Replacement of Neanderthals by Modern Humans Series

Emiliano Bruner
Naomichi Ogihara
Hiroki C. Tanabe *Editors*

Digital Endocasts

From Skulls to Brains

Springer

Replacement of Neanderthals by Modern Humans Series

Edited by

Takeru Akazawa
Research Institute, Kochi University of Technology
Kochi 782-8502, Japan
akazawa.takeru@kochi-tech.ac.jp

Ofer Bar-Yosef
Department of Anthropology, Harvard University
Cambridge, Massachusetts 02138, USA
obaryos@fas.harvard.edu

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Emiliano Bruner • Naomichi Ogihara •
Hiroki C. Tanabe
Editors

Digital Endocasts

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Editors
Emiliano Bruner
CENIEH
Burgos, Spain

Naomichi Ogihara
Keio University
Yokohama, Japan

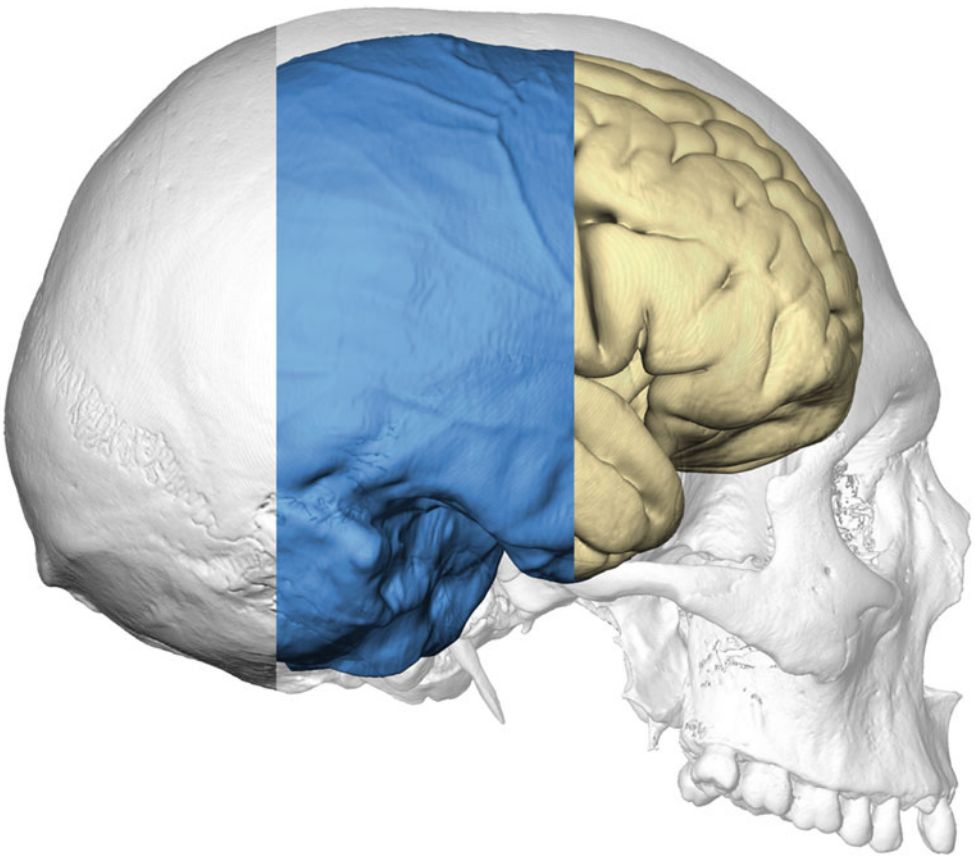
Hiroki C. Tanabe
Nagoya University
Nagoya, Japan

Replacement of Neanderthals by Modern Humans Series
ISBN 978-4-431-56580-2 ISBN 978-4-431-56582-6 (eBook)
DOI 10.1007/978-4-431-56582-6

Library of Congress Control Number: 2017957848

Printed on acid-free paper

This Springer imprint is published by Springer Nature
The registered company is Springer Japan KK
The registered company address is: Chiyoda First Bldg. East, 8-1 Nishi-Kanda Chiyoda-ku, 101-0065 Tokyo, Japan



Brain, endocast, and skull digital reconstruction (courtesy of Simon Neubauer)

Preface

In recent years, computer-based techniques have led to a noticeable renaissance of most anatomical disciplines, involving new challenges and re-introducing old problems. Digital anatomy has represented a major advance in the visualization and exploration of anatomical elements, and computed morphometrics has supplied numerical and statistical tools for analyzing anatomical systems using proper quantitative approaches. Before this "pixel revolution," anatomy was often limited by reduced sample sizes and by methodological difficulties associated with physical dissections. Working with bodies, most of all when dealing with humans, implies a limited availability of individuals, difficulties in management and administration, and large and complex histological preparations. Furthermore, dissections only allow the study of the anatomical components outside of their functional conditions. Digital tools can be used to investigate large samples with an extreme resolution and within their biological context, preventing most of those limitations, which, decades ago, contributed to a sort of "freezing" of the anatomical fields, slowing down their development and often impeding the efficient dissemination of their achievements. Once the computed tools had become available on a large scale and many forgotten topics had been recovered from past literature, we realized that we still lacked much information regarding our own anatomy. In fact, we have spent the last decades principally investigating molecules and microscopic features, but we do not yet have a robust knowledge of our bones and vessels. For many macroanatomical traits, we still ignore the variations, influences, and developmental processes that generate the phenotypic variability of our species. Importantly, some of these anatomical traits may be crucial not only from an evolutionary perspective, but also from a medical point of view.

Physical dissections and other non-digital approaches are still mandatory and essential, but the complementary potentialities of these computed methods are outstanding. Nonetheless, as usual, power must be accompanied by adequate control of its capacities and limitations. Most of these methods are based on very complex and complicated technical and numerical assumptions and criteria that rely on elaborate programs, devices, and algebraic transformations, and they are based on an important background integrating electronics, informatics, and statistics. Therefore, the entangled numerical elaboration associated with these digital models requires competence and caution. Frequently, programs are sufficiently "user-friendly" to allow a basic manipulation of the data without any comprehensive knowledge of the processes involved. This usability further increases the possibility of a superficial use, interpretation, or understanding, of the actual outputs of a computerized analysis. Multidisciplinarity is, indeed, strictly required in such a complicated methodological context.

Most anatomical disciplines have taken advantage of these methodological changes, but one that probably has been particularly privileged by these digital approaches is neuroscience. Structural and functional imaging has induced a considerable revolution in all kinds of brain studies, including evolutionary neuroanatomy. This book is part of the 5-year (2010–2014) project "Replacement of Neanderthals by Modern Humans: Testing Evolutionary Models of Learning" (RNMH), funded by the Japanese Government (Ministry of Education, Culture, Sports, Science, and Technology, Grant-in-Aid for Scientific Research on Innovative Areas No. 22101001) and coordinated by Professor Takeru Akazawa. The project is based on a multidisciplinary approach, integrating cultural anthropology, biological sciences, and engineering, to investigate and compare cognitive and cultural capacities in modern humans and Neanderthals, and to make inferences on their respective learning abilities. This new volume of the RNMH Series is dedicated to brain evolution and paleoanthropology, focusing on recent advances in all those research areas investigating the brain form in extinct species. The book includes chapters on craniology, digital techniques, endocast reconstruction, craniovascular traits, surface analyses, landmarking, and on the relationships between the brain and the braincase. Furthermore, the volume includes chapters concerning the principal brain districts, and reviews the current knowledge regarding their evolution in humans and in nonhuman primates. The aim is to supply a comprehensive and updated reference on the challenges, advances, and limitations associated with the study of the brain form and functions in fossils, introducing the current state of the art and future directions of human paleoneurology.

Burgos, Spain — Emiliano Bruner
Yokohama, Japan — Naomichi Ogihara
Nagoya, Japan — Hiroki C. Tanabe

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On the Making of Endocasts: The New and the Old in Paleoneurology

1

Ralph L. Holloway

Abstract

Making endocasts with latex rubber has been around for many years. This chapter describes my methods which were not original and some of the experiences encountered. Other methods, using plaster of Paris, various silicon-based rubbers, and Admold (dental caulk), for sectioned crania are examined and their relative merits and problems compared, such as damage to original specimens, deterioration with time (especially with latex rubber), and tensile strength of silicon-based molds. The resolution is as good as it can get, compared to "virtual" endocasts. These older methods have largely been succeeded by the making of "virtual" endocasts through various scanning procedures, with numerous advantages such as being noninvasive of original fossil specimens, immediate coordinates for morphometric analyses, scan data sharing and replication, and production of actual virtual endocasts through 3-D printing.

Keywords

Brain endocasts • Latex • Silicon • Dental caulk • "Virtual" endocasts

1.1 Introduction

Emi Bruner's invitation to contribute an introductory chapter is a real challenge, particularly given his expressed desire for me to describe making endocasts with latex rubber. It might be useful to situate that process within a larger canvas of what is and has happened in paleoneurology regarding endocast studies and what is being studied and how (see Holloway 2014 for more extended discussion of paleoneurology).

From what I have gleaned from Tilly Edinger's (1975) massive (257 pages!) annotated bibliography, the earliest publication goes back to 1804. Pages 183–257 are devoted to the Hominidae, and there is a very fine forward by Professor Bryan Patterson which describes in great detail how the bibliography came to be. Clearly, paleoneurology has played an important role in the zoological sciences. When I wrote my dissertation (Holloway 1964), I had no idea that there was such a vast history and had only read papers devoted to questions of human brain evolution, although I was aware of and had admired Edinger's (1949) work on the evolution of the horse brain. Kotchetkova's book and endocasts were not available until Harry Jerison made it so. F. Symington, G.E. Smith, F. Weidenreich, C.U. Kappers, F. Tilney, C.J. Connolly, and G.H.W. Schepers were the fodder from which I came to the erroneous conclusion that endocasts were not of very much use in hominid evolution, as they seldom showed any reliable details, thanks to meningeal conspiracies and cisterna of cerebrospinal fluid covering areas where one needed details to be able to separate the cerebral lobes accurately. It was their volumes that were useful. Ironically, thanks to a lack of facilities at Columbia for doing histological work (Golgi-Cox) on primate brains ("if we do not know what is happening in the brains of Aplysia, the sea-slug, how can we possibly know what is

R.L. Holloway (✉)
Department of Anthropology, Columbia University, New York, NY 10027, USA
e-mail: rlh2@columbia.edu

E. Bruner et al. (eds.), *Digital Endocasts*, Replacement of Neanderthals by Modern Humans Series,
DOI 10.1007/978-4-431-56582-6_1

happening in primate brains. . .” from a Nobel laureate), my forays into dendritic branching were confined to rats (Holloway 1966). This led me to once again look at endocasts, and a semester’s leave to work in P.V. Tobias’ lab at Wits (University of Witwatersrand) in Johannesburg, South Africa, sealed my fate as a paleoneurologist. I knew the Taung endocast couldn’t be some 500+ ml (cc), and I thus leapt into assessing its volume and morphology. I came back in 1971–1972 for a full year of research on the australopithecines and also worked with the Leakeys in Nairobi, Kenya, and on some of the Indonesian hominins in Teuku Jacob’s lab in succeeding years, as well as the Solo specimens in Frankfurt, Germany. My goals at that time were finding accurate volumes and making endocast reconstruction that I thought were accurate.

