred across the entire surface of the brain for a relatively large number of specimens representing diverse hominin taxa that lived during the last several million years. We are also using these methods to address questions concerning the evolution of cortical asymmetry. Although the research with Zilles' team is in a preliminary stage, I believe that the novel technique they invented for studying endocasts will yield more information about hominin brain evolution than I (or others) ever dreamt possible! Once again, it was fortunate that I had actual specimens in my collection that could be subjected to this hitherto-unknown method of analysis using advanced medical imaging technology.

This brief discussion has provided a few examples of the direction in which the so-called field of paleoneurology is headed as the 21st century begins to unfold. Although studies of hominin brain evolution are constrained by limitations of available sources of data (confined essentially to little more than a handful of fossilized braincases), the ever-evolving CT and MRI technology in combination with advances in creative software for computer graphics and analyses of virtual endocasts holds much promise for contributing to our future knowledge. As Spoor et al. point out[10], the field has already gone through its initial 'pretty pictures' phase that marveled at the possibilities of producing beautiful images, and the true scientific merit of using advanced medical imaging techniques to understand evolutionary processes has now become abundantly clear.

Acknowledgements

I am deeply grateful to the colleagues with whom I have collaborated in the study of hominin endocasts including Horst Seidler and his colleagues in Austria, Karl Zilles and his team in Germany, Michael Vannier, Charles Hildebolt, and Glenn Conroy. They have been very generous with their time and resources. Without their collaboration and friendship, I would not be privy to the 'magic' needed to study hominin brain evolution.

REFERENCES

1. SEIDLER, H., D. FALK, C. STRINGER, H. WILFIG, G. B. MULLER, D. ZUR NEDDEN, G. W. WEBER, W. RECHEIS, J.-L. ARSUAGA, J. Hum. Evol., 33 (1997) 691. — 2. ZUR NEDDEN, D., R. KNAPP, K. WICKE, W. JUDMAIER, W. A. MURPHY, H. SEIDLER, W. PLATZER, Radiology, 193 (1994) 269. — 3. FALK, D., K. R. GIBSON (Eds.): Evolutionary anatomy of the primate cerebral cortex. (Cambridge University Press, Cambridge, 2001). — 4. SPOOR, F., N. JEFFERY, F. ZONNEVELD, Imaging skeletal growth and evolution. In: O'HIGGINS, P., M. COHN (Eds.): Development, growth and evolution: Implications for the study of the hominid skeleton. (Linnean Society of London, London, 2000). — 5. ZOLLIKOFER, C. P. E., M. S. PONCE DE LEON, R. D. MARTIN, P. STUCKI, Nature, 375 (1995) 283. — 6. CONROY, G. C., M. W. VANNIER, Science, 26 (1984) 456. — 7. CONROY, G. C., M. W. VANNIER, Endocranial volume determination of matrix-filled fossil skulls using high-resolution computed tomography. In: TOBIAS, P. V. (Ed.): Hominid evolution: Past, present and future. (Alan R. Liss, New York, 1985). — 8. CONROY, G. C., M. W. VANNIER, P. V. TOBIAS, Science, 247 (1990) 838. — 9. FALK, D., T. B. GAGE, B. DUDEK, T. R. OLSON, J. Hum. Evol., 29 (1995) 591. — 10. SPOOR, F., N. JEFFERY, F. ZONNEVELD, J. Anat., 197 (2000) 61. — 11. CONROY, G. C., G. W. WEBER, H. SEIDLER, P. V. TOBIAS, A. KANE, B. BRUNSDEN, Science, 280 (1998) 1730. — 12. FALK, D., Science, 280 (1998) 1714. — 13. FALK, D., J. C. REDMOND, JR., J. GUYER, G. C. CONROY, W. RECHEIS, G. W. WEBER, H. SEIDER, J. Hum. Evol., 38 (2000) 695. — 14. FALK, D.: Evolution of the brain and cognition in hominids. (American Museum of Natural History James Arthur Lecture, New York, 1992). — 15. FALK, D.: Braindance: Revised and expanded edition. (University Press of Florida, Gainesville, 2004). — 16. VEKUA, A., D. LORDKIPANIDZE, G. P. RIGHTMIRE, J. AGUSTI, R. FERRING, G. MAISURADZE, A. MOUSKHELISHVILI, M. NIORADZE, M. PONCE DE LEON, M. TAPPEN, M. TVALCHRELIDZE, C. ZOLLIKOFER, Science, 297 (2002) 85. — 17. BALTER, M., A. GIBBONS, Science, 297 (2002) 26. — 18. FALK, D., C. HILDEBOLT, J. CHEVERUD, L. A. P. KOHN, G. FIGIEL, M. VANNIER, J. Neurosci. Meths., 39 (1991) 185. — 19. SEMENDEFERI, K., A. LU, N. SCHENKER, H. DAMASIO, Nature Neurosciences, 5 (2002) 272. — 20. FALK, D., C. E. MACLEOD, H. MOHLBERG, K. ZILLES., Am. J. Phys. Anthropol., 34 Suppl. (2002) 68.

D. Falk

Department of Anthropology, Florida State University, 1847 West Tennessee Street, Tallahassee, Florida 32304, USA
e-mail address: dfalk@fsu.edu

EVOLUCIJA MOZGA HOMININA – NOVO STOLJEĆE, NOVE SMJERNICE

SAŽETAK

Studija evolucije mozga hominina usmjerena je na unutrašnjost fosiliziranih lubanjskih jama. Primijenjene su nove tehnike – trodimenzionalna kompjutorska tomografija (CT) i prikazivanje pomoću magnetske rezonance (MRI) – za vizualizaciju i mjerenje »virtualnog endokasta« lubanjskih jama u kombinaciji s naprednim metodama kompjuterske grafike i programa za dobivanje relevantnih podataka koje su transformirale način na koji su fosili lubanja analizirani te poboljšali kvalitetu paleoneuroloških istraživanja. Premda CT prikaz se češće koristi za fosile lubanja, nova metoda koja kombinira visoku rezoluciju MRI fizičkog endokasta, elektronička rekonstrukcija nedostajućih dijelova i iskrivljavanje rezultirajućeg virtualnog endokasta trenutno se razvija i ima veliki potencijal za buduće studije evolucije mozga u hominina. Primjena CT i MRI tehnika već je rezultirala u iznenađujućim novim nalazima, koji su ukratko prikazani. Uzbudljiva otkrića o evoluciji mozga hominina očekuju se tijekom 21. stoljeća.