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Preface

We can probably say that any field of knowledge is concerned with anthropology, dealing with some general or specific aspects of the biology or of the culture of humankind. Similarly, we can also say that any field of knowledge is about brain, the brain itself being the central director organizing the information of such a perspective. This is why human sciences and brain sciences have always had blurred and debated boundaries. On the one hand, we have the "hard fields" commonly recognized to be essential in neuroscience, nowadays mostly focused on molecular and cellular levels. At the same time, plenty of disciplines orbit around this conventional core, mixing and integrating heterogeneous dynamics. We are used to organizing things (including science) using separate "boxes" and labels, and we feel uncomfortable with such a scarcely defined topic. However, the difficulties in organizing a defined structure for the study of the human brain are implicit within the nature of the subject. The image of a core of fields is an illusory picture generated from our reductionist tendency, a need to handle single small pieces like, in this case, cells and molecules. The human brain is about everything, and its study suffers from a circular and tautological indetermination principle, in which the observer and the observed are the same entity. Although we may be partially aware of the bias this can induce, we totally ignore the actual effects of such circularity. In recent decades, many holistic approaches have attempted to escape these reductionist excesses, integrating different sources of information, large-scale perspectives, and multidisciplinary programs. Although results are probably still preliminary, the effort is valuable and necessary. An example is the field of neuroanthropology, which considers the integration between brain and environment by evaluating the relationship between biology and culture, and attempting to disentangle the dichotomy between organic and superorganic components of the mind. In an evolutionary context, another example is given by cognitive archaeology that interprets the cultural evidence of the archaeological record through the cognitive evidence of the current neuropsychological fields. It is undeniable that the multidisciplinary integration between anthropology, medicine, neuroscience, and social sciences will be a major key in future discoveries in human brain biology and evolution. Theories and advances in extended mind and embodiment will be probably decisive to change paradigms, possibly leading to epistemological shifts and new levels of interpretation.

While this new attempt to integrate knowledge is supporting some recent pioneering perspectives, technology is supplying a parallel and necessary methodological enhancement. In the last decade, digital tools in anatomy and morphometrics allowed to rediscover topics and issues left apart more than 50 years ago. Thanks to biomedical imaging, virtual modeling, and computed statistics, anatomy has become again a central issue in biology and evolution. Methods in anthropology and paleontology have been particularly empowered by these new toolkits, and "morphometrics" represents nowadays a specialized professional field.

One of the disciplines which have benefited most from the technical improvement of digital morphometrics is paleoneurology. In its early times, it mainly concerned the study of the cranial capacity and brain volume, its variations and differences among extinct and living hominoids, and the allometric study of the encephalization processes. The physical molding of the endocranial cavity and the production of endocranial casts also supported inferences on sulcal patterns and brain morphology. Nonetheless, paleontological study of the brain anatomy has been hampered for a long-time due to the elusive nature of its main target, namely providing inferences on brain structure from bone remains. Apart from the intrinsic limits of the field, methodological problems associated with the reconstruction of the brain form have represented a relevant limiting factor. The contribution of digital anatomy in this sense has been decisive, promoting in the last decade a new age of paleoneurological studies. As always, influent technical advances are difficult to control in their earliest stages of application, and caution is recommended to avoid excesses based on an improper use of the methodological power. Nevertheless, the crucial contribution of these tools in paleoneurology and evolutionary neuroanatomy has been essential.

In October 2012, an international symposium on *Human Paleoneurology* was organized at the National Research Center for Human Evolution in Burgos, Spain. The conferences, supported by the Instituto Tomás Pascual, were aimed at connecting people working on different aspects of brain evolution. The works presented during the conference were conveniently reorganized and extended, before being collected in this book. In the introduction Ralph Holloway, a pioneer in paleoneurology, offers a critical review of the main challenges still constraining the field. The chapter by Laura Reyes and Chet Sherwood introduce current topics in evolutionary neuroanatomy. Philipp Gunz presents major technical advances and digital tools. Emiliano Bruner discusses functional craniology, supplying a general review of the state of the art in paleoneurology. Simon Neubauer analyzes brain size and brain shape changes during hominid evolution, introducing issues associated with allometry and heterochrony. Natalie Uomini adds a behavioral component, including laterality, asymmetries, and language. Dietrich Stout and Erin Hecht integrate neurobiological and archaeological evidence, reviewing the current analytical methods in brain imaging. Fred Coolidge, Tom Wynn, Leee Overmann, and Jim Hicks discuss topics in cognition and archaeology, ranging from sleep to working memory. Finally, a collection of images displays endocasts

