

A frontal lobe surface analysis in three archaic African human fossils: OH 9, Buia, and Bodo

Amélie Beaudet ^{a,*} and Emilio Bruner ^b

^a Department of Anatomy, University of Pretoria, PO Box 2034, 0001 Pretoria, South Africa

^b Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain

* Corresponding author.

E-mail address: beaudet.amelie@gmail.com (A. Beaudet).

Abstract

The evolution of the frontal lobes represents a major issue in paleoneurology. In this survey, we used a surface analysis to describe the frontal morphology of three relevant East African specimens from early and middle Pleistocene: OH 9, UA 31, and Bodo. When compared with a modern human endocast, UA 31 and Bodo display a flatter dorso-lateral surface, while OH 9 shows a general flattening of the whole dorsal morphology. OH 9 is the specimen with older chronology and with orbits more separated from the prefrontal cortex than in UA 31 and Bodo. The morphology of these three specimens is in agreement with the hypothesis that increase of the frontal curvature is due to the shifting of the facial block under the anterior cranial fossa. Apart from variations in size and general proportions, surface analysis can be useful in analyzing morphological changes localized in specific cortical areas. The three fossils are used as case study to discuss and review some relevant issues concerning frontal lobe evolution and paleoneurology.

Keywords

Human evolution
Paleoneurology
Prefrontal cortex
Anterior cranial fossa
Endocasts
Deformation-based models

1. Introduction

Frontal lobes are considered key cerebral areas in human brain evolution, particularly because of the role of the prefrontal cortex in executive functions and language (e.g., Kringelbach and Rolls, 2004; Petrides and Pandya, 1999; Rajkowska and Goldman-Rakic, 1995; Schenker et al., 2010). Nonetheless, there are still uncertainties on the scaling rules between frontal lobes and the rest of the brain in humans when compared with other primates (Barton and Venditti, 2013; Smaers, 2013). Although it is acknowledged that extant human frontal lobes are absolutely larger as compared to those of other primate taxa, critical studies report that the relative size of the frontal lobe is similar across hominoids, and that humans do not have the larger frontal lobe that would be expected from a primate brain of the human size (Semendeferi et al., 1997, 2002). Furthermore, investigations of the evolutionary rate of changes in the frontal lobes suggest that the frontal cortex did not evolve especially fast relative to other brain regions in the human lineage (Barton and Venditti, 2013). However, it has been claimed that the volume of human prefrontal white matter exceeds the volume predicted from primate trends based on the size of non-prefrontal cerebral white matter (Rilling, 2006; Schoenemann et al., 2005, but see Barton and Venditti, 2013). Moreover, the human prefrontal cortex is more convoluted than expected for a primate of our brain size and is among the most gyrfified cerebral areas (Rilling and Insel, 1999; Zilles et al., 1988).

Endocranial casts (endocasts) constitute a proxy for investigating and quantifying variations in brain size, brain shape and neocortical surface morphology in extinct species (Falk, 2014; Holloway, 1978; Holloway et al., 2004; Neubauer, 2014). Paleoneurological surveys have provided a general perspective on the morphological evolution of the frontal lobes in our genus. The derived *Homo*-like features of the frontal lobes, notably a prominent bossing in left inferior frontal convolution (Broca's area), a specific sulcal organization (horizontal and ascending branches of the lateral fissure) and cortical asymmetries (larger right frontal volume) have been present in the earliest human representatives for 2 million years (Falk, 1983; Schoenemann, 2013; Tobias, 1987). Also the general curvature of the frontal lobe profile has not displayed major changes at least in the last half-million years, especially when compared with the marked variations of the outer cranial districts (Bookstein et al., 1999). Modern humans tend to show more bulging frontal squama, but such increased curvature is likely to be a structural consequence due to the reduction of the facial block, which is furthermore positioned under the anterior cranial fossa (Bruner et al., 2013, 2014). Such spatial position between face and braincase requires an increased frontal curve, which, in this case, must be interpreted as a secondary structural consequence of the cranial architecture and not as a primary functional variation of the brain. Interestingly, both modern humans and Neanderthals display relatively wider frontal lobes when compared with less derived hominids (Bruner and Holloway, 2010). Nonetheless, these two species are also the only ones in which the frontal lobes are positioned almost entirely onto the orbital roof. Therefore, during morphogenesis, vertical development of the prefrontal cortex is constrained by the upper face, and lateral redistribution of the brain mass can simply be a secondary structural adjustment. Nonetheless, the interpretation of the frontal widening in modern humans and Neanderthals as a structural consequence is challenged by specimens like Maba, in which a derived face-braincase position is associated with narrow frontal lobes (Wu and Bruner, 2016).

In this study, we evaluate the morphology of the frontal lobes in three archaic human specimens from East Africa, as to evidence and quantify their frontal lobe differences in terms of spatial variations. The three fossils span from early to middle Pleistocene, covering a time span of about 0.8 Ma: the Early Pleistocene (c. 1.4 Ma) *H. erectus* specimen OH 9 from Olduvai Gorge, Tanzania (Antón, 2003; Deino, 2012; Leakey, 1961, 1966; Rightmire, 1979; Tamrat et al., 1995); the *H. erectus-ergaster* specimen UA 31 from the late early Pleistocene (1 Ma) assemblage of Uadi Aalad, Eritrea (Abbate et al., 1998; Albianelli and Napoleone, 2004; Bigazzi et al., 2004; Bruner et al., 2016; Ghinassi et al., 2015; Macchiarelli et al., 2004); and the *H. heidelbergensis* specimen Bodo 1 from the early middle Pleistocene (c. 0.6 Ma) deposits of the Middle Awash, Ethiopia (Clark et al., 1994; Conroy et al., 1978, 2000; Rightmire, 1996).

Unfortunately, quantitative analyses in paleoneurology are limited by different methodological restrictions. First, fossil samples are generally scarce, hampering adequate statistical inferences and robust quantitative tests. The morphology of the upper areas of the frontal lobes can be frequently reconstructed, because the thick frontal squama can more easily resist taphonomic and diagenetic processes. In contrast, the orbital side is generally fragmented and lost in the fossil record, because it is associated with the thin and fragile floor of the anterior cranial fossa. A second limit concerns the completeness of the sulcal imprints. During morphogenesis, the physical interaction between the frontal areas (housed in the anterior cranial fossa) and the facial block generates some spatial conflicts, and the intermediate bone layers are forced to mold between two different developmental systems (the brain and the face). As a result, the bone is particularly rich in imprints, most of all on the orbital surface (*digital impressions*). Despite the good correspondence between brain circumvolutions and their imprints in this district, the traces are, however, partial and incomplete, with some areas void of morphological information. Le Gros Clark and colleagues (1936) compared six chimpanzee crania and corresponding brains and, despite the conclusion that “very little information can be extracted in regard to sulcal pattern from the majority of our endocranial casts of the chimpanzee” (p. 267), they reported the identification of crucial sulci, such as the fronto-orbital sulcus. More recently, similar investigations were performed on a *Macaca* sample using virtual extraction of the endocasts and revealed that locations of most of the cerebral sulci could be inferred from the inner surface of the cranium (Kobayashi et al., 2014). Imprints are more pronounced for small brains, while they are more smoothed in larger endocasts. Humans, having the largest brain among primates, generally show less clear sulcal patterns than apes or cercopithecoids do. A third problem deals with the lack of a strict correspondence between morphological traits and functional brain areas, also for frontal areas involved in language like Brodmann's areas 44 and 45 (Amunts et al., 1999). These same areas display a noticeable individual variability and caution is needed in making inferences about morphological trends or distributions (Keller et al., 2009). Needless to say that a fourth limit is the lack of any biological information that goes beyond the gross superficial morphology, and endocasts cannot provide reliable information on tissues, cells, or molecular levels.