Most of this history can be found in Holloway (2008) and Holloway et al. (2004), which I prefer not to recount here, particularly all of the controversial history with Dean Falk and Harry Jerison who are also leading experts in paleoneurology. In the late 1970s, I adopted the stereoplotting method described by Oyen and Walker (1977), which employed an apparatus that measured surface point length from a central homologous center in polar coordinates; some of the initial work is published in Holloway (1981). This was in the era of punched IBM cards and SPSS multivariate analyses. Fortunately, the equipment fell apart from so many measurements, and I was thus spared having to continue those studies (see Chap. 9 of this book).

The 1970s and 1980s were also an era in which I endocast close to 200+ ape endocasts from crania I borrowed from several museums, in addition to many of the australopithecines and early *Homo*. Close to 100 modern human endocasts were made from the lab collection of crania at Columbia and the American Museum of Natural History.

I can only hope that several hundred endocasts I have made survive the changing environments and will prove to be a useful collection for those wishing to pursue paleoneurological studies.

As I see it, there are about five ways of making endocasts:

1. I think the earliest attempts were to pour plaster of Paris directly into the crania (obviously not through the foramen magnum) probably first coating the internal table of the bone with shellac. The foramina of the cranial base would first be plugged, and delicate structures such as the clinoid processes and dorsal sellae, cribriform plate, as well as open cracks, or missing portions would be protected with plasticine or cotton wadding. These could only be done on the calva, cranial base portions, and not the whole, unless there were postmortem cracks or glue joints that could be separated and rejoined after the cast was extracted.
2. Similar to the above was the use of alginate, but in this case, the alginate cast formed a mold which could be covered with some other material which then could be a mold for a plaster endocast. As I recall from using it a few times, the material had no tear strength.
3. Liquid latex of varying consistencies became a standard in making endocasts. My earliest forays into this adventure were derived from what previous paleoneurologists (e.g., Len Radinsky 1967 and Tilly Edinger 1929, 1949) were using. The latex I used was called Admold, and it came from the Bronx, usually in gallon containers, with the consistency of a thin milk shake. I often added a small amount of red dye to effect a pink rather than crème complexion, which I thought made endocast details easier to see. To make the latex into “rubber” required a heat treatment, at about 100 °C and for about an hour. This was often done in various ovens, autoclaves, etc. This vulcanized the latex into a sheet with great tensile strength and flexibility, as the vulcanized product was extracted through the foramen magnum of the cranium. In addition to becoming something of an expert on making endocasts, I became an expert on handheld hair dryers that could be used in three different continents with different electrical voltages, outlets, etc. I was surely a host’s pain in the neck for requesting such equipment and various stands (Bunsen burners a favorite) to hold the hair dryer so as to avoid the necessity of slave labor, etc. Nobody in their right mind would want to hold a hair dry in their hand for hours at a time! If dried and vulcanized properly, the extraction process could begin. This simply means getting the dried vulcanized endocast out of the skull, and that meant pulling it out through the foramen magnum for complete crania. I always used talcum or baby powder inside the endocast to prevent sticking when the endocast was collapsed. I would carefully release the endocast by using a finger (usually middle, but not with hylobatids, etc.) to initially detach the rubber from the foramen magnum and would apply some talcum power to that released interface as I worked the rubber into a completely collapsed state within the cranium. Now came the fun part: extracting the collapsed rubber endocast through the foramen magnum. This was done very gently mm by mm, collapsing the endocast as it peeled away from the bony surface and finally being rewarded with a pleasant-sounding “POP” (place the tip of the tongue on inner upper lip and flick forcefully forward and downward, and you will hear the sound of a latex rubber endocast emerging from the cranium). I then usually floated the endocast in water and filled it with liquid plaster to prevent distortion. After that, the foramen magnum area was capped with latex or plasticine, and the product was now ready for water displacement and various measurements with calipers and measuring tape.

Schoenemann et al. (2007) showed that this introduced only minor distortions, mostly confined to the basal region. Most of the early endocasts I made have undergone degeneration or caramelization (Fig. 1.1). I remember in particular the ones I made in Kenya and the Solo endocasts I made in Frankfurt while von Koenigswald was still alive. These were particularly difficult to make, as I recall it was during a very hot summer spell in Frankfurt, and I was working in my underwear. I made the layers too thin, also. These casts should be done again, but CT scanning is the way to go with such fragile specimens these days. The KNM-ER 1470 endocast (Fig. 1.2) was a special challenge. I wanted to stabilize the dimensions of the total latex, vulcanized in situ, so, much to Richard Leakey's temporary horror, I poured plaster into the latex-lined skull and told Richard to come back the next day. After the plaster had set, I simply dissolved the glued joints with acetone and, after the endocast was free, glued the cranial fragments back as they were. The Indonesian *Homo erectus* endocasts I made back in the 1970s were difficult, particularly Sangiran 10, 12, and 17. (See Holloway et al. 2004a for discussions, analysis, descriptions of fossil hominin endocasts.)

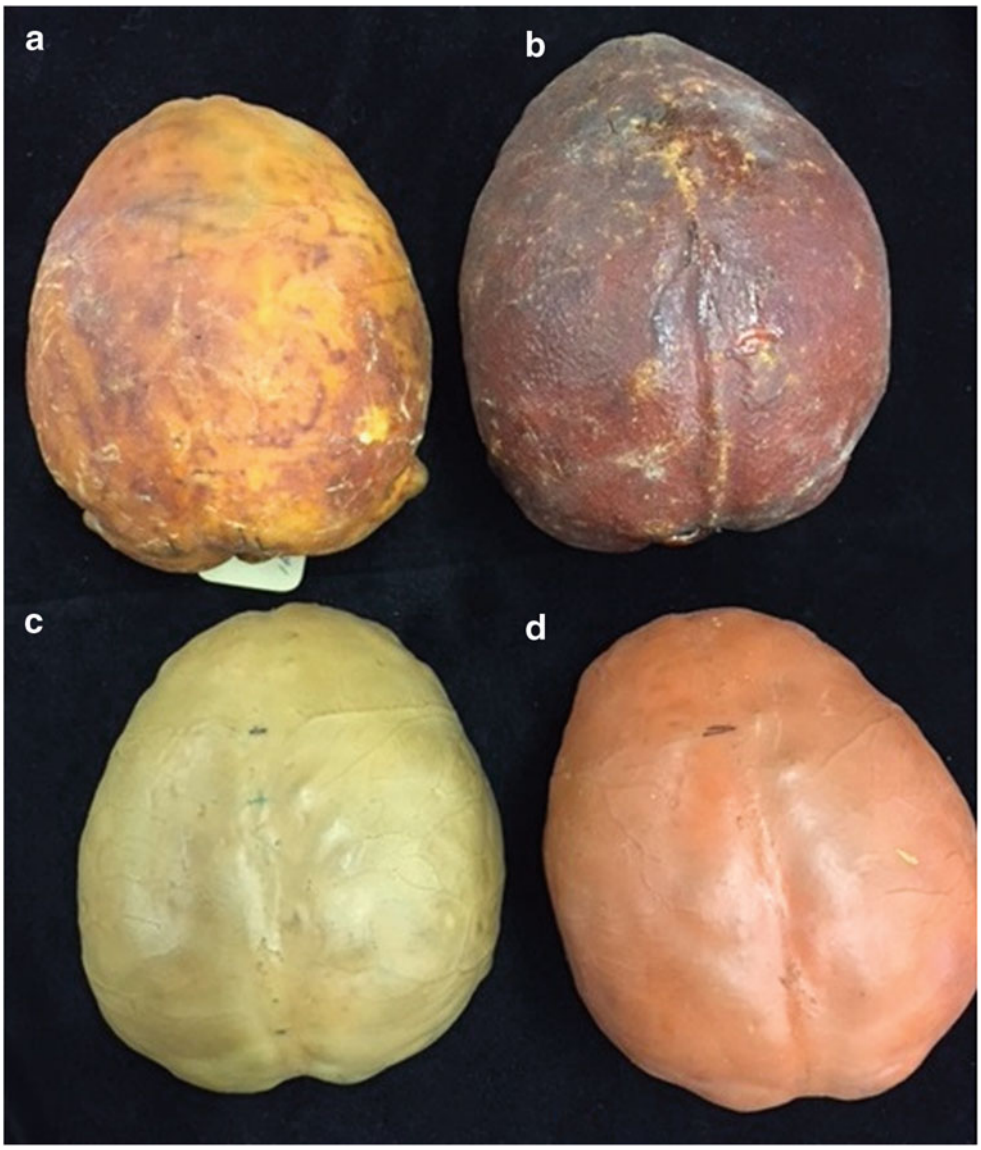

Fig. 1.1 Rubber latex endocasts showing various degrees of caramelization. (**a**, **b**) are gorillas; (**c**, **d**) are bonobos, the later showing pink coloration from adding red dye to Admold liquid latex

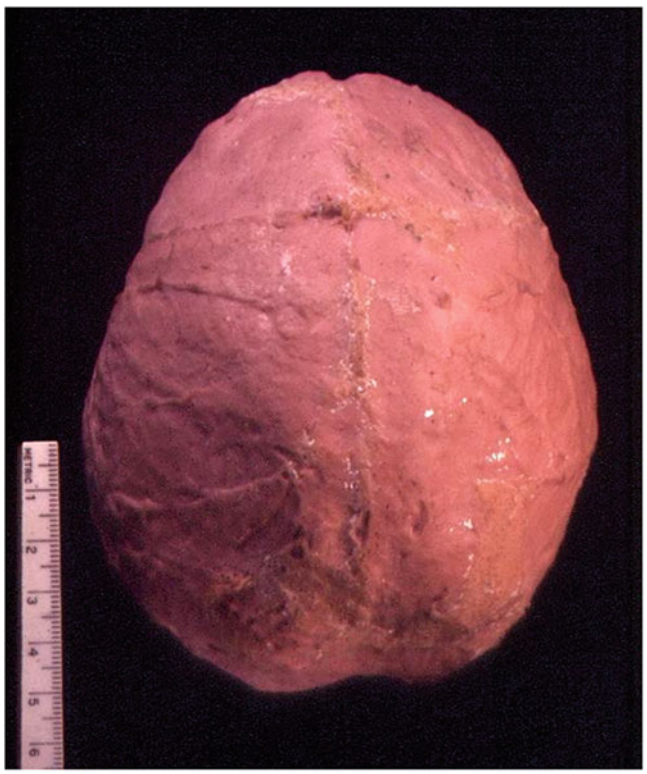

Fig. 1.2 The original KNM-ER 1470 *Homo rudolfensis* I made in Nairobi

Fig. 1.3 Ralph Holloway making an endocast using Dentsply

4. Various silicon casting products, e.g., Xantopren, became the standard way of making excellent casts of any of the bony elements of hominins during the 1960s and 1970s and are still used today. These molds were difficult to make and required considerable skill in making two halves tethered in plasticine and ending up with as small a flash line as possible. I used this method on a few of the australopithecines, such as Taung and SK 1585. The tensile strength was poor, compared to latex rubber, but the details were extremely fine as they were with latex. I still have some of those molds which do not deteriorate as does latex. Most of the wonderful Wenner-Gren casts were done this way, thanks to the skill of my friend and colleague, Dr. Alan Mann.
5. A variation of the above technique that I used when making endocasts on sectioned materials was to use a dental molding material such as Dentsply Aquasil LV Caulk, which was extruded through a gun that combined two compounds which would cure in 5 or less minutes (Fig. 1.3). This approach is wonderful on sectioned crania, or cranial fragments, but the casts have no tensile strength and, on modern human crania, require some skill in getting a thin flash line when the two halves are joined together and must be thick enough to avoid distortion. A small portion of two compounds, SmoothOn 320 A and B, mixed, is introduced through the foramen magnum, and the endocast rotated around so that the viscous compound would coat the entire endocast as it hardened while curing. The details of the endocranial surface are superb. The shelf life of these endocasts is unknown, but far longer than any of the latex rubber endocasts. Besides, they are usually a very pretty green or blue color (Fig. 1.4). Additional tools essential to such cast making are sharp scalpels to remove excess material along the flash line.