of representative fossil and living hominoids, digitally reconstructed by José Manuel de la Cuétara.

This volume is a synthesis of many current perspectives aimed at integrating studies in brain evolution, connecting anthropology with neurosciences. The target is to provide a general view of the present topics, methods, limits, and problems, encountered by those who decide to approach paleoneurology in the age of multidisciplinarity, digital anatomy, and computed morphometrics.

Burgos, May 2014   Emiliano Bruner

Contents

Chapter 1
Introduction: Paleoneurology, Resurgent!

Ralph Holloway

Abstract   Much has happened in the study of paleoneurology since the turn of the 20th Century involving increasing sophistication of digital methods which permit a variety of statistical and imaging techniques that are replacing the older methods of studying endocasts, which have relied upon plaster/latex rubber copies of fossil materials and mostly qualitative statements regarding morphology and those correlations with structural and functional studies from neuroanatomy. Today, non-invasive imaging techniques allow for immediate study of b both qualitative and multivariate quantitative approaches to both fossil specimens and modern human endocranial variation. Nevertheless, a critical examination of several recent paleoneurological papers suggest that too little familiarity with actual neuroanatomy and reliance instead on digitized descriptions and statistical techniques is leading to hypotheses that fly in the face of actual neuroanatomical details. We need a much better understanding of modern human and ape neuroanatomical patterns as well as more fossil specimens, and in particular, better ethics of sharing digital information.

Keywords   Cerebral asymmetries · Endocasts · Paleoneurology · Reorganization · Striate cortex reduction

It was not that long ago that those of us doing paleoneurology and actively making and studying endocasts could probably have fit into a London phone booth, albeit with protest. Of course, study of the evolution of the brain, in general, has always been a popular subset of the Zoological sciences (think of the Edingers, Tilly, and father Ludwig, C. Ariens Kappers, F. Weidenreich, the Jesuit scholar CJ Connolly, H. Jerison, I. Kotchekova, to mention but a few), including Anthropology. It seems to have finally dawned on a growing number of paleoanthropologists that the most direct evidence for hominin (and hominid) brain evolution is to be found by

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studying the only really direct evidence, those sometimes ugly, seldom complete, and data-impoverished objects we call endocasts, moot with regard to almost all cerebral morphology. Ecological opportunities are conspicuously available in paleoneurology, particularly given the age profile of its current combatants….

It is no secret that endocasts provide few cortical convolutional details and this understanding has a long and controversial history (Symington 1916; Clark et al. 1936; Hirschler 1942; Bailey and Bonin 1951; Keith 1931; Ariens-Kappers 1934; Balzeau and Gillissen 2010; Black 1932; Edinger 1949; Grimaud-Herve 1997; Holloway et al. 2001, 2010; Holloway 2012; Radinsky 1968; Shellshear and Smith 1934; Weidenreich 1936, 1941, 1943; Wu et al 2006), and it is embarrassing to remember that such a highly regarded neuroanatomist as Smith (1926) regarded the Piltdown endocast as having an extremely primitive pattern, more so than in *Homo erectus* from Indonesia. Connolly's (1950) book is more or less our "bible" on these issues, which also provided ontogenetic, and comparative "racial" observations, based on the collections at the Smithsonian Institute. Nevertheless, endocasts are the closest we can come to what was once an actual living brain, and is what I describe as the only true "direct" evidence regarding hominin brain evolution (Holloway 1964, 1996, 2009; Holloway et al. 2004). The goal of course is to synthesize the "direct" paleoneurological evidence with the rest of the fossil record, archaeological materials, particularly stone tools, living sites, faunal associates, current neuroscience, and human behavioral/social adaptations gleaned from comparative neuroscience and animal studies.