Despite these limitations, the availability of recently developed computer-based analytical tools allowing high-resolution digital imaging and modeling of the endocranial casts disclosed new perspectives in comparative paleoneurology (Gunz et al., 2009; Weber and Bookstein, 2011; Zollikofer, 2002; Zollikofer et al., 1998). Digital data promote new methods in quantitative analysis of endocranial shape, notably through geometric morphometric methods (e.g., Bruner, 2004; Gunz, 2015; Bruner et al., 2003; Neubauer et al., 2010) and registration of surfaces from the correspondence of anatomical landmarks (e.g., Specht et al.,

2007). However, methodological approaches based on landmarks and semi-landmarks are limited by the paucity of anatomical references on the brain surface. In this context, landmark-free methods that characterize shape via deformation-based models may represent an additional tool for registration and quantitative comparison of endocranial variations (Beaudet, 2015; Beaudet et al., 2016; Durrelman et al., 2012a). Accordingly, in this study, we present a deformation-based surface analysis of the frontal lobes in OH9, UA 31 and Bodo in comparison to the extant human condition, after digital reconstruction of the endocasts (Fig. 1). The aim of the study was to show the application of surface analysis to specific paleoneurological cases, and to evaluate whether these three specimens present a chronological pattern of variation in the morphology of their frontal lobes.

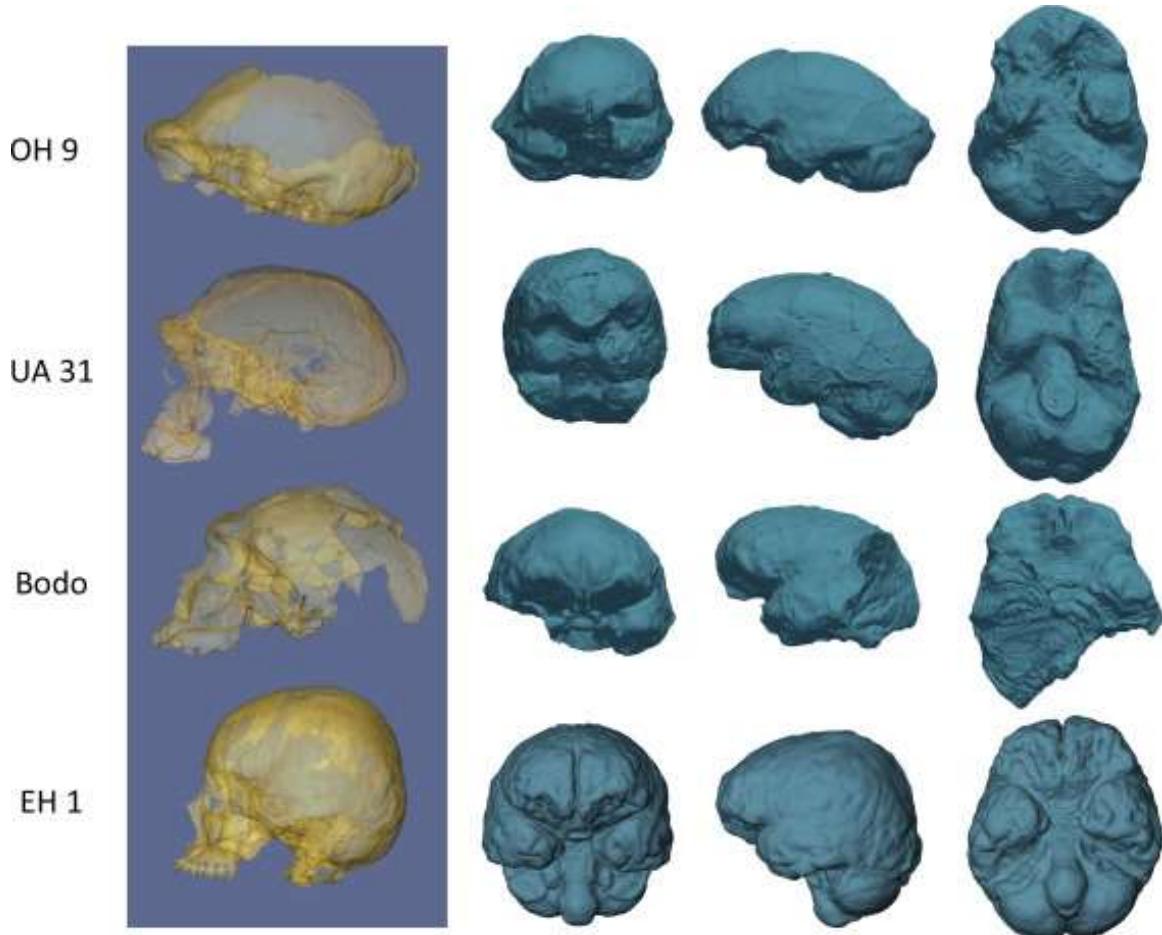


Fig. 1. Virtual rendering of the cranium and endocast in OH 9, UA 31, Bodo, and one extant human subject (EH 1). Images not to scale.

2. Material and methods

2.1. Material

The OH 9 specimen yielded by Bed II at Olduvai Gorge consists of a partially preserved braincase, including the supraorbital structures and much of the basicranium, lacking the face as well as the top and right side of the vault (Leakey, 1961; Rightmire, 1979). Leakey (1961) reported similarities between the OH 9 braincase and specimens from Steinheim, Broken

Hill, and Saldanha, considered early *Homo*. When discussing the diagnosis and phylogenetic position of the new species *Homo habilis* and paleobiodiversity at Olduvai Gorge, Leakey (1966) classified OH 9 as *Homo erectus*. Holloway et al. (2004) identified on the endocast a strong left occipital petalia and asymmetry in cerebellar lobes. The cranial capacity was estimated at 1067 cm³ (Holloway, 1973; Schoenemann, 2013).

The Bodo specimen was discovered in the Awash River Valley at the Bodo d'Ar site, and it consisted of an almost complete face and partial neurocranium (Conroy et al., 1978). Initial description reported affinities in overall appearance with archaic middle Pleistocene *Homo* crania (e.g., Kabwe, Petralona, Arago 21). However, Bodo has been suggested to be “intermediate” in its anatomy between *Homo erectus* and later Pleistocene humans (Conroy et al., 1978, 2000; Rightmire, 1996) and was included in the *Homo heidelbergensis* hypodigm. Regarding the external endocranial aspect, Holloway et al. (2005) described a “striking 30 mm long frontal torus just anterior to the left *pars triangularis* region of Broca's cap” shared with Kabwe and potentially specific to *Homo heidelbergensis* (Holloway et al., 2004, 2005). However, the overall shape of the prefrontal and orbital regions is similar to both Neanderthal and modern human and asymmetries in the Broca's caps are consistent with the extant human condition (Holloway et al., 2004, 2005). The encephalization quotient estimates in Bodo fall below the values found in samples of early late Pleistocene to extant *H. sapiens* (both fossil and recent) and Neanderthals despite an extant human-sized brain (1250 cc) (Conroy et al., 2000; Schoenemann, 2013).