1.2 Some Concluding Remarks

All of the above five methods are "old," and each one has some potential to alter the bony surface, whether fossil or recent. The "new" refers, of course, to the use of CT, laser, and micro-CT scanning of the original fossil or specimen, and these methods are totally nondestructive. What results are a large number of scan sections, often at 0.5 mm intervals or lower. Obviously the quality of endocranial details will depend on the initial state of the fossil, the interval distance between slices, and the software package used to produce a "virtual" endocast. An immediate advantage is that not only

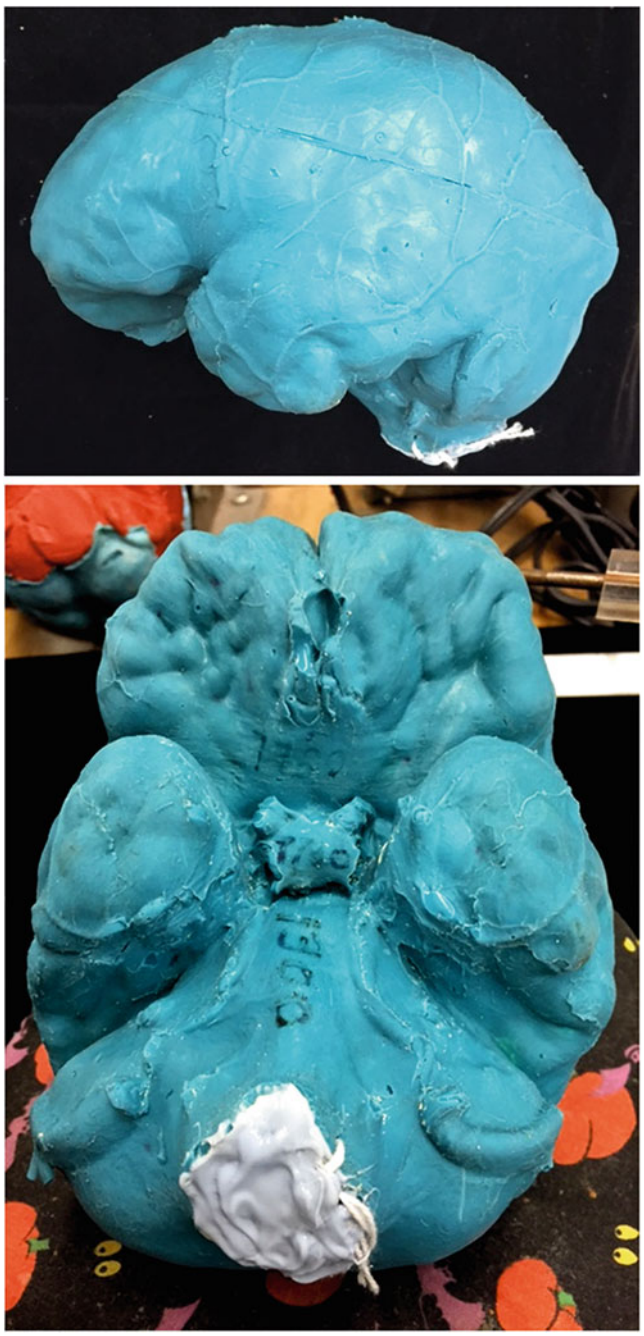

Fig. 1.4 *Above*: modern human endocast made with Dentsply (note flash line through the calva). *Below:* basal view of same modern human endocast

is the original fossil not damaged, nor mailed around various continents: the digital record is there, permanent, easy to upload and download to whoever might want to study the "virtual" result. The LB1 *Homo floresiensis* is a good example (Falk et al. 2005) or some of the recent works by Carlson et al. (2011), Neubauer et al. (2012), Gunz et al. (2009), Weber et al. (2012), Bruner and Manzi (2005), Zollikofer and Ponce de León (2013), etc. The *Homo naledi* fragments are available on MorphoSource.

Indeed, many of the endocasts made through methods 1–5 can themselves be scanned and be available as a repository of digital "virtual" endocasts. Almost all of the 200+ latex rubber endocasts of anthropoids I made during the 1970s have been scanned and are available through ORSA at the University of Pennsylvania, collected under the auspices of Drs. Janet Monge and Tom Schoenemann. This is an important process, as one of the problems with latex rubber is its gradual degradation or caramelization. The 80+ endocasts of modern humans (Figs. 1.5 and 1.6) I made during the last decade have also been scanned. Many of the plaster and plastic endocasts of hominins from my collection have also been scanned.

Interestingly, the various methods used to derive the volume of endocasts are not a constant. A remarkable collection of museum crania collected by Dr. Lynn Copes (2012) has been segmented by me, and the volumes derived (using Analyze 11) are often at variance with the recorded seed or shot volumes previously recorded, which are almost always higher in volume that those derived from either water displacement, CT, or laser scans, the latter two methods yielding volumes based on voxel counts. The last three methods yield only minor differences. Water displacement is tricky, in that the rubber or silicon has some degree of hydrophilia, and it is not uncommon for a rubber endocast to increase in volume by very small amounts as the number of immersions advances. This not always a good method for klutzes. . . Of course, while hitting that button in the software package saying "volume" is so convenient, it would be wise to remember that counting voxels is only as accurate as the initial segmentation that was done.

The new techniques of making virtual endocasts include algorithms for obtaining volumes, allow for measuring between points defined on the virtual surface, permit free rotation for both viewing and measurements, and also allow for correcting distortions, adding missing fragments, and reconstructing whole endocast portions based on sophisticated morphometric algorithms. One can even have some haptic experiences when one holds an actual endocast made from a 3-D printer using the CT scan data, but such experiences cannot match the haptic sensations with rubber or silicon, or even plaster endocasts, where the resolution is perfect.

Newer than "new" are my present experiences with working on the endocranial remains of *Homo naledi* (Berger et al. 2015). Here the authors have provided the entire world with the opportunity to freely download the CT sections of many of the remains for their analyses. When I did so (first I asked permission, after all I am "old school"), I sent the files over to my colleague Will Vanti in the library to print on their 3-D machine. What came back were brilliant red piece of plastic of both ecto- and endocranial surfaces (Fig. 1.7). Using Dentsply (see above), I made endocasts of DH1, DH3, and DH1. The first set, at 150 μm, didn't show any details I felt I

Fig. 1.5 Modern human crania and their endocasts

Fig. 1.6 File cabinet showing 80 modern human endocasts and microcephalics (*bottom row*)

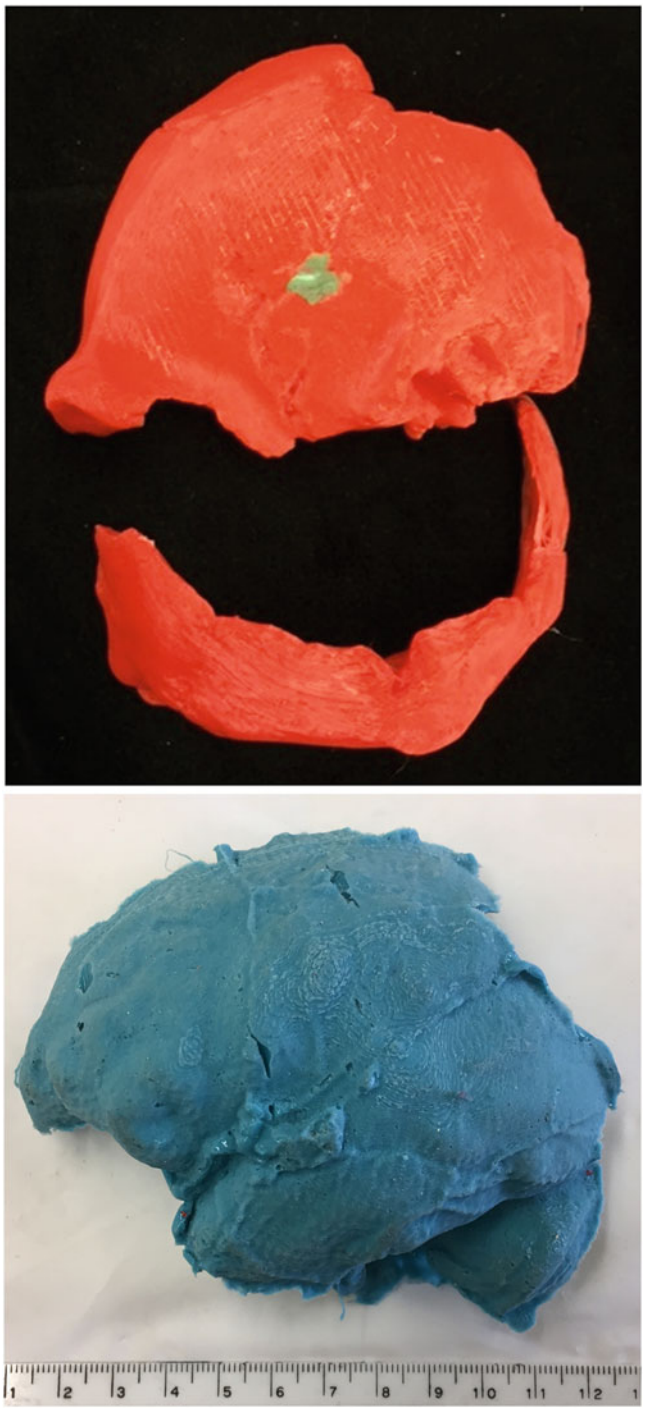

Fig. 1.7 *Above*: 3-D prints of some of the *Homo naledi* fragments from MorphoSource scans. *Upper* is frontal fragment, *bottom* is occipital fragment. *Below*: 3-D print of frontal endocranial surface of *Homo naledi*

could trust, so I asked Will if we could go to a finer resolution. Limited at 100 μm, the endocasts began to show some sulcal relief. I contacted the senior authors of the eLife paper and asked for help. Most importantly, I am working with another author, Dr. Heather Garvin, whose skills at illustrating this piece in different angles, with varied lighting, have made it possible to identify many endocranial features.