Today, it is becoming difficult to stay on top of the paleoneurological game, particularly if we include all of its speculation, and simply impossible to stay on top of the neurosciences. Nevertheless, the field of paleoneurology is in an expansive phase, even if ignored by most physical anthropologists, whether postcranial or dental specialists, and archaeologists (see Holloway 1997, 2008, 2009, for a brief history). I would like to offer a speculation as to why, aside from the obvious interest in human brain evolution: paleoneurology is becoming an aesthetic and a digital turn-on for younger scholars born with mice in hand. Not that art did not exist earlier as any study of the papers by Retzius, Ariens Kappers, Weidenreich, and many others would show, in their illustrations and lists of linear and arc measurements, but today's software programs such as Amira, Analyze, Osirix, ITK-SNAP, Endex, to mention a few, offer both aesthetic and morphometric delights that surely must satisfy paleoneurological nerds, even dinosaurs like myself. One need only look at the beautiful images produced by Dean Falk and colleagues on LB1, Bruner, Weber, Neubauer, Gunz, Schoenemann, Balzeau, Gilissen, Grimuad-Hervé, Subsol, Thibaut, and Wu. Add to this virtual virtuosity sophisticated statistical packages and the advancement of morphometric techniques e.g., mirror-imaging, spline analysis, and algorithms for correcting some forms of distortion, add missing data points, and one can see much advancement over the days when endocast reconstruction reliability was scored between 1–4 (Holloway 1970). In short, these advances have made it possible to evolve a Paleoneurology that is more empirical, quantitative, advancing actual hypotheses for testing, and perhaps most importantly, the sharing of endocast data, where

colleagues can challenge each other's reconstructions and interpretations, given, of course, there exists a wholesome intellectual environment, and not a sheer competitive landscape brought on by a dearth of academic jobs available for an overabundance of paleoneurologists.

Nevertheless, I remember fondly the good old days of pouring liquid latex into skulls, vulcanizing them, and extracting the endocast out from the foramen magnum with a satisfying expanding pop, hoping that the sella turcica was not included. Or, using Dentsply on sectioned crania and getting beautiful blue (or green) endocranial portions that hopefully would last forever with exquisite detail, as the molding was meant for dental crowns. When the endocasts were incomplete, as was the case for almost all of the African, Indonesian, and European ones I reconstructed since 1969, (see Holloway et al. 2004 for examples), the sculptor became alive and happy as I tried to add plasticine to the missing regions based on other endocasts of the same taxon that were more complete. Of course, that is a route for reducing endocranial volumetric variance, but one where decades of experience should count for something! Nor was there any lack of pleasure in dunking the endocast into various sized beakers to see if Archimedes' Principle really worked across the taxa! Currently, one just hits the "volume" key in the software package, and voila! a volume with three (or more) decimal places appears! Sad to say, however, that the roughly 200 ape endocasts I made during the '70's have deteriorated, their latex surfaces growing caramelized as I write this article. Fortunately, almost all of these have been scanned and are available at ORSA, University of Penn, under the directorship of Drs. Janet Monge and Tom Schoenemann.

Next was the task of sharing one's work with one's colleagues, and making sure that the home of the discovered crania was given an endocast, which meant then molding the endocast reconstruction and mailing them off to various parts of the world, which was not an easy, or enjoyable task. These were usually done by exchanging endocasts between respective collections, which could be difficult for those with nothing to exchange! Today, not only can one send the reconstruction or original electronically, but one can even make a 3-D model from the scan data. Just consider the beautiful reconstruction of the Malapa (MH1) endocast done by Berger, Carlson et al. (2011) from South Africa. Contrast that with the inability of myself to get a copy of the Daka endocast after doing the description and made to return the original cast without making a copy. The same for the Konso specimen. The lesson being, of course, that politics is still a major barrier to full academic sharing between fossil discoveries and major research centers which control the CT scan data of the specimens and are loath to share until every last pixel and voxel have been described. Even then politics tends to overcome our better instincts.

Of course, advances in technologies and electronic manipulations of data do not necessarily guarantee more reliable error-free results. Considerable neuroanatomical knowledge is still required, collections need expansion, morphology still needs identification and interpretation, and individual biases still play their nefarious roles in selective perception, segmenting, measuring, etc. The classic "garbage-in garbage-out" meme always remains a possibility, even with sharing

of data. Having now segmented some 500+ modern human endocasts from museum crania using Analyze 11, ITK-SNAP, I know full well how it is possible to err in interpreting objects slice-by-slice, and selecting points with the mouse. Working segmentation with fossils still containing adhering debris is extremely challenging, particularly when the fossils are fragmented and/or distorted, as in several of the Neandertal (e.g., Forbes Quarry, Skhul 9, Amud), *Homo erectus*, and australopithecine specimens, e.g., Stw505, Hadar AL 444. Below are some examples of where the "new" and "virtual" raises some issues and doubts. Weber et al. (2012) have a nice paper on how some of the defects can be corrected.

The exchanges between Dean Falk and me over the decades can serve as prime examples of the above. Consider our recent exchanges in the American Journal of Physical Anthropology (Falk and Clarke 2007, 2012a, b; Holloway and Broadfield 2011, 2012a, b). Here, the issue was using a modern technique of mirror-imaging (truly modern?) the right side of the Taung endocast and finding a new volume of 382 ml, quite different than my 402 ml volume published in 1970, which was quite different than the 525 cc volume published by Dart. Inherent in the above arguments was the notion that somehow using laser scans and mirror-imaging was a real improvement over my (Holloway 1970) defining a midline, scribing it, and sanding it down to the midline, and multiplying the resulting hemi-endocast volume by 2, assuming hemispheric symmetry. When their results were published (Falk and Clarke 2007), it was apparent that they had not only not defined a midline explicitly by defining actual anatomical landmarks, but their mirror image showed a visible asymmetry between left and right sides, hence our critical response. The quest by Falk and colleagues to assert that my earlier works on australopithecine endocasts (Falk et al. 2000) provided inflated endocasts does not appear to have much support, judging by the recent Neubauer et al. (2012) paper. Nevertheless, despite our disagreement, the work by Falk and Clarke on that specimen is valuable and suggests that such methods and challenges to prior research is useful and welcome.

Another more recent example where disagreement is necessary is the error in the Falk et al. (2012) paper claiming that the Taung specimen had an open metopic suture and anterior fontanelle, which permitted an adaptation around some "pelvic dilemma", so that the prefrontal lobe could expand thus indicating prefrontal reorganization. The Fig. 1 of their article, a medical CT scan of the Taung specimen, clearly indicates a labeled metopic suture and anterior fontanelle. The frontal bone is without any trace of a metopic suture either on the external or internal bony table, and all that can be found is a small remnant just superior to nasion. This feature alone probably invalidates their claims. When a microCT Scan was done, it became apparent that there was no metopic suture, no anterior fontanelle, but that the remnants of cortical bone on the left side of the endocast which ended at the superior sagittal sinus was what led to their medical CT scan suggesting a metopic suture (Holloway et al. 2013a, b). Here, the error is understandable given the medical CT scan, and an example where additional, more advanced technology can provide a different explanation. Of course, matters were not helped by the claim that many of the early hominins of the genus *Homo* had

metopic sutures (as if they were like that claimed for Taung). A careful look at original descriptions of the fossils indicated that metopic sutures, if present (most were not) were confined to the regions between nasion and glabella, which the micro-CT scan data shows to be the for the Taung endocast. But their study proves useful because it forces the field to re-examine these older fossils with the newest techniques available, and to sharpen our inferences regarding the evolution of the brain and in particular, the prefrontal lobes. Here of course, it is convolutional details rather than metric widening of the prefrontal lobe that is the key to understanding when such reorganization might have taken place.

One could hardly be unaware that Falk and I have been arguing about the lunate sulcus on the Taung endocast for decades, yet neither Falk nor Keith ever provided quantitative support for their placement of the lunate sulcus in a cercopithecoid (*Papio*, *Macaca*) position, whereas a large sample of chimpanzee lunate sulci positions transferred to the Taung endocast violate the transverse sulcal morphology in the anterior occipital and posterior parietal lobe, thus strengthening the argument for a more posterior placement, and thus suggesting neural reorganization prior to brain enlargement (Holloway 1984, 1985; Holloway et al. 2003). The issue of placement is critically important to our understanding as to when and where (on the brain) reorganization took place between the *Homo* lineage and the Last Common Ancestor. This controversy is curiously injected in very useful and interesting study of Einstein's brain by Falk (2009) and Falk et al. (2013) where they make reference to the lunate sulcus as not being homologous between apes and hominins, based on a misreading of Allen et al. (2006), ignoring the importance of partial homology. The point I am trying to make here, is that even after 85 years of study of the Taung endocast, controversies continue. Most of these arguments could have been avoided by a careful study of the actual anatomy of the specimen by independent researches rather than just the two of us, rather than relying on newer techniques (e.g., mirror-imaging, medical CT scan, etc.) that avoid confronting the anatomy. Indeed, other australopithecine endocasts were relegated to the pongid level: consider that to suggest that the *Australopithecus afarensis* 162-28 specimen was not showing reorganization and retaining a pongid pattern, Falk (1985) had to rotate the endocast so that the cerebellar lobes protruded beyond the occipital lobes, done by having the poor beast with its face on the ground, or bipedally hunched over rather like the more villainous representations of the Hunchback of Notre Dame. Even metric analysis was of no avail in that argument.

Sample size is also a matter that impedes accurate understanding of anatomical differences between taxa. Falk et al. (2009) argued that LB1 (*Homo floresiensis*) had the derived character state of a projecting occipital lobe over the cerebellum, but in fact all pongids show that character. Fossils are of course rare, and sampling a major problem in attempting to justify taxonomic arguments as well as functional interpretations, and ultimately evolutionary trajectories., but comparative materials such as modern human and pongid endocasts are abundant. Indeed 5 of

the 7 so-called "derived" features of the LB1 *Homo floresiensis* endocast are shared with apes, including hylobatids. The recent paper by Kubo et al. (2013) using microCT scan data on the cranium of LB1 and the resulting endocranial volume of 426 cc, claiming their volume is a better estimate than previously published values of roughly 400 cc. However, the Fig. 2 of their paper shows that their reconstruction of a virtual endocast does not correct for the obvious bulge of the right side of LB1 cranium, and thus the endocast which has been pointed out in other papers. In my humble opinion, even microCT scan data still requires an appreciation of distortion which should be obvious to the naked eye. It should be noted, however, that while I am taking some of my colleagues to task here, I am sure some of my earlier works are worthy of similar critiques, and indeed, without disagreement, how can this field possibly advance?

Morphometric analyses have become much more sophisticated. As is apparent in this volume, much progress in this area can be attributed to the Editor, Emiliano Bruner, who I have had the pleasure of working with over the past few years. I hope I will not be regarded as traitorous to the cause of quantitative morphometric advances in paleoneurology when I retain a strong skepticism that these methods truly solve any issues, despite their extremely important function of providing tests of actual hypotheses regarding taxonomic verity and possible evolutionary changes in morphometry and supposedly behavioral function. My skepticism is based on that hard rock that we in these sciences confront: small sample sizes of individuals that are almost always incomplete (consider just how many basicrania there are for *Homo erectus*, Neandertals, etc.), or distorted. Nevertheless, the recent paper by Bruner et al. (2014) has some very beautiful illustrations of how the field of cranial/endocranial morphometrics has progressed. Still, I have little faith that shape patterns between Neandertals and modern *Homo*, for example, have any functional significance that can be rigorously tested, although the assertions are sometimes amazing, as exemplified by the recent Pearson et al. (2013). Here is it is claimed that given Neandertal large orbits, and thus large occipital lobes, they were, in essence, somewhat cortically deficient in their parietal lobes, and thus not up to modern *Homo* cognitive and sociality levels. These conclusions came from a reliance on statistical theatre that made one correction after another to primary data. However, that is a minor criticism, given that the authors never asked whether larger Neandertal faces might mean larger orbits, perhaps requiring some allometric adjustment. Additionally, these authors never bothered to closely examine the actual occipital lobe morphology in Neandertals. If they had, they would have found considerable differences in size and pattern variation. Needless to say, they did not provide any measurements of primary visual striate cortex, or area 17 of Brodmann, which cannot really be defined on these endocasts, thus making it impossible to know if indeed the size of the posterior parietal lobe was less in Neandertals than modern in *Homo*. Area 17 is also quite variable in volume in modern Australian Aborigines, being some 20 % larger that in Europeans (Klekamp et al. 1994). Holloway and Schoenemann (2014) have taken considerable

pains to show how variable Neandertal occipital cortices appear, and how variable these are in modern humans. In essence, morphometry trumped morphology, and its relationship to behavioral function, namely visual competence and cognitive application.

Even more recently, Barton and Venditti (2013) have provided opinions regarding the relative size of the frontal/prefrontal lobe in humans and argue that its size is what would be expected for a primate with our brain size, and thus it was unlikely that evolution worked to select larger prefrontal lobes. Curious was the lack of reference to von Bonin's (1948) paper which demonstrated this, and as noted my several of my early papers. Missing was any sense that the organization of the frontal lobe could well have changed through selection pressures without manifest increases in relative size. One wonders how bonobos and chimpanzees differ in social behavior and relative size of their prefrontal lobes, without considering fiber/cellular organization, and inter-connectivity with the rest of the brain.

The recent 2013 AAPA Meetings in Knoxville had a stellar presentation on the reconstruction of the *Sahelanthropus* endocast (Bienvenu et al. 2013). One can only marvel at the hard work done in creating a virtual endocast from that badly fragmented (internal table of bone) and distorted specimen! The conclusion that the prefrontal lobe showed human-like organization rather than that of a pongid flies in the face of what we see on prefrontal lobes of chimpanzees and bonobos. Again, it would appear that possible bias and speculation precedes careful morphological comparison.

As can be seen in this paper, there is a lot of newer work, methodological approaches, and even controversial issues happening in paleoneurology, this one small part of the neurosciences in general. I would hope for another 50 years to see where it all goes…and I have not even touched on comparative neuroscience….

References

Ariens-Kappers CU (1934) The fissuration on the frontal lobe of *Sinanthropus pekinensis*. Proc K Ned Akad Wet 36:802–812

Allen JS et al (2006) Looking for the lunate sulcus: a magnetic resonance imaging study in modern humans. Anat Record Part A 288A:867–876

Bailey P, von Bonin G (1951) The isocortex of man. University of Illinois Press, Urbana

Balzeau A, Gilltssen E (2010) Endocranial shape asymmetries in *Pan paniscus, Pan troglodytes* and *Gorilla gorilla* assessed via skull based landmark analysis. J Human Evol 59:54–69

Barton RA, Venditti C (2013) Human frontal lobes are not relatively large. Proc Natl Acad Sci USA 110:9001–9006

Bienvenu T et al (2013) The endocast of *Sahelanthropus tchadensis*, the earliest known hominid. Am J Phys Anthropol S56:80–81

Black D (1932) The brain cast of *Sinanthropus*, a review. J Comp Neurol 56:361–366

von Bonin G (1948) The frontal lobe of primates: cytoarchitectural studies. Res Publ Assoc Res
    Nerv Ment Dis 27 (1):67–83
Bruner E et al (2014) Functional craniology and brain evolution: from paleontology to
    biomedicine. Front Neuroanat 8:19
Carlson KJ et al (2011) The endocast of MH1, *Australopithecus sediba*. Science 333:1402–1406
Connolly CJ (1950) The external morphology of the primate brain. CC Thomas, Springfield
Clark WE et al (1936) The endocranial cast of the chimpanzee. J Roy Anthropol Inst Grt Brit
    Ireland 66:249
Edinger T (1949) Paleoneurology versus comparative brain anatomy. Brain endocasts: the
    paleoneurological evidence. Wiley-Liss, New York, pp 273–282
Falk D (1985) Apples, oranges and the lunate sulcus. Am J Phys Anthropol 67:313–315
Falk D et al (2000) Early hominid brain evolution: a new look at old endocasts. J Hum Evol
    38:695–717
Falk D (2009) New information about Albert Einstein's brain. Front Evol Neurosci 1:3
Falk D et al (2009) LB1's virtual endocast, microcephaly, and hominin brain evolution. J Hum
    Evol 57:597–607
Falk D, Clarke R (2007) Brief communication: new reconstruction of the Taung endocast. Am J
    Phys Anthrop 134:529–534
Falk D, Clarke R (2012a) Letter to the editor: response to Holloway and Broadfield's critique of
    our reconstruction of the Taung virtual endocast. Am J Phys Anthropo 148:483–485
Falk D, Clarke R (2012b) Letter to the editor: reply to Holloway and Broadfield's letter to the
    editor regarding the Taung endocast. Am J Phys Anthrop 149:327–328
Falk D et al (2013) The cerebral cortex of Albert Einstein: a description and preliminary analysis
    of unpublished photographs. Brain 136:1304–1327
Falk D et al (2012) Metopic suture of Taung (*Australopithecus africanus*) and its implications for
    hominin brain evolution. PNAS 1119752109
Grimaud-Herve D (1997) L'evolution de L'enchephale Chez *Homo Erectus* et *Homo Sapiens*.
    CNRS Editions, Paris
Hirschler P (1942) Anthropoid and human endocranial casts. Noord-Hollandsche Witgevers
    Maatschappen, Amsterdam
Holloway RL (1964) Some aspects of quantitative relations in the primate Brain. PhD
    Dissertation, University of California, Berkeley
Holloway RL (1984) The Taung endocast and the lunate sulcus: a rejection of its anterior
    placement. Am J Phys Anthropol 64:285–287
Holloway RL (1985) The past, present, and future significance of the lunate sulcus. In: Tobias PV
    (ed) Hominid evolution: past, present, and future. A. R. Liss Inc., New York, pp 47–62
Holloway RL (1996) Evolution of the human brain. Chapter 4. In Lock A, Peters C (eds)
    Handbook of human symbolic evolution. Oxford University Press, New York, pp 74-116
Holloway RL (2008) The human brain evolving: a personal retrospective. Ann Rev Anthropol
    37:1–19
Holloway RL et al (2013a) Metopism and early brain evolution. Am J Phys Anthropol
    S56:150–151
Holloway RL, Broadfield DC, Carlson K (2013b) Metopism and early human brain evolution.
    Am J Phys Anthropol 150(S56):150–151
Holloway RL, Schoenemann PT (2014) The occipital lobes of Neandertal brans, orbit size, and
    cognition: what is the evidence for Neandertal cognitive inferiority? Am. J. Phys. Anthrop.
    S58:143–144
Holloway RL, Broadfield DC, Yuan MS (2004) The human fossil record: vol. 3: brain endocasts:
    the paleoneurological evidence. Schwartz JH, Tattersall I (eds) Wiley-Liss, New York
Holloway RL, Broadfield DC (2011) Technical note: the midline and endocranial volume of the
    Taung endocast. Am J Phys Anthropol 146:319–322

Holloway RL, Broadfield DC (2012a) Letter to the editor: response to Falk and Clarke regarding Taung midline. Am J Phys Anthropol 143:326

Holloway RL, Broadfield DC (2012b) Letter to the editor: reply to Falk and Clarke on Taung Virtual endocast midline and volume. Am J Phys Anthropol 149:326

Holloway RL (1970) Australopithecine endocast (Taung specimen, 1924): a new volume determination. Science 168:966–968

Holloway RL (1997) Neuroanatomy, comparative. In Spencer F (ed) History of physical anthropology: an encyclopedia, vol 2 (M–Z). Garland Publishing, Inc., New York, pp 732–743

Holloway RL, Broadfield DC, Yuan MS (2001) Revisiting australopithecine visual striate cortex: newer data from chimpanzee and human brains suggest it could have been reduced during australopithecine times. In: Falk D, Gibbon KR (eds) Evolutionary anatomy of the primate cerebral cortex. (A Festschrift for Dr. Harry Jerison.) Cambridge University Press, Cambridge, pp 177–186

Holloway RL, Broadfield DC, Yuan MS (2003) Morphology and histology of chimpanzee primary visual striate cortex indicate that brain reorganization predated brain expansion in early hominid evolution. Anat Rec 273A:594–602

Holloway RL (2009) Brain fossils: endocasts. In: Squire LR (ed) Encyclopedia of neuroscience, vol 2. Academic Press, Oxford, pp 253–261

Holloway RL (2012) The issue of brain reorganization in Australopithecus and early hominids: Dart had it right. Chapter 9. In: Reynolds SC, Gallagher A (eds) African genesis: perspectives on hominin evolution. Cambridge University Press, Cambridge, pp 163–180

Holloway RL, Schoenemann T, Monge J (2010) The hobbit brain: some doubts about its "derived features". Am J Phys Anthropol 141(S50):130

Keith A (1931) New discoveries relating to the antiquity of man. Williams and Norgate Ltd, London

Klekamp G et al (1994) Morphomrtric study on the postnatal growth of the visual cortex of Australian aborigines and Caucasians. Jurnal fur Hirnforschung 35(4):541–548

Kubo D, Kono RT, Kaifu Y (2013) Brain size of Homo floresiensis and its evolutionary implications. Proc Royal Soc B 280:20130338

Neubauer S et al (2012) Endocranial volume of Australopithecus africanus: new CT-based estimates and the effects of missing data and small sample size. J Hum Evol 62:498–510

Pearce E, Stringer C, Dunbar R (2013) New insights into differences in brain organization between neanderthals and anatomically modern humans. Proc R Soc B 280:1758

Radinsky L (1968) Evolution of somatic sensory specialization in otter brains. J Comp Neurol 134:495–505

Shellshear JL, Smith GE (1934) A comparative study of the endocranial cast of Sinanthropus. Philos Trans R Soc Lond B 223:469–487

Smith GE (1926) Casts obtained from the brain cases of fossil man. Nat Hist 26:294–299

Symington J (1916) Endocranial casts and brain form: a criticism of some recentspeculations. J Anat Physiol 11:111–130

Weber GW et al (2012) Digital South African fossils: morphological studies using reference-based reconstruction and electronic preparation. In: Reynolds SC, Gallagher A (eds) African genesis: perspectives on hominin evolution. The Guilford Press, Cambridge: New York, pp 298–316

Weidenreich F (1936) Observations on the form and proportions of the endeocranial casts of Sinanthropus pekinensis, other hominids, and the great apes. Paleontogica Sinica (B) VII:1–50

Weidenreich F (1943) The skull of *Sinanthropus pekinensis*: a comparative study on a primitive hominid skull. Paleontol Sin New Ser 10:108–113

Weidenreich F (1941) The brain and its role in the phylogenetic transformation of the human skull. Trans Am Philos Soc 31:321–442

Wu XJ, Schepartz L, Falk D, Liu W (2006) Endocast of Hexian *Homo erectus* from south China. Am J Phys Anthropol 130:445–454

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Ralph L. Holloway started his education as a metallurgical engineer at Drexel Institute, but took a turn toward a BS in Geology, 1959, at the University of New Mexico. In 1964, he received his Ph.D. in anthropology from the University of California, Berkeley, and has been teaching and doing research at Columbia University since then. His main area of expertise is the evolution of