OH 9 and Bodo were CT-scanned by X-ray tomography at Innsbruck (Austria) with a spatial resolution of 0.47 × 0.47 × 1 mm and of 0.49 × 0.49 × 1 mm, respectively. The digital data were provided by the Institute of Anthropology, University of Vienna, Austria (Digital Archive of Fossil Hominoids). The digital extraction and reconstruction of OH 9 and Bodo endocraniala were performed through the Endex® software, which is particularly suitable for crania that preserve an empty endocranial cavity (Subsol et al., 2010) (Fig. 1).

The cranium UA 31 is part of the assemblage from Uadi Alad, Danakil depression of Eritrea, and includes a well-preserved braincase, a large part of the facial skeleton, and the base (Abbate et al., 1998; Macchiarelli et al., 2004). The cranium of UA 31 presents a combination of *Homo erectus*-like and derived morphoarchitectural features shared with middle Pleistocene specimens (rev. in Bruner et al., 2016). The consensual terminology of *H. erectus*-like representative is mostly used (e.g., Bruner et al., 2016; Macchiarelli et al., 2004). The metric comparisons of the UA 31 endocast performed in Bruner et al. (2016) suggest a general archaic morphology shared with *Homo erectus* specimen, although the endocast displays pronounced dolichocephalic proportions and a narrow cranial base, constraining the temporal lobes and increasing the parietal curvature. The UA 31 endocranial volume is 995 cc (Bruner et al., 2016). In the present study we used the digital replica of the high-quality resin mold of the UA 31 endocast obtained after synchrotron X-ray radiation microtomography (SR-μCT) performed at the European Synchrotron Radiation Facility of Grenoble, France (isometric voxel size: 0.35 mm) in 2003 (Bruner et al., 2016).

No evidence of significant plastic deformation/distortion of the frontal lobes was reported in early and subsequent descriptions of these three fossil specimens (Bruner et al., 2016; Holloway et al., 2004; Leakey, 1961; Rightmire, 1979). We compared these specimens with the endocast of an extant human adult individual (EH 1) selected from the anonymized human clinical records of the Pasteur Hospital in Toulouse, France (El Khoury et al., 2014). The patient was scanned by medical computed-tomography (CT) with a spatial resolution of

$0.48 \times 0.48 \times 0.8$ mm. For a descriptive purpose, we also used in this study the cranium and endocast of an adult chimpanzee from the “Royal Museum for Central Africa” (Tervuren, Belgium) scanned with a spatial resolution of $0.38 \times 0.36 \times 0.8$ mm (El Khoury et al., 2014).

2.2. Deformation-based models

The morphology of the frontal lobes in the three fossil specimens was compared to the extant human condition through a landmark-free deformation-based model (Durrleman et al., 2012a). This approach differs substantially from landmark-based methods because it is not based on prior definition of homologous points, but on geometrical correspondences between continuous surfaces (see Durrleman et al., 2012a for further details). This method is particularly appropriate for comparing overall shapes and local orientation in the field of computational anatomy (Durrleman et al., 2014; Glaunès and Joshi, 2006), and more particularly to describe accurately complex 3D surface changes (Durrleman et al., 2012a). The deformation-based models have been demonstrated to be a useful tool for the registration of surface variation in primate endocranial ontogenetic trajectories, revealing both global and local changes (Durrleman et al., 2012a). These models also supply a valuable contribution to taxonomic and evolutionary studies (Beaudet, 2015; Beaudet et al., 2016; Dumoncel et al., 2014).

The comparison between surfaces is computed via the software Deformetrica (<http://www.deformetrica.org/>) dedicated to the statistical analysis of the 2-3D shape data, which includes registration process (deformation between two sets) and atlas construction (computation of an average object from a set of objects, e.g., Beaudet, 2015; Beaudet et al., 2016; Durrleman et al., 2012b). In our study, we specifically focused on the application dealing with the registration process.

As a pre-processing step, the frontal lobes were virtually separated from the rest of the endocranial surface according to a geometric criterion, along a plane defined by three landmarks placed at the junction between the temporal and frontal lobes corresponding to the anterior extremity of the Sylvian fissure (one landmark per hemisphere) and at the maximum anterior extension of the left temporal pole (Fig. 2). The fossils’ surfaces were firstly rigidly aligned in position, orientation, and scale with respect to the extant human specimen, using the iterative closest point (ICP) algorithm. The deformations from the fossil specimens to the extant human individual were mathematically modeled as a diffeomorphism; i.e. a one-to-one deformation of the 3D space that is smooth, invertible and with a smooth inverse (Durrleman et al., 2012a, b, 2014; Glaunès and Joshi, 2006). The deformation is computed using an iterative optimization algorithm described in Durrleman (2010). The algorithm yields deformation fields, which are the parameters of non-linear deformations registering one surface to another. They are distributed in a 3D grid enclosing the surfaces and common to all the registrations procedures (see Durrleman, 2010 for further technical details).

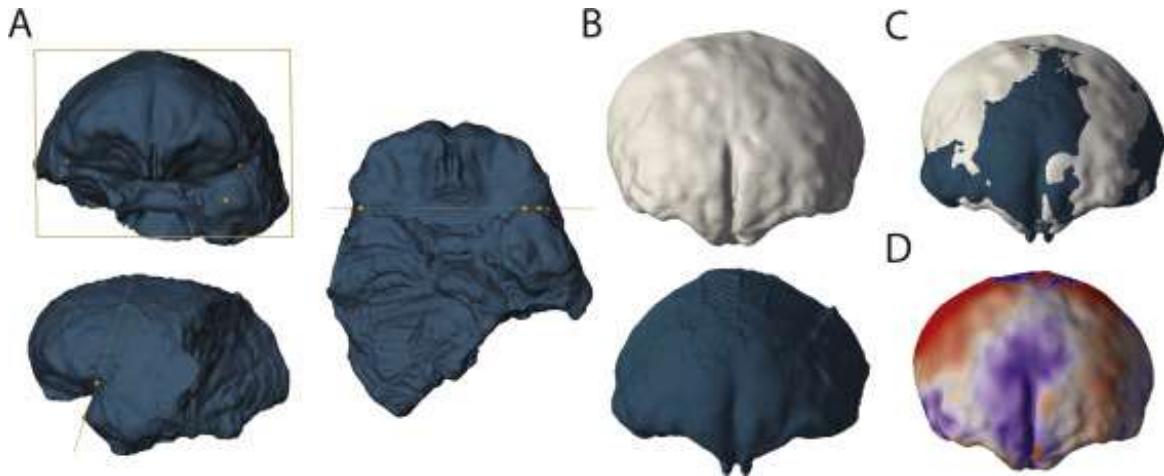


Fig. 2. Virtually rendered surfaces of the Bodo (dark green) and extant human (EH 1, light grey) endocasts. Cut plane corresponds to the best-fit plane passing through three landmarks positioned at the junction between the temporal and frontal lobes corresponding to the anterior extremity of the Sylvian fissure (one landmark per hemisphere) and at the maximum anterior extension of the left temporal pole (A) and isolates the frontal region from the rest of the endocast (B). The isolated frontal surface of Bodo is aligned onto the extant human surface (C). Colour map shows areas of more bulging (red) and flatter (blue) surfaces in the extant human endocast, when compared with the fossil one (D).

The magnitude and orientation of the surface differences according to the deformation process were signed and rendered by color maps from dark blue (negative values: flatter surface in the extant endocast) to red (positive values: more bulged surface in the extant endocast).

3. Results

Fig. 3 shows the surface differences between the three fossil specimens and the extant human endocast. In all three specimens, the frontal surface was generally flatter and longer than in the modern human endocast. Although the pattern was similar in the three extinct fossils, some minor specific differences can be detected. UA 31 and Bodo displayed flatter dorso-lateral surfaces, with the modern specimen showing bulging areas roughly centered on the posterior regions of the second frontal convolution. In general, in all cases the modern morphology was associated with increased bulging along the second frontal gyrus, more prominent on the left hemisphere. In addition, in OH9 frontal flattening was more pronounced and involved the whole posterior surface, including the central region. The three fossils also showed flatter orbital surfaces. In general, this registration does not reveal wider Broca's cap in the modern endocast, except when compared with UA 31 left side. Minor asymmetries in the surface mapping cannot be properly considered here, being possibly influenced by issues associated with the degree of completeness of the fossil or with idiosyncratic local variations.

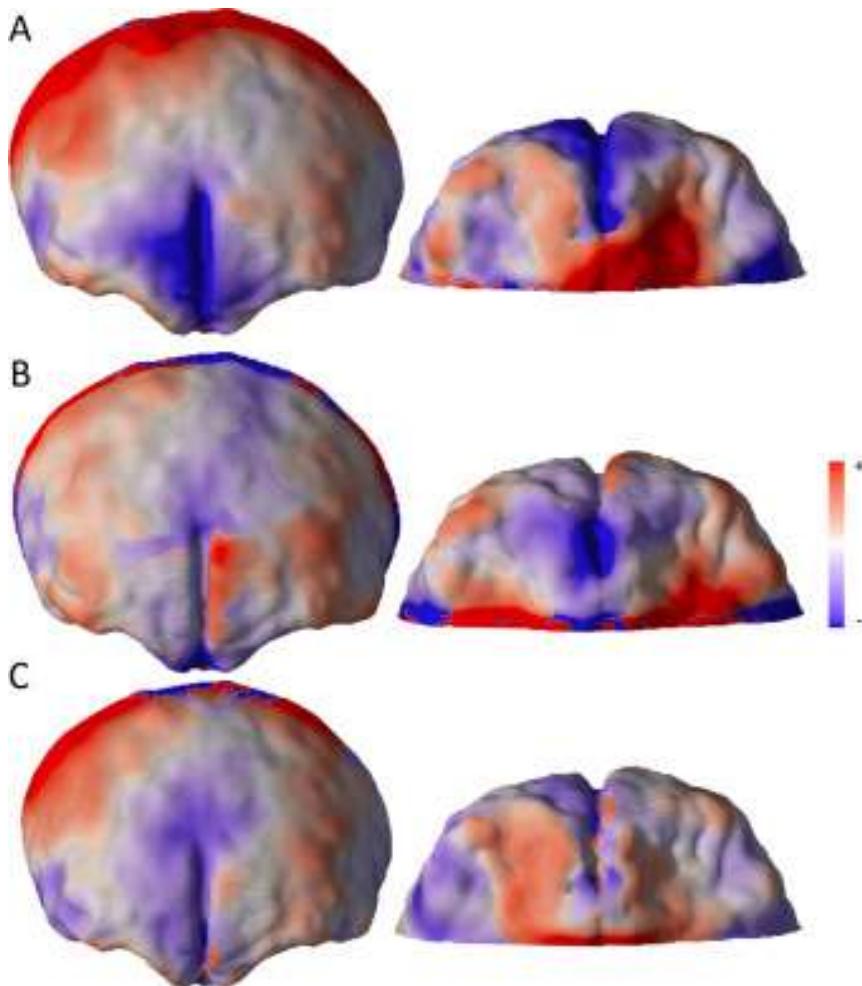


Fig. 3. Comparative maps of morphological deformations in frontal lobes from OH 9 (*H. erectus*) (A), UA 31 (*H. erectus-ergaster*) (B) and Bodo (*H. heidelbergensis*) (C) to EH1 (extant human), in anterior (left column) and inferior (right column) views. Cumulative displacement variations are signed and rendered by a pseudo-color scale ranging from dark blue (highest negative values) to red (highest positive values) on the extant human surface. Images not to scale.

In synthesis, this surface comparison suggests that our modern human endocast has wider dorso-lateral frontal lobes and taller orbital areas when compared with UA 31 and Bodo. The dorsal bulging of the frontal lobes is more pronounced and extended when compared with the oldest specimen, OH 9 (Fig. 3).

4. Discussion

The phylogenetic history of the human genus spans 2 million years and three continents. Taking into consideration the noticeable geographical and chronological variability in primates, at both inter- and intra-specific level, caution is recommended when dealing with single specimens. A further caution is necessary when analyzing endocasts of fossil taxa; information on the relationships between endocranial anatomy and brain functions is elusive and scanty, hampering strict associations between endocranial morphology and cerebral capacities. Within the limits inherent to the paleoneurological studies, endocasts represent the only direct evidence of brain evolution, and morphometric analyses of the external endocranial surface may reveal gross anatomical changes along the evolutionary lineages. In this study, we compared the surface of the anterior cranial fossa, a morphological proxy for

the prefrontal cortical areas, in three early to middle Pleistocene East African *Homo* specimens, using a modern human endocast as reference.

Our modern human endocast shows a relative bulging of the dorso-lateral surfaces, of the middle longitudinal curvature (second frontal gyrus) and of some orbital areas (Fig. 4). When compared with the oldest specimen, OH 9, the whole posterior surface is more bulging. These three specimens are generally assigned to archaic human species, namely *H. erectus/ergaster* (OH9 and UA 31) and *H. heidelbergensis* (Bodo). These two archaic taxa display allometric differences due to a larger brain size in the latter (both in absolute and relative terms—Rightmire, 2004, 2008) but, at present, no group-specific differences have been described in their endocranial morphology and proportions (Bruner, 2004; Bruner et al., 2003, 2015). The OH 9 endocast is similar to the endocasts from Zhoukoudian in terms of gross morphology, although in general the frontal proportions do not show marked differences between early and middle Pleistocene samples (Bruner et al., 2015, 2016). Nonetheless, if these three specimens are representative of their respective phylogenetic groups, we can tentatively hypothesize that frontal bulging has involved both an early change of the whole dorsal surface and a second change more localized on the dorso-lateral surfaces. Further specimens are necessary to evaluate whether such change might be associated with human evolution from early to middle Pleistocene, or from more archaic morphotypes (*H. erectus/ergaster*) to more derived ones (*H. heidelbergensis*). UA 31 is currently interpreted as *H. erectus/ergaster*, but this analysis suggests that its frontal morphology is more similar to Bodo's than to OH 9's.

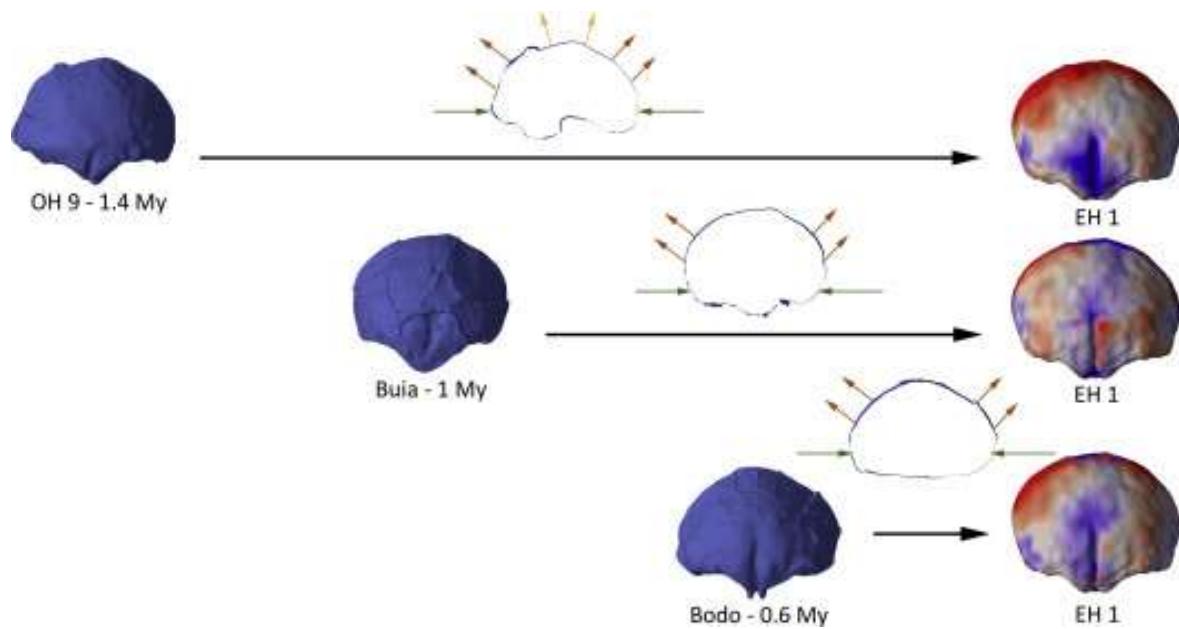


Fig. 4. A synthetic view (manual sketch) of the differences between the three fossil specimens and the modern human reference. When compared with the oldest specimen, OH 9, the modern human endocast displays a general bulging of the whole dorsal surface, while compared with UA 31 and Bodo it shows most of all a relative enlargement of the dorso-lateral areas. Changes are summarized by green (lateral), brown (dorso-lateral) and yellow (dorsal) arrows.

As already mentioned, the anterior cranial fossa is involved in complex morphogenetic processes in which the braincase and the facial block (the orbits and the ethmomaxillary system) are involved in spatial competition and reciprocal structural influences. Such a multifactorial process is necessarily constrained by functional and structural limits and, in general, it may be difficult to properly recognize primary causes and secondary consequences

of a given evolutionary change. In paleoneurology, a primary brain variation can be recognized if secondary adjustments due to cranial constraints can be ruled out (Bruner, 2015). Frontal lobe lateral widening has been hypothesized to be the result of vertical constraints associated with decreasing distance between frontal lobes and orbits (Bruner and Holloway, 2010), and frontal bulging has been hypothesized to be the secondary results of the curvature necessary to integrate the braincase with the face, positioned under the anterior fossa in more encephalized human species (Bruner et al., 2013). In chimps, orbits are positioned in front of the frontal lobes while in modern humans orbits are below the frontal lobes, therefore having shifted in a posterior and inferior position (Fig. 5). Apparently, OH 9 and Bodo display an intermediate morphology, with the former showing a less derived morphotype (i.e. larger distance between orbits and lobes; Fig. 5). Although this area is less complete in Buia, in this specimen the orbits also stood out in a more anterior position (see fig. 3 in Bruner et al., 2016). Hence, frontal curvature of these fossils fits the structural hypothesis: OH 9 has the most anterior orbits, and the flatter frontal lobes, as opposite to the modern morphotype. Ectocranially, these spatial changes also influence the expression of the browridge (Lieberman, 2000), which is more pronounced in those species with larger separation between orbits and frontal lobes.

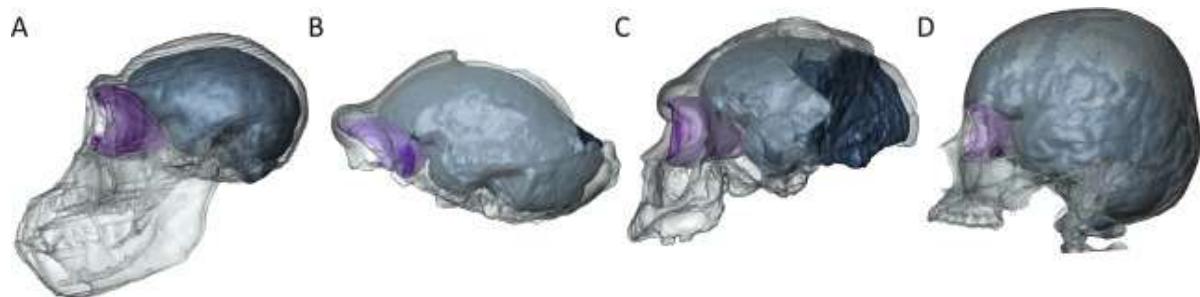


Fig. 5. Digital reconstruction of cranium (light grey), endocast (blue), and orbits (purple) in a chimpanzee (A), OH 9 (B), Bodo (C), and the recent human subject (D). Images not to scale.

The lateral expansion of the frontal lobes (in this case, the absence of) is more difficult to interpret. Considering that a proportional volumetric increase of the frontal lobes in apes and humans has not been patently recognized (Rilling, 2006; Semendeferi et al., 1997), most shape variations should be assumed to be a matter of geometry and mass redistribution and not of specific cortical expansion. As mentioned, the hypothesis of frontal widening due to facial constraints in large-brained human species is challenged by fossils like Maba, which has a derived facial morphology and position, but a plesiomorph brain form with narrow prefrontal areas (Wu and Bruner, 2016). Interestingly, the endocast of Maba has generalized human proportions, and it is very similar to the endocast of Bodo (Wu and Bruner, 2016), but their frontal bulging is very different: frontal curvature is derived in Maba, but plesiomorph in Bodo, which resembles the phenotype observed in Kabwe or Ceprano (Bruner et al., 2013). This result seems to suggest that facial position may influence the degree of frontal bulging but not necessarily the degree of frontal widening. In this case frontal bulging and widening may be two independent characters and a structural effect can be more easily hypothesized for the former. If frontal widening is not a secondary consequence of structural constraints, the question should be asked whether frontal widening could represent a primary change of brain morphology due to either change in specific local cortical organization (some areas become larger, some other smaller) or to changes to the system of connections. In fact, the morphology of the cortical surface has been hypothesized to be sensitive to mechanical forces associated with physical properties of neurons and of their fibers (Tallinen et al., 2016; Toro

and Burnod, 2005; Van Essen, 1997). All these interpretations are speculative and it has to be considered that all these characters exhibit a noticeable intraspecific variation and that few specimens are not sufficient for validating specific evolutionary hypotheses.

Also the fact that this model does not reveal changes at the third frontal gyrus and Broca's cap should be interpreted with caution. Apart from individual variation and idiosyncratic traits, we must take into account that surface analyses do not include anatomical information such as cerebral boundaries, homology, or specific anatomical elements. Therefore, these procedures compare surfaces but do not consider specific anatomical correspondence, apart from a general geometrical one. Moreover, our definition of the frontal lobes is strictly geometrical and follows neither anatomical nor structural references. In the specific case of Broca's cap, the recognition of its morphological features can be problematic even in brain samples (Keller et al., 2009), which suggests that there are still some general aspects of the brain gross morphology that remain unresolved.

This study suggests that the evolution of the frontal lobes in the human genus should be considered not only in terms of curvature or lateral proportions. Specific morphological analysis of their surface may reveal some localized cortical variations (for example the dorso-lateral expansion). Current brain mapping is integrating information on cytoarchitecture, functions, connections, biochemistry and genetics to provide a comprehensive view of the brain parcellation (Glasser et al., 2016). In this sense, future perspectives in paleoneurology deal with two major targets. First, more specimens are needed to provide reliable and consistent quantification of patterns and variation. Second, improving morphometric tools would allow the identification of specific and localized cortical areas in terms of cytoarchitectonic organization involved in phylogenetic changes.

As a final remark it must be stressed that, even if a primary brain change can be identified, and even if the area involved is crucial for some specific cognitive performance, a traditional interpretation of this change as consequence of a direct selective pressure can be misleading. Our brain morphology is more susceptible to non-genetic factors, when compared with the brain morphology of apes (Gómez-Robles et al., 2015). The brain is a plastic organ, extremely sensitive to environmental influence, and our species is responsible for a very special kind of environment: culture. Brain changes can be the result of a genetic selection for some neural aspects, but also the result of environmental influences and behavioral training. Intermediate situations, like genetic selection for plasticity or epigenetic effects between culture and genes, are also possible (Bruner and Iriki, 2016). In all cases, cognitive changes may leave no traces on brain anatomy but, in contrast, marked variations in brain anatomy are likely to be associated with behavioral differences. That's why paleoneurological studies on the frontal lobes are necessary for ruling out cranial constraints, eventually revealing actual cortical modifications.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgments

Access to the record of the UA 31 fossil specimen from Buia, Eritrea, has been allowed within an ongoing scientific collaboration with the “Eritrean-Italian Danakil Expedition: Anthropo-Archaeological and Geo-Paleontological Research Project”. For granting access to

the comparative material, we are grateful to the AMIS (Toulouse) laboratory. We are grateful to Roberto Macchiarelli for promoting this study, and for his constant help and suggestions during the preparation of this paper. This paper is part of a special issue edited by Roberto Macchiarelli and Clément Zanolli, entitled “*Hominin biomechanics, virtual anatomy and inner structural morphology: from head to toe. A tribute to Laurent Puymerail*”. AB would like to express her gratitude to Laurent Puymerail for his patience as co-supervisor, his support as colleague and, more importantly, for his presence as friend. For scientific contribution and/or discussion we are grateful to J. Braga (Toulouse), J. Dumoncel (Toulouse), S. Durrleman (Paris), E. Gilissen (Tervuren), A. Oettlé (Pretoria), G. Subsol (Montpellier) and J.F. Thackeray (Johannesburg). This work was granted access to the HPC resources of CALMIP supercomputing center under the allocation 2016-[P1440] attributed to the laboratory AMIS (Toulouse). EB is funded by the Spanish Government (CGL2015-65387-C3-3-P). AB is funded the Erasmus Mundus program “A European and South African Partnership on Heritage and Past+” (AESOP+ program).

References

- Abbate, E., Albianelli, A., Azzaroli, A., Benvenuti, M., Tesfamariam, B., Bruni, P., Cipriani, N., Clarke, R.J., Ficcarelli, G., Macchiarelli, R., Napoleone, G., Papini, M., Rook, L., Sagri, M., Medhin Tecle, T., Torre, D., Villa, I., 1998. A one-million-year-old Homo cranium from the Danakil (Afar) Depression of Eritrea. *Nature* 393, 458–460.
- Albianelli, A., Napoleone, G., 2004. Magnetostratigraphy of the Homo-bearing Pleistocene Dandiero Basin (Danakil Depression, Eritrea). *Riv. Ital. Paleont. Strat.* 110 (Suppl.), 35–44.
- Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H.B., Zilles, K., 1999. Broca’s region revisited: cytoarchitecture and intersubject variability. *J. Comp. Neurol.* 412, 319–341.
- Antón, S.C., 2003. Natural history of *Homo erectus*. *Yearb. Phys. Anthropol.* 46, 125–170.
- Barton, R.A., Venditti, C., 2013. Human frontal lobes are not relatively large. *Proc. Natl. Acad. Sci. U.S.A.* 110, 9001–9006.
- Beaudet, A., 2015. Caractérisation des structures crânio-dentaires internes des cercopithécoïdes et étude diachronique de leurs variations morphologiques dans la séquence Plio-Pléistocène sud-africaine. Univ. Toulouse (PhD dissertation).
- Beaudet, A., Dumoncel, J., de Beer, F., Dupoyer, B., Durrleman, S., Gilissen, E., Hoffman, J., Tenailleau, C., Thackeray, J.F., Braga, J., 2016. Morphoarchitectural variation in South African fossil cercopithecoid endocasts. *J. Hum. Evol.* 101, 65–78.
- Bigazzi, G., Balestrieri, M.L., Norelli, P., Oddone, M., Tewolde, M.T., 2004. Fission-track dating of a tephra layer in the Alat formation of the Dandiero Group (Danakil Depression, Eritrea). *Riv. Ital. Paleont. Strat.* 110 (Suppl.), 45–49.
- Bookstein, F., Schafer, K., Prossinger, H., Seidler, H., Fieder, M., Stringer, C., Weber, G.W., Arsuaga, J.L., Slice, D.E., Rohlf, F.J., Recheis, W., Mariam, A.J., Marcus, L.F., 1999. Comparing frontal cranial profiles in archaic and modern Homo by morphometric analysis. *Anat. Rec.* 257, 217–224.

- Bruner, E., 2004. Geometric morphometrics and paleoneurology: brainshape evolution in the genus *Homo*. *J. Hum. Evol.* 47, 279–303.
- Bruner, E., 2015. Functional craniology and brain evolution. In: Bruner, E.(Ed.), Human Paleoneurology. Springer, Switzerland, pp. 57–94.
- Bruner, E., Holloway, R.L., 2010. A bivariate approach to the widening of the frontal lobes in the genus *Homo*. *J. Hum. Evol.* 58, 138–146.
- Bruner, E., Iriki, A., 2016. Extending mind, visuospatial integration, and the evolution of the parietal lobes in the human genus. *Quatern. Int.* 405, 98–110.
- Bruner, E., Athreya, S., Manuel de la Cuétara, J., Marks, T., 2013. Geometric variation of the frontal squama in the genus *Homo*: frontal bulging and the origin of modern human morphology. *Am. J. Phys. Anthropol.* 150, 313–323.
- Bruner, E., Bondioli, L., Coppa, A., Frayer, D.W., Holloway, R.L., Libsekal, Y., Medin, T., Rook, L., Macchiarelli, R., 2016. The Endocast of the One-Million-Year-Old Human Cranium from Buia (UA 31), Danakil Eritrea. *Am. J. Phys. Anthropol.* 160, 458–468.
- Bruner, E., de la Cuétara, J.M., Masters, M., Amano, H., Ogihara, N., 2014. Functional craniology and brain evolution: from paleontology to biomedicine. *Front. Neuroanat.* 8, 19.
- Bruner, E., Grimaud-Hervé, D., Wu, X., de la Cuétara, J.M., Holloway, R., 2015. A paleoneurological survey of *Homo erectus* endocranial metrics. *Quatern. Int.* 368, 80–87.
- Bruner, E., Manzi, G., Arsuaga, J.L., 2003. Encephalization and allometric trajectories in the genus *Homo*: evidence from the Neandertal and modern lineages. *Proc. Natl. Acad. Sci. U. S. A.* 100, 15335–15340.
- Clark, J.D., De Iliciuehn, J., Schick, K., Han, W., White, T., WoldeGabriel, G., Walter, R., Suwa, G., Asfaw, B., Vrba, E., Haile-Selassie, Y., 1994. African *Homo erectus*: old radiometric ages and young Oldowan assemblages in the Middle Awash Valley, Ethiopia. *Nature* 264, 1907–1910.
- Conroy, G.C., Jolly, C.J., Cramer, D., Kalb, J.E., 1978. Newly discovered fossil hominid skull from the Afar depression, Ethiopia. *Nature* 276, 67–70.
- Conroy, G.C., Weber, G.W., Seidler, H., Recheis, W., Zur Nedden, D., Mariam, J.H., 2000. Endocranial capacity of the bodo cranium determined from three-dimensional computed tomography. *Am. J. Phys. Anthropol.* 113, 111–118.
- Deino, A.L., 2012. ⁴⁰Ar/³⁹Ar dating of Bed I, Olduvai Gorge, Tanzania, and the chronology of early Pleistocene climate change. *J. Hum. Evol.* 63, 251–273.
- Durrleman, S., (Ph.D. dissertation) 2010. Statistical models of currents for measuring the variability of anatomical curves, surfaces and their evolution. Université Nice-Sophia Antipolis.

- Durrleman, S., Pennec, X., Trouvé, A., Ayache, N., Braga, J., 2012a. Comparison of the endocranial ontogenies between chimpanzees and bonobos via temporal regression and spatiotemporal registration. *J. Hum. Evol.* 62, 74–88.
- Durrleman, S., Prastawa, M., Charon, N., Korenberg, J.R., Joshi, S., Gerig,G., Trouvé, A., 2014. Morphometry of anatomical shape complexes with dense deformations and sparse parameters. *NeuroImage* 101,35–49.
- Durrleman, S., Prastawa, M., Korenberg, J.R., Joshi, S., Trouvé, A., Gerig,G., 2012b. Topology preserving atlas construction from shape data without correspondence using sparse parameters. In: Ayache, N.,Delingette, H., Golland, P., Mori, K. (Eds.), MICCAI 2012, Part III. LNCS,vol. 7512. Springer, Heidelberg, pp. 223–230.
- Dumoncel, J., Durrleman, S., Braga, J., Jessel, J.-P., Subsol, G., 2014. Landmark-free 3D method for comparison of fossil hominins and hominids based on endocranum and EDJ shapes. *Am. J. Phys. Anthro-pol.* 153 (110) (abstract).
- El Khoury, M., Braga, J., Dumoncel, J., Nancy, J., Esclassan, R., Vaysse,F., 2014. The human semicircular canals orientation is more similar to the bonobos than to the chimpanzees. *Plos One* 9 (4), e93824,<http://dx.doi.org/10.1371/journal.pone.0093824>.
- Falk, D., 1983. Cerebral cortices of East African early hominids. *Science* 221, 1072–1074.
- Falk, D., 2014. Interpreting sulci on hominin endocasts: old hypotheses and new findings. *Front. Hum. Neurosci.* 8, 134.
- Ghinassi, M., Oms, O., Papini, M., Scarciglia, F., Carnevale, G., Sani, F.,Rook, L., Delfino, M., Pavia, M., Libsekal, Y., Bondioli, L., Coppa, A.,Frayer, D.W., Macchiarelli, R., 2015. An integrated study of the Homo-bearing Aalat stratigraphic section (Eritrea): an expanded continental record at the Early-Middle Pleistocene transition. *J. Afr. Earth Sci.* 112,163–185.
- Glasser, M.F., Coalson, T.S., Robinson, E.C., Hacker, C.D., Harwell, J., Yacoub,E., Ugurbil, K., Andersson, J., Beckmann, C.F., Jenkinson, M., Smith, S.M.,Van Essen, D.C., 2016. A multi-modal parcellation of human cerebral cortex. *Nature* 536, 171–178.
- Glaunès, J.A., Joshi, S., 2006. Template estimation from unlabeled pointset data and surfaces for computational anatomy. In: Pennec, X., Joshi,S. (Eds.), Proceedings of the International Workshop on the Mathematical Foundations of Computational Anatomy. Copenhagen, pp.29–39.
- Gómez-Robles, A., Hopkins, W.D., Schapiro, S.J., Sherwood, C.C., 2015. Relaxed genetic control of cortical organization in human brains compared with chimpanzees. *Proc. Natl. Acad. Sci. U. S. A.* 112,14799–14804.
- Gunz, P., 2015. Computed tools for paleoneurology. In: Bruner, E. (Ed.),Human paleoneurology. Springer, Zurich, pp. 39–55.

Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G.W., Bookstein, F.L., 2009. Principles for the virtual reconstruction of hominin crania. *J. Hum. Evol.* 57, 48–62.

Holloway, R.L., 1973. New endocranial values for the East African early hominids. *Nature* 243, 97–99.

Holloway, R.L., 1978. The relevance of endocasts for studying primate brain evolution. In: Noback, C.R. (Ed.), *Sensory Systems of Primates*. Plenum Press, New York, pp. 181–200.

Holloway, R.L., Broadfield, D.C., Yuan, M.S., 2004. *The Human Fossil Record: Brain Endocasts, the Paleoneurological Evidence*. Wiley-Liss, Hoboken.

Holloway, R.L., Yuan, M.S., Broadfield, D.C., 2005. The Bodo endocast: a strange frontal lobe. . . Am. J. Phys Anthropol 126 (Suppl. 40), 118(abstract).

Keller, S.S., Crow, T., Foundas, A., Amunts, K., Roberts, N., 2009. Broca's area: Nomenclature, anatomy, typology and asymmetry. *Brain Lang.* 109, 29–48.

Kobayashi, Y., Matsui, T., Haizuka, Y., Ogihara, N., Hirai, N., Matsumura, G., 2014. Cerebral sulci and gyri observed on macaque endocasts. In: Akazawa, T., Ogihara, N., Tanabe, H.C., Terashima, H. (Eds.), *Dynamics of learning in Neanderthals and modern humans*, Volume 2. Springer, Japan, pp. 131–137.

Kringelbach, M.L., Rolls, E.T., 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Prog. Neurobiol.* 72, 341–372.

Le Gros Clark, W.E., Cooper, D.M., Zuckerman, S., 1936. The Endocranial Cast of the Chimpanzee. *J. Roy. Anthropol. Inst.* 66, 249–268.

Leakey, L.S.B., 1961. New finds at Olduvai Gorge. *Nature* 189, 649–650.

Leakey, L.S.B., 1966. *Homo habilis*, *Homo erectus* and the australopithecines. *Nature* 209, 1279–1281.

Lieberman, D., 2000. Ontogeny, homology and phylogeny in the hominid craniofacial skeleton. The problem of the browridge. In: O'Higgins, P., Cohn, M. (Eds.), *Development, growth and evolution: Implications for the study of hominid skeletal evolution*. Academic Press, London, pp. 85–122.

Macchiarelli, R., Bondioli, L., Chech, M., Coppa, A., Fiore, I., Russom, R., Vecchi, F., Libsekal, Y., Rook, L., 2004. The late Early Pleistocene human remains from Buia, Danakil Depression, Eritrea. *Riv. It. Paleont. Strat.* 110 (Suppl.), 133–144.

Neubauer, S., 2014. Endocasts: possibilities and limitations for the interpretation of human brain evolution. *Brain Behav. Evol.* 84, 117–134.

- Neubauer, S., Gunz, P., Hublin, J.-J., 2010. Endocranial shape changes during growth in chimpanzees and humans: a morphometric analysis of unique and shared aspects. *J. Hum. Evol.* 59, 555–566.
- Petrides, M., Pandya, D.N., 1999. Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. *Eur. J. Neurosci.* 11, 1011–1036.
- Rajkowska, G., Goldman-Rakic, P.S., 1995. Cytoarchitectonic definition of prefrontal areas in the normal human cortex: II. Variability in locations of areas 9 and 46 and relationship to the Talairach Coordinate System. *Cereb. Cortex* 5, 323–337.
- Rightmire, G.P., 1979. Cranial remains of *Homo erectus* from Beds II and IV, Olduvai Gorge, Tanzania. *Am. J. Phys. Anthropol.* 51, 99–115.
- Rightmire, G.P., 1996. The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene? *J. Hum. Evol.* 31, 21–39.
- Rightmire, G.P., 2004. Brain size and encephalization in early to mid-Pleistocene *Homo*. *Am. J. Phys. Anthropol.* 124, 109–123.
- Rightmire, G.P., 2008. *Homo* in the Middle Pleistocene: hypodigms, variation, and species recognition. *Evol. Anthropol.* 17, 8–21.
- Rilling, J.K., 2006. Human and non-human primate brains: are they allometrically scaled versions of the same design? *Evol. Anthropol.* 15, 65–67.
- Rilling, J.K., Insel, T.R., 1999. The primate neocortex in comparative perspective using magnetic resonance imaging. *J. Hum. Evol.* 37, 191–223.
- Schenker, N.M., Hopkins, W.D., Spoorer, M.A., Garrison, A.R., Stimpson, C.D., Erwin, J.M., Hof, P.R., Sherwood, C.C., 2010. Broca's area homologue in chimpanzees (*Pan troglodytes*): probabilistic mapping, asymmetry, and comparison to humans. *Cereb. Cortex* 20, 730–742.
- Schoenemann, P.T., 2013. Hominid brain evolution. In: Begun, D. (Ed.), *A companion to paleoanthropology*. Wiley-Blackwell, Chichester, pp. 136–164.
- Schoenemann, P.T., Sheehan, M.J., Glotzer, L.D., 2005. Prefrontal white matter volume is disproportionately larger in humans than in other primates. *Nat. Neurosci.* 8, 242–252.
- Semendeferi, K., Damasio, H., Frank, R., Van Hoesen, G.W., 1997. The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. *J. Hum. Evol.* 32, 375–388.
- Semendeferi, K., Lu, A., Schenker, N., Damasio, H., 2002. Humans and great apes share a large frontal cortex. *Nat. Neurosci.* 5, 272–276.

- Smaers, J.B., 2013. How humans stand out in frontal lobe scaling. Proc.Natl. Acad. Sci. U. S. A. 110, E3682.
- Specht, M., Lebrun, R., Zollikofer, C.P.E., 2007. Visualizing shape transformation between chimpanzee and human braincases. Vis. Comput. 23, 743–751.
- Subsol, G., Gesquière, G., Braga, J., Thackeray, F., 2010. 3D automatic methods to segment “virtual” endocasts: state of the art and future directions. Am. J. Phys. Anthropol. 141 (Suppl. 50), 226–227(abstract).
- Tallinen, T., Chung, J.Y., Rousseau, F., Girard, N., Lefèvre, J., Mahadevan, L., 2016. On the growth and form of cortical convolutions. Nat. Phys. 12, 588–593.
- Tamrat, E., Thouveny, N., Taïeb, M., Opdyke, N.D., 1995. Revised magnetostratigraphy of the Plio-Pleistocene sedimentary sequence of the Olduvai Formation (Tanzania). Palaeogeogr. Palaeoclimatol. Palaeoecol. 114, 273–283.
- Tobias, P.V., 1987. The brain of *Homo habilis*: a new level of organization in cerebral evolution. J. Hum. Evol. 16, 741–761.
- Toro, R., Burnod, Y., 2005. A morphogenetic model for the development of cortical convolutions. Cerebral Cortex 15, 1900–1913.
- Van Essen, D.C., 1997. A tension-based theory of morphogenesis and compact wiring in the central nervous system. Nature 385, 313–318.
- Weber, G.W., Bookstein, F.L., 2011. Virtual Anthropology: a guide to a new interdisciplinary field. Springer, London.
- Wu, X., Bruner, E., 2016. The endocranial anatomy of Maba 1. Am. J. Phys. Anthropol. 160, 633–643.
- Zilles, K., Armstrong, E., Schleicher, A., Kretschmann, H.J., 1988. The human pattern of gyration in the cerebral cortex. Anat. Embryol. 179, 173–179.
- Zollikofer, C.P.E., 2002. A computational approach to paleoanthropology. Evol. Anthropol. 11, 64–67.
- Zollikofer, C.P.E., Ponce De León, M.S., Martin, R.D., 1998. Computer-assisted paleoanthropology.