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Digital Reconstruction of Neanderthal and Early *Homo sapiens* Endocasts

2

Naomichi Ogihara, Hideki Amano, Takeo Kikuchi, Yusuke Morita, Hiromasa Suzuki, and Osamu Kondo

Abstract

Endocranial morphology is currently the most useful source of information available for estimating the brain morphology and, hence, possible differences in cognitive ability in fossil hominins. Recently, computed tomography has been widely used to construct digital models of the endocranial cavity. With ongoing advances in computer-assisted morphological techniques, digital endocasts allow detailed analyses of morphological variability between hominin fossils and modern humans. This paper reviews digital reconstructions and morphological analyses of fossil endocasts and presents the digital reconstructions of complete endocasts of specimens of four Neanderthals and four early *Homo sapiens* based on CT scan data. Possible differences in the brain structure between Neanderthals and early *Homo sapiens* were identified based on a three-dimensional geometric morphometric analysis of the reconstructed endocasts. Our results demonstrated that ecto- and endocranial shapes are quantitatively different between Neanderthals and early *Homo sapiens*. The cranium of early *Homo sapiens* shows relative enlargement of the cerebellar region and relative expansion of the parietal area, possibly indicating that neuroanatomical organization is different between the two species.

Keywords

Fossil • Brain • Cerebellum • Geometric morphometrics

2.1 Introduction

Endocranial morphology is currently the most useful source of information available for estimating brain morphology and, hence, possible differences in cognitive ability in fossil hominins. Therefore, efforts have traditionally been made to construct casts from original fossil crania. Specifically, silicone rubber was poured onto the internal surface of fossil braincases through the foramen magnum to make a cast, and the extracted rubber cast was then filled with plaster to stabilize the shape of the cast. To analyze variation in morphology of the cranial cavity, linear dimensions were measured, and sulcus patterns were identified on the plaster endocasts (Holloway et al. 2004; Holloway 2008). However, although great care was taken to construct plaster endocasts, considerable deformation occurs, and errors of about 2 mm reportedly exist on the overall endocranial surfaces of plaster endocasts (Schoenemann et al. 2007).

Recently, the use of X-ray computed tomography (CT) for morphological analyses of fossil materials has become more widespread. This technique is now one of the most widely used methods to acquire and analyze the

N. Ogihara (✉) • H. Amano • T. Kikuchi • Y. Morita
Department of Mechanical Engineering, Faculty of Science and Technology, Keio University, Yokohama 223-8522, Japan
e-mail: ogihara@mech.keio.ac.jp; hideki_amano_0307@yahoo.co.jp

H. Suzuki
Department of Precision Engineering, Graduate School of Engineering, University of Tokyo, Tokyo 113-8656, Japan
e-mail: suzuki@den.t.u-tokyo.ac.jp

O. Kondo
Department of Biological Sciences, Graduate School of Science, University of Tokyo, Tokyo 113-0033, Japan
e-mail: kondo-o@bs.s.u-tokyo.ac.jp

E. Bruner et al. (eds.), *Digital Endocasts*, Replacement of Neanderthals by Modern Humans Series,
DOI 10.1007/978-4-431-56582-6_2

morphology of fossil specimens in the field of physical anthropology (Zollikofer and Ponce de León 2005; Gunz et al. 2009; Weber and Bookstein 2011; Ogihara et al. 2015). Using CT, the endocranial surface can also be determined, allowing construction of three-dimensional (3D) virtual models of the endocranial surfaces without damaging the original specimen. The spatial resolution of medical CT is about 0.3 mm, much smaller than the overall error of conventional plaster endocasts. Furthermore, using digital modeling, glue and plaster can be removed from the original specimen to separate the fragments constituting the fossil cranium, allowing reassembly of these fragments (Kikuchi and Ogihara 2013). Missing regions of the reassembled cranium can be geometrically or statistically interpolated. If the reconstruction is conducted using a digital model, deformations can be corrected based on geometric processing technologies, such as spatial warping techniques (Ogihara et al. 2006; Gunz et al. 2009). Therefore, digital endocasts hold great promise for more precise morphological comparisons of endocranial surfaces among different species in the human lineage.

The first morphological study of the hominin endocranium using digital endocasts was published in 1990, when Conroy et al. (1990) reported the endocranial capacity of *Australopithecus africanus* (MLD37/38) from 3D reconstructed digital endocasts. Since then, assessment of endocranial capacity and morphology based on digital endocasts has become increasingly common for working toward understanding the evolution of the human brain (Conroy et al. 1998, 2000a, b; Seidler et al. 1997; Recheis et al. 1999; Tobias 2001; Neubauer et al. 2004, 2012; Coqueugniot et al. 2004; Balzeau et al. 2005, 2013; Falk et al. 2005; Falk and Clarke 2007; Wu et al. 2008; Berger et al. 2010; Carlson et al. 2011; Kranioti et al. 2011; Kubo et al. 2011; Benazzi et al. 2011, 2014; Neubauer 2014; Amano et al. 2015). Furthermore, more detailed analyses of morphological variability in the endocranial shape have recently been carried out due to ongoing advances in geometric morphometric techniques (Neubauer et al. 2009, 2010).

The present paper reviews digital reconstructions and morphological analyses of fossil endocasts. We also present digital reconstructions of endocasts of four Neanderthal and four early modern human crania. We then describe possible differences in the brain structure between Neanderthals and early modern humans that were identified based on a 3D geometric morphometric analysis of the reconstructed endocasts of the fossil crania to infer possible differences in cognitive ability in fossil hominins.

2.2 Digital Reconstruction of Endocasts

An X-ray CT scanner is essentially a 3D shape digitizing device that captures both the external and internal structures comprising a biological specimen. Therefore, CT is an ideal tool for studying 3D morphology of endocasts. Figure 2.1 shows the process of constructing a digital endocast using a CT scanner. The first step is to obtain CT scan data of the original cranium. From a series of consecutive cross-sectional images of the specimen, the bony object region is segmented by thresholding, and its 3D isosurface is generated as a triangular mesh model using a computer graphics algorithm, such as the marching cubes algorithm (Fig. 2.1).

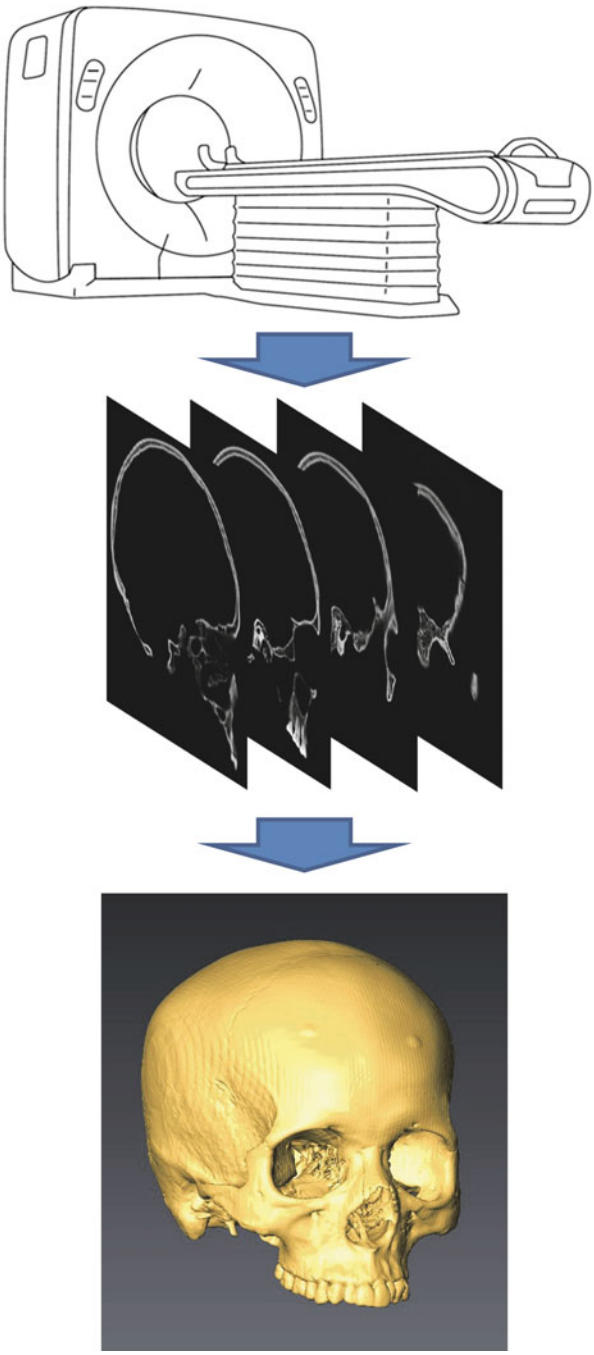

Fig. 2.1 Process of reconstructing a digital model of a cranium using an X-ray CT scanner (Ogihara et al. 2015) (Reprinted with the permission from the Anthropological Society of Nippon)

To create a digital endocast, the external surface of the cranium should be removed. For this, the external neurocranial surface is first selected using a paintbrush tool (Fig. 2.2a), and the selected surface is deleted. If the cranium is viewed from above, the internal surface of the cranial base is visible because the internal neurocranial surface facing inferiorly is invisible (transparent) because the surface facing inward is viewed from the back (Fig. 2.2b). Therefore, the internal surface including the basicranial surface can be entirely selected by the paintbrush tool. By selecting and deleting the inverse of the selected endocranial surface, the complete endocranial surface can be selected (Fig. 2.2c).

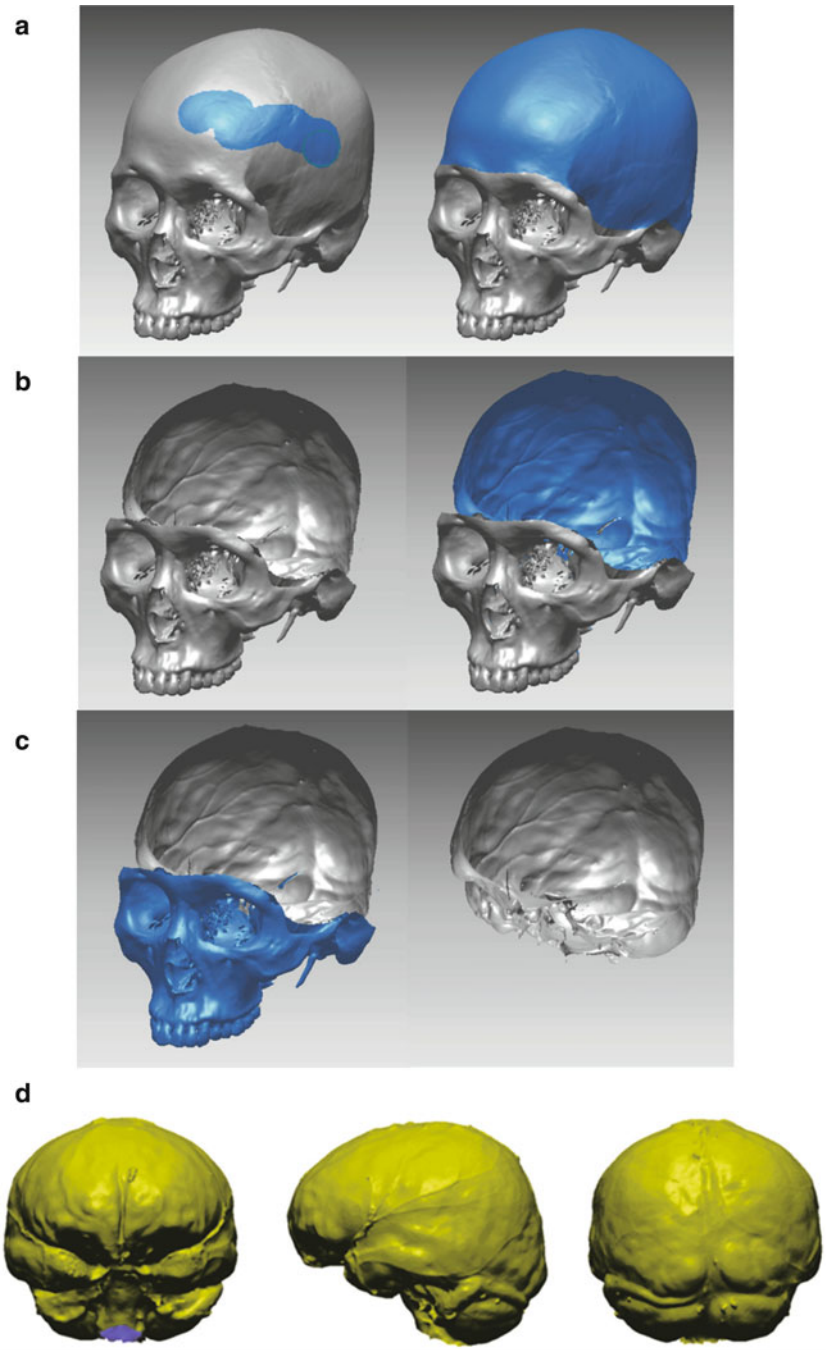

Fig. 2.2 Removal of the external surface of a cranium. (**a**) A paintbrush tool is used to select the external neurocranial surface. (**b**) The selected external surface is removed, and the entire internal surface is selected by the paintbrush tool. Note that the internal cranial surface is facing inward. Therefore, the concave surface of the occipital region is visible. (**c**) By selecting the inverse of the selected endocranial surface, the endocranial surface can be selected. (**d**) Holes on the surfaces such as the foramen magnum and neural foramina are filled using the fill-hole command, and normal vectors of the surface mesh triangles are flipped to the opposite direction to generate a closed surface model of the endocranium

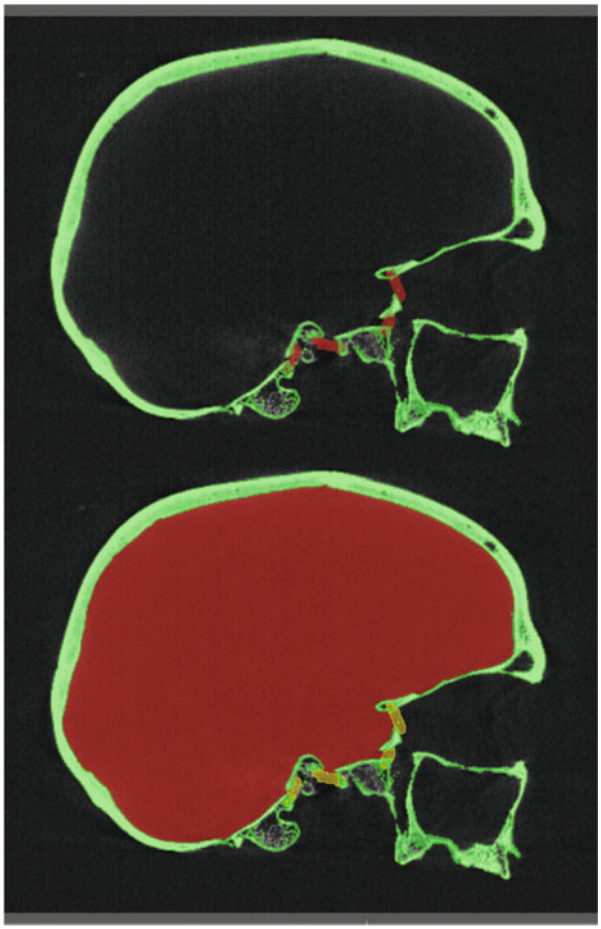

Fig. 2.3 Extraction of an endocranial cavity on a cross-sectional image using a region-growing algorithm

Lastly, holes on surfaces such as the foramen magnum and neural foramina are filled using a fill-hole command. Normal vectors of the surface mesh triangles are flipped to the opposite direction to generate a complete, closed surface model of the endocranium (Fig. 2.2d) (Morita et al. 2015).

Another possible way to construct a digital endocast is to extract the endocranial cavity on each cross-sectional image using the so-called region-growing algorithm (Fig. 2.3). Specifically, an initial seed is assigned in the endocranial cavity of each image. Then, the region is expanded until the region reaches the edge that is determined by thresholding prior to the region growing. To do so, openings due to foramina and nerve canals should be manually closed by drawing lines before beginning the digital reconstruction. This process is repeated for all consecutive cross-sectional images, and a 3D surface of the segmented volume is generated to create an endocast (Kubo et al. 2011).

These manual reconstructions of digital endocasts are, however, time-consuming and require patience. Therefore, efforts have also recently been made to computationally extract an endocast surface from a stack of CT images (Michikawa et al. 2017). In this extraction method, the seed is placed, and foramina and canals are closed automatically, with the assumption that the endocast is the largest cavity in the images. Although it takes hours to manually create a cranial endocast, the automatic method requires less than 10 min, hopefully facilitating morphological studies of endocasts. The automatically and manually constructed endocasts have been confirmed to be identical (Michikawa et al. 2017).

However, cranial fossils are usually fragile and only partially preserved. Accurate interpolation of missing parts in fossil crania is therefore essential for correct estimation of endocranial and, thus, brain morphology. For this, geometric interpolation using a spline function and statistical interpolation using multivariate regression have been proposed (Gunz et al. 2009). Geometric interpolation using a spline function interpolates a missing part based on data mapped from a complete reference specimen (Fig. 2.4). Specifically, common existing anatomical landmarks and semi-landmarks are digitized on the reference. Then, a deficient cranium and the deformation function from the reference to the target damaged cranium are defined based on the digitized common landmarks. The thin-plate spline (TPS) function is widely used for such a deformation function. Using this function, the reference cranium is matched to the damaged cranium to compensate for its missing parts. If many reference samples are used for interpolation, the degree of uncertainty in interpolation can also be evaluated (Gunz et al. 2009).

On the other hand, statistical interpolation is based on multivariate regression estimates of missing coordinates based on a sample of complete specimens as a reference database (Fig. 2.5). Specifically, multivariate regressions are calculated with the missing coordinates as dependent variables and other remaining coordinates as independent variables. These equations are then applied to predict missing cranial parts. For example, Amano et al. (2014) attempted to mathematically interpolate missing coordinates of crania based on a reference database of cranial morphology and successfully demonstrated the efficacy of the interpolation method (Fig. 2.5). However, estimation of missing landmarks on the basicranial region is reportedly difficult, possibly due to the low correlation between the shape of the basicranium and the rest of the cranium. See Gunz et al. (2009) and Ogihara et al. (2015) for more details about the interpolation methods.

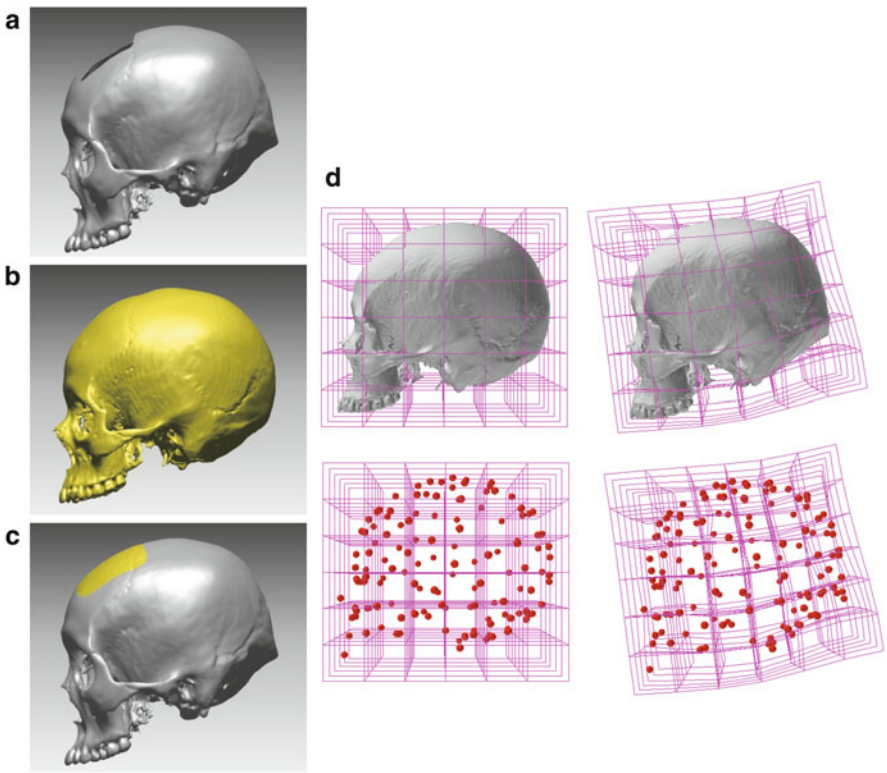

Fig. 2.4 Geometric interpolation using a thin-plate spline (TPS) function. (**a**) A deficient cranium with a missing region. (**b**) A complete reference cranium. (**c**) The missing portion of the deficient cranium is interpolated by warping the complete reference cranium. (**d**) The TPS function is widely used as a deformation function. Common existing anatomical landmarks and semi-landmarks are digitized on the reference and deficient cranium. The deformation function from the reference to the target damaged cranium is defined based on the digitized common landmarks

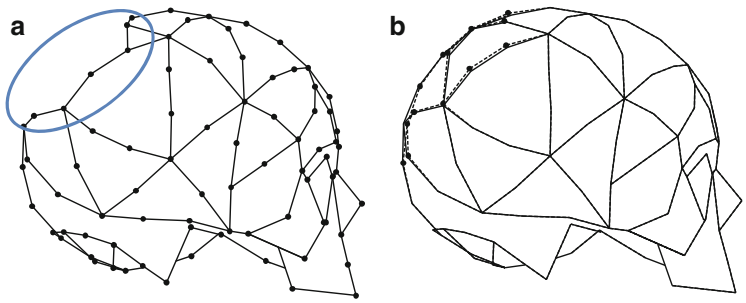

Fig. 2.5 Statistical interpolation based on multivariate regression. Coordinates of missing landmarks on a virtual deficient cranium (**a**) are estimated by calculating multivariate regressions with the missing coordinates as dependent variables and the other remaining coordinates as independent variables (**b**) (Amano et al. 2014)

2.3 Endocasts of Neanderthals and Early *Homo sapiens*

Using the above techniques, we performed digital reconstruction of digital endocasts of specimens of four Neanderthals and four early *Homo sapiens* as shown in Fig. 2.6. The four Neanderthals are Amud 1 (Suzuki and Takai 1970) (dated 50,000–70,000 years old; Valladas et al. 1999; Rink et al. 2001), Forbes' Quarry 1 (Busk 1865) (no dating information), La Chapelle-aux-Saints 1 (Boule 1908; Bouyssonie et al. 1909) (dated 47,000–56,000 years old; Grün and Stringer 1991), and La Ferrassie 1 (Capitan and Peyrony 1909) (dated 43,000–45,000 years old; Guerin et al. 2015). The four early *Homo sapiens* are Cro-Magnon 1 (Lartet 1868; Broca 1868) (dated 28,000 years old; Henry-Gambier 2002), Mladeč 1 (Szombathy 1925) (dated 31,000 years old; Wild et al. 2005), Qafzeh 9 (Vandermeersch

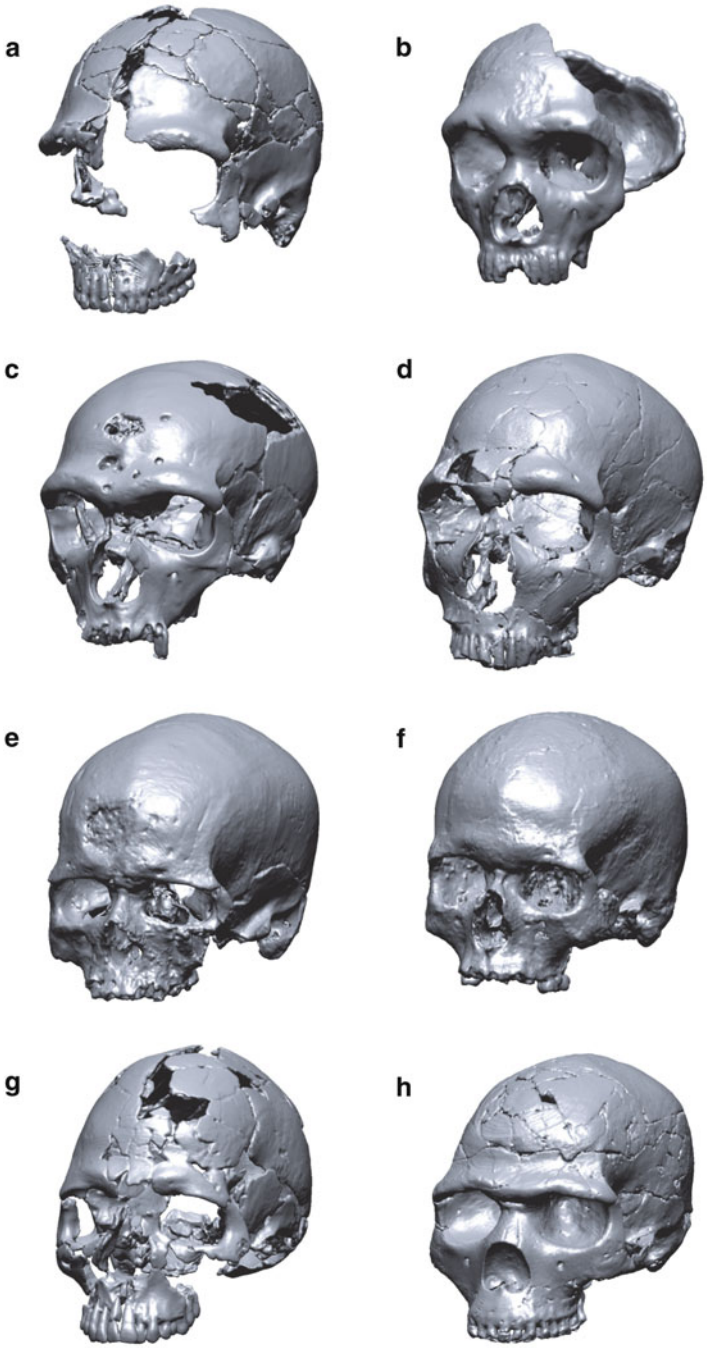

Fig. 2.6 Fossil crania of specimens of Neanderthals (**a**–**d**) and early *Homo sapiens* (**e**–**h**) used in the present study. (**a**) Amud 1, (**b**) Forbes' Quarry 1, (**c**) La Chapelle-aux-Saints, (**d**) La Ferrassie 1, (**e**) Cro-Magnon 1, (**f**) Mladeč 1, (**g**) Qafzeh 9, (**h**) Skhul 5

1981) (dated 90,000–120,000 years old; Valladas et al. 1988; Schwarcz et al. 1988; Grün and Stringer 1991), and Skhul 5 (McCown and Keith 1939) (dated 100,000–135,000 years old; Mercier et al. 1993; Grün et al. 2005) (Fig. 2.6).

For Amud 1, we first digitally removed the adhesive and plaster from the original CT data and isolated and disassembled the original cranial fragments comprising the fossil based on segmentation procedures such as thresholding and region-growing techniques (Fig. 2.7). These fragments were then mathematically reassembled in a virtual environment based on joint smoothness (Kikuchi and Ogihara 2013). The missing facial, basicranial, and endocranial regions were geometrically interpolated using a composite Neanderthal cranium (La Chapelle-aux-Saints 1 cranium whose missing central basicranial areas were interpolated by matching the Forbes' Quarry 1 cranium

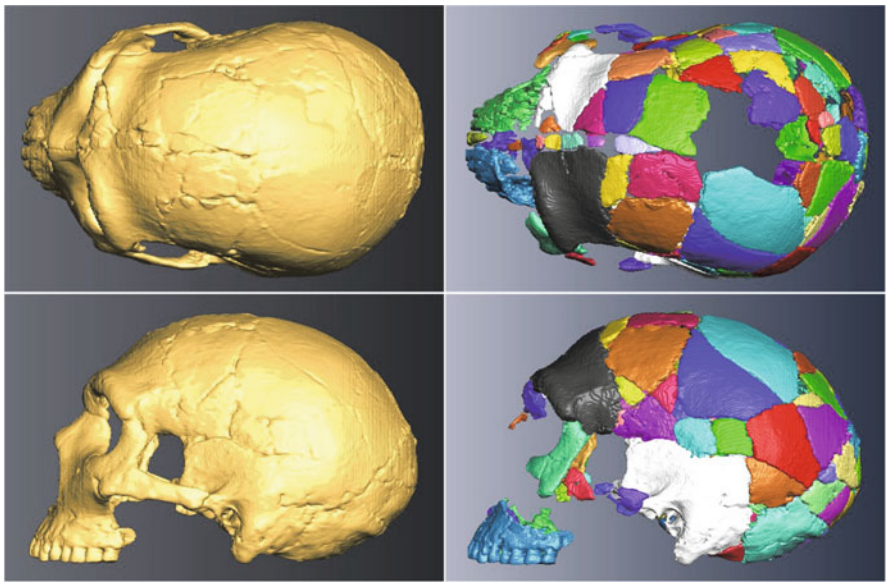

Fig. 2.7 Digital models of Amud 1 as originally reconstructed by Suzuki (1970) with (*left*) and without (*right*) plaster. The cranium is composed of numerous fragmented pieces, and substantial portions of the facial and basicranial regions are missing

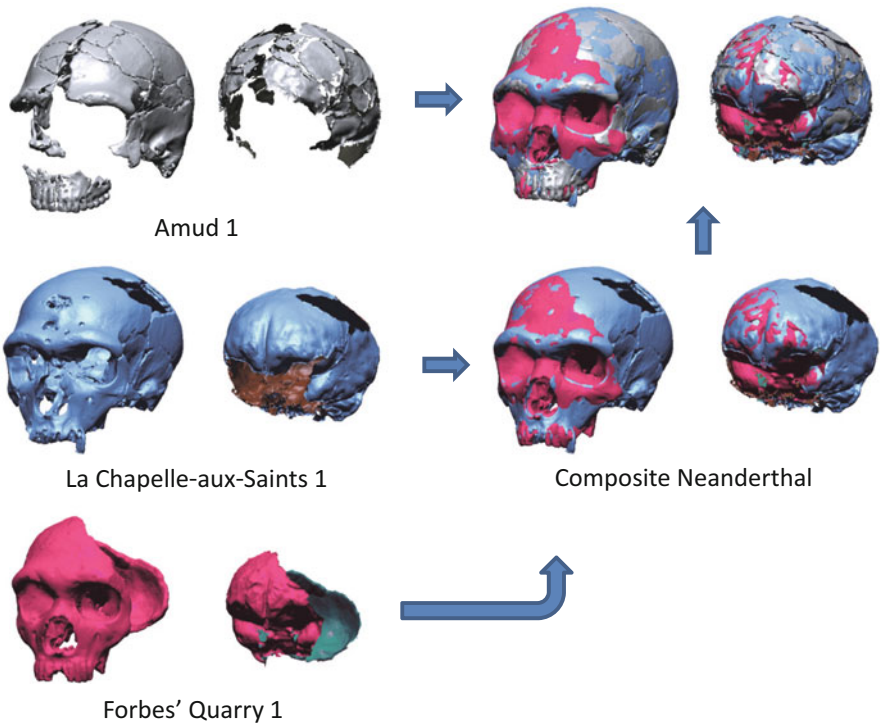

Fig. 2.8 Virtual reconstruction of the Amud 1 cranium (Amano et al. 2015) (Reprinted with the permission from John Wiley & Sons)

using a TPS function) as a reference cranium (Fig. 2.8). The remaining openings were compensated by matching a modern Japanese cranium (KUMA-554) using the TPS deformation, and the reconstruction was completed. Virtual reconstruction of the Amud 1 cranium is described in detail in Amano et al. (2015).

In the Forbes' Quarry 1 cranium, the basal region including the frontal lobe was preserved, but most of the left side was missing. The missing regions of the Forbes' Quarry 1 cranium were interpolated by warping the La Chapelle-aux-Saints 1 cranium (Fig. 2.9). The remaining openings were compensated by matching the modern Japanese cranium

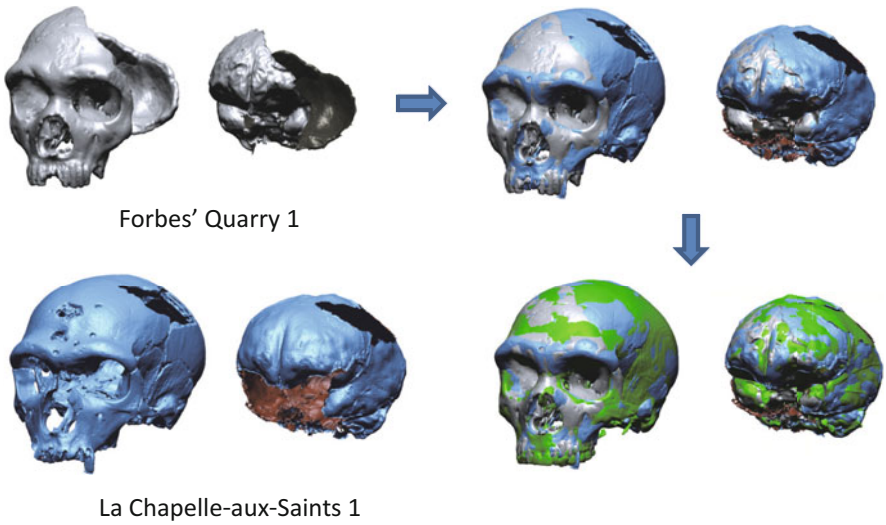

Fig. 2.9 Virtual reconstruction of the Forbes' Quarry 1 cranium

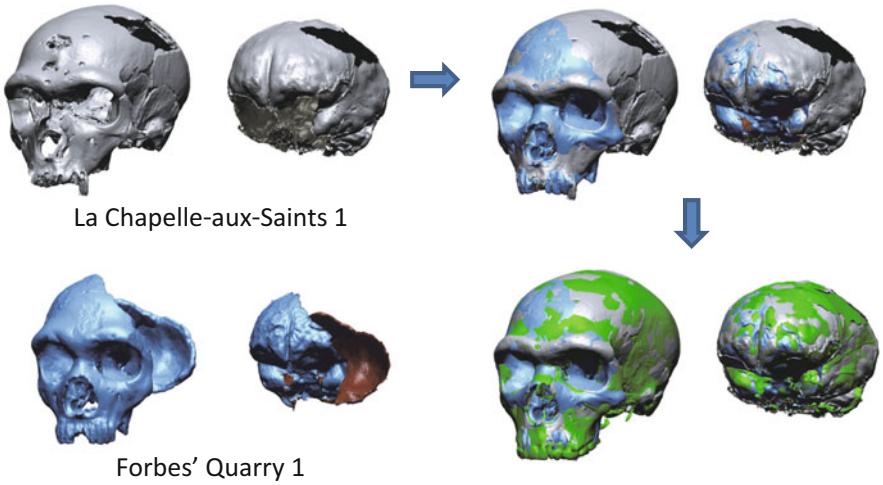

Fig. 2.10 Virtual reconstruction of the La Chapelle-aux-Saints 1 cranium

(KUMA-554) using the TPS deformation. The damaged portion of the skull was not reconstructed using the reflection of the opposite side because of possible cranial shape asymmetry.

The La Chapelle-aux-Saints 1 cranium was almost complete except for central basicranial areas. The missing basicranial region was interpolated by matching the Forbes' Quarry 1 cranium (Fig. 2.10). The remaining openings were compensated by matching the modern Japanese cranium (KUMA-554) using the TPS deformation.

In the La Ferrassie 1 cranium, the neurocranium and the occipital bone were preserved, but the anterior basal region was missing. The missing basicranial region was interpolated by matching the Forbes' Quarry 1 cranium (Fig. 2.11). The remaining openings were compensated by matching the modern Japanese cranium (KUMA-554) using the TPS deformation.

The fossil crania of the early *Homo sapiens* specimens were generally better preserved. We digitally removed the stone matrix and plaster where necessary and extracted well-preserved endocranial surfaces. For the Cro-Magnon 1, Qafzeh 9, and Skhul 5 crania, the modern Japanese cranium (KUMA-554) was matched onto the fossil endocasts to compensate for the missing surface areas to obtain complete endocranial surfaces (Fig. 2.12). The endocast of the Mladeč 1 is almost perfectly preserved except for a small deficit at the edge of the foramen magnum. We therefore did not use a reference cranium but rather used the fill-hole tool to compensate for the small missing surface.

To define a deformation function from one cranial specimen to another for interpolation, a set of homologous landmark coordinates that can be observed on both specimens must be obtained. For this, we acquired 62 anatomical

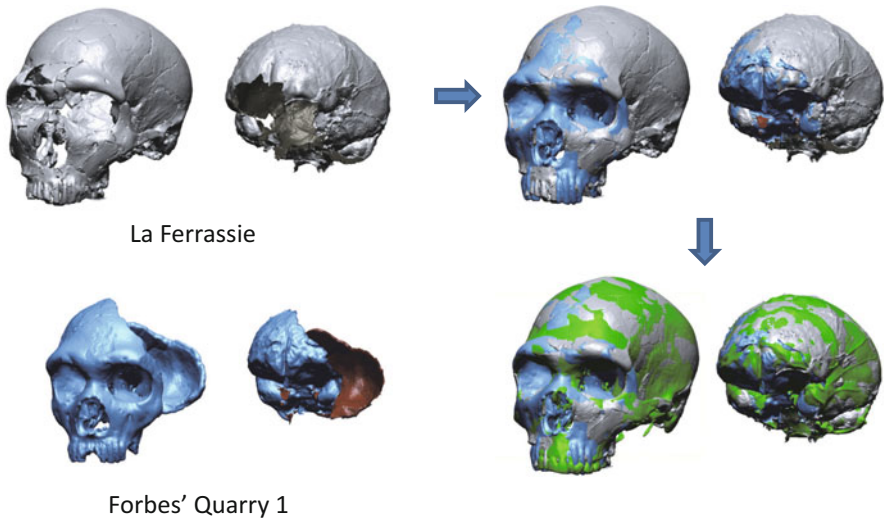

Fig. 2.11 Virtual reconstruction of the La Ferrassie 1 cranium

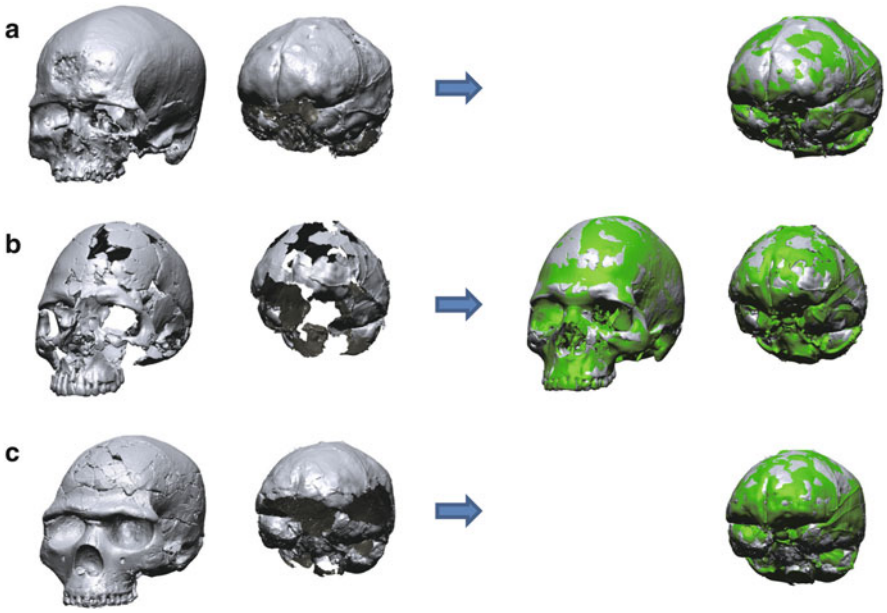

Fig. 2.12 Virtual reconstruction of the fossil crania of early *Homo sapiens*. (**a**) Cro-Magnon 1, (**b**) Qafzeh 9, (**c**) Skhul 5

landmarks on the external surface and 14 equally spaced points along curves approximated by Bazier functions (Morita et al. 2013) (Fig. 2.13). We also defined a total of 85 sliding semi-landmarks across the entire neurocranial surface based on the shortest paths between pairs of anatomical landmarks and equally spaced points along the curves (Morita et al. 2013). Similarly, we defined 30 anatomical landmarks on the endocranial surface and 22 equally spaced points along endocranial curves as well as 133 surface endocranial sliding semi-landmarks (Fig. 2.13). See Amano et al. (2015) for landmark definitions.

The 3D reconstructions of the digital endocasts are presented in Fig. 2.14 (see Appendix for the six-sided views). As shown in Fig. 2.14, endocranial surfaces of the four Neanderthal and four early *Homo sapiens* crania were successfully reconstructed in a virtual environment. The endocranial volumes of Neanderthals, Amud 1, Forbes' Quarry 1, La Chapelle-aux-Saints 1 and La Ferrassie 1, were 1736 cc, 1183 cc, 1512 cc and 1671 cc, respectively, and those of early Homo sapiens, Cro-Magnon 1, Mladeč 1, Qafzeh 9, and Skhul 5, were 1589 cc, 1596 cc, 1424 cc, and 1395 cc, respectively. Such virtual reconstruction of the complete geometry of the fossil

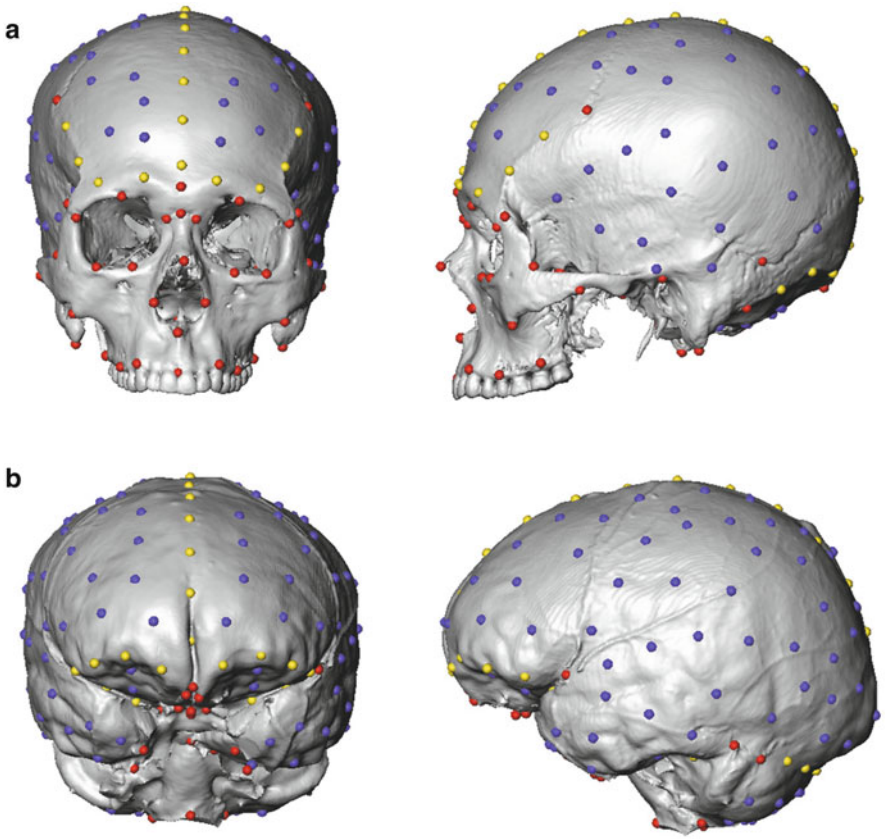

Fig. 2.13 Landmarks used to define thin-plate spline functions for geometric interpolation of the fossil crania (Amano et al. 2015). (**a**) Ectocranial landmarks. (**b**) Endocranial landmarks (Reprinted with the permission from John Wiley & Sons)

crania allows detailed comparative analysis of ecto- and endocranial morphology between the two species.

2.4 3D Morphometrics of Endocasts

Studies on endocasts have historically focused on endocranial volume (ECV), which can be used to approximate brain size (Falk 2012). Such studies have clearly demonstrated that the ECV of hominins has increased during the process of human evolution (Hublin et al. 2015). However, brain evolution and encephalization are not just a matter of size but also a matter of structure and organization. Therefore, researchers have tried to identify sulcus patterns on the extracted virtual endocasts (Holloway et al. 2004; Holloway 2008; Falk 2014). However, identifying cortical features such as imprints of sulci and gyri on the endocranial surface is actually very difficult. Although imprints of sulci and gyri extracted from crania are somewhat pronounced in nonhuman anthropoids, such as macaques (Kobayashi et al. 2014), and in human children (Zollikofer and Ponce de León 2013), such imprints are very subtle on the human adult cranium. Figure 2.15 shows a comparison of a modern human cranium and the brain enclosed in it. Here the CT and magnetic resonance images from one male participant were registered to each other to maximize mutual information between the CT and magnetic resonance images (Ogihara et al. 2015). Endocast and brain surfaces were then 3D reconstructed. As shown in Fig. 2.15, the sulcal patterns are generally not visible on the internal surface of the adult human cranium. The same is true for the adult chimpanzee cranium, although the imprints are quite prominent on the cranium of a juvenile chimpanzee (Fig. 2.16). Therefore, identification of cortical features and the relative size of brain regions from the fossil endocranial surfaces in Neanderthals and early *Homo sapiens* is currently quite difficult. However, the quality of imprints may be related to the spatial resolution of medical CT. Micro-CT may provide finer details about imprints than medical CT.

To quantitatively analyze the overall shape of the endocranial cavity, researchers have traditionally measured a set of linear metric variables taken from physical or virtual endocasts, such as maximum length, chords, and distances between two anatomical landmarks, and analyzed the difference in endocranial shape based on indices (ratios) or multivariate analyses (Falk et al. 2000, 2005; Broadfield et al. 2001; Balzeau et al. 2012, 2013). However, a set of linear measurements may have limited applicability in the analysis

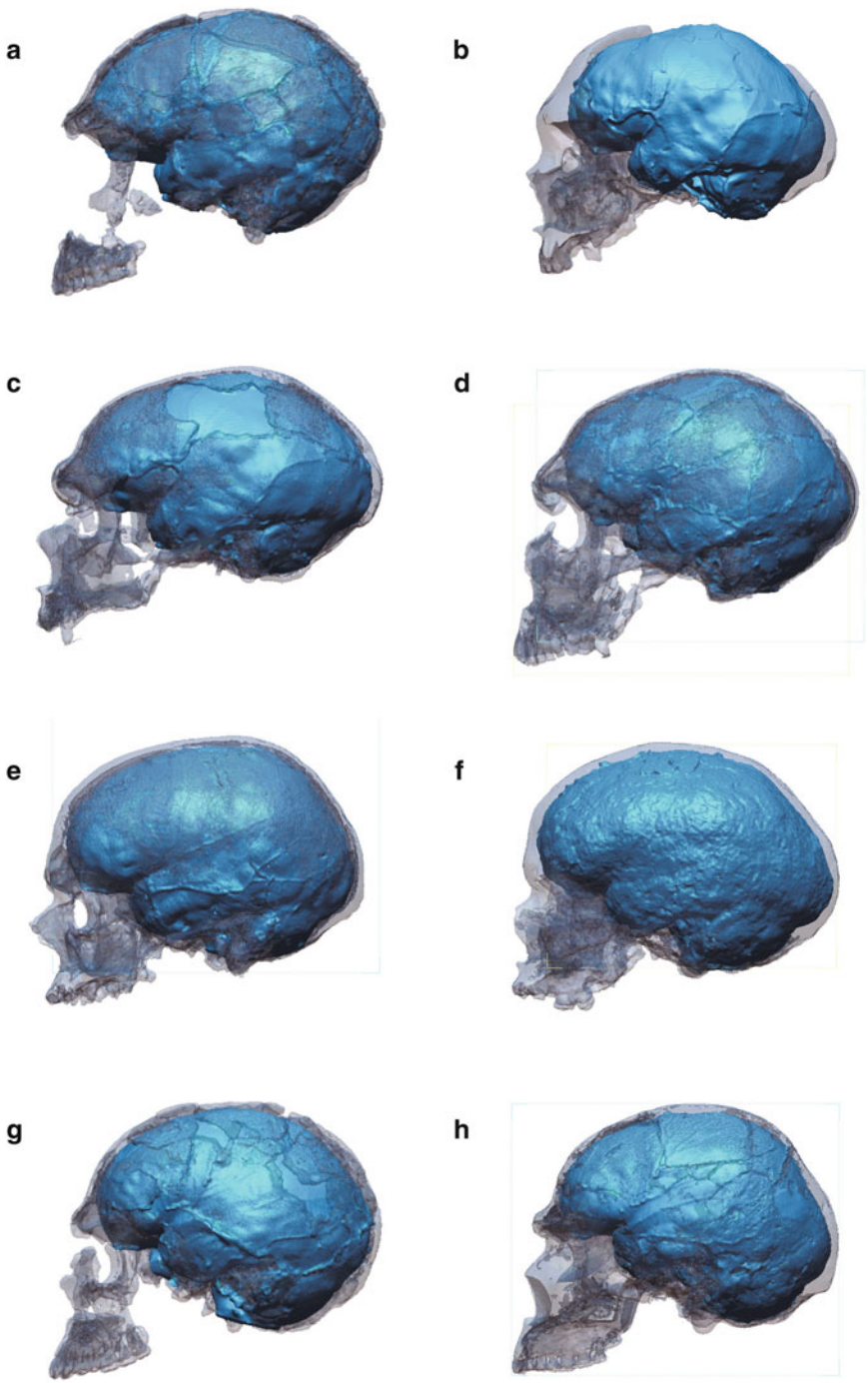

Fig. 2.14 Digital endocasts of specimens of Neanderthals (**a**–**d**) and early *Homo sapiens* (**e**–**h**). (**a**) Amud 1, (**b**) Forbes' Quarry 1, (**c**) La Chapelle-aux-Saints, (**d**) La Ferrassie 1, (**e**) Cro-Magnon 1, (**f**) Mladeč 1, (**g**) Qafzeh 9, (**h**) Skhul 5

of endocranial shape (Holloway 1981), because the overall spatial relationships of landmarks in each endocast are not preserved in the conventional multivariate analyses based on a set of linear measurements.

Thus, with a 3D geometric morphometric technique, a quantitative approach used to analyze shape variations based on landmark coordinates (Bookstein 1991; O'Higgins 2000; Adams et al. 2004; Slice 2005; Mitteroecker and Gunz 2009) was recently applied for quantitative comparisons of endocranial morphology. In these studies, homologous landmarks were digitized on the surface of each specimen, and landmark coordinates were normalized by centroid size for size-independent shape analysis. Landmark coordinates were then registered using the Procrustes method, and shape

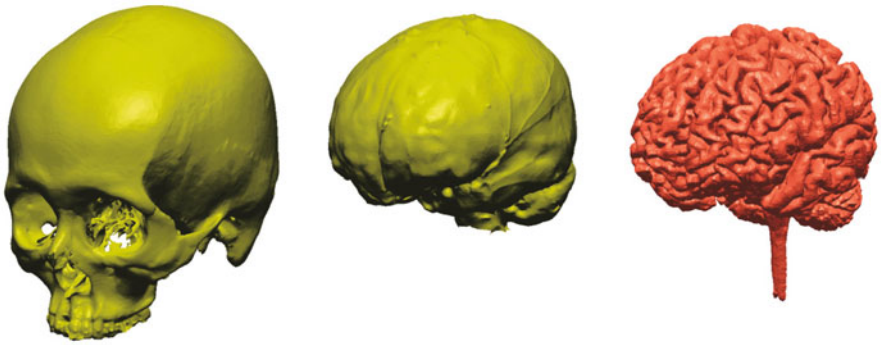

Fig. 2.15 Comparison of a human cranium and the brain enclosed in it (Ogihara et al. 2015). The CT and magnetic resonance images from one male participant were registered to each other to maximize mutual information between the CT and magnetic resonance images. Note that the sulcal patterns are not visible on the internal surface of the adult human cranium (Reprinted with the permission from the Anthropological Society of Nippon)

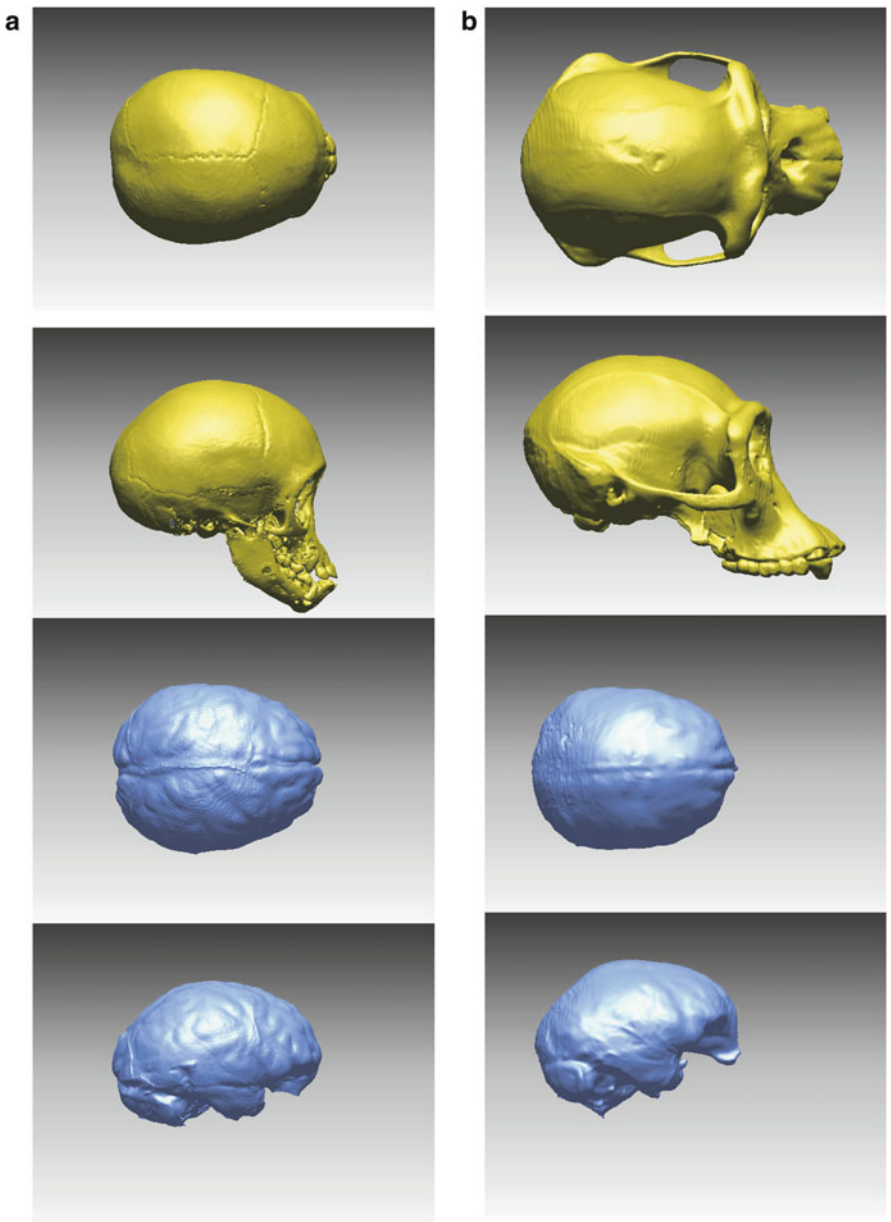

Fig. 2.16 Endocasts of a juvenile (**a**) and an adult female (**b**) chimpanzee. Note that imprints of sulci and gyri on the endocranial surface are somewhat prominent in the juvenile chimpanzee but not in the adult chimpanzee. The juvenile chimpanzee is a formalin-fixed specimen (JMC-3788), and the adult chimpanzee is a dry bone specimen (Musa), both housed at the Japan Monkey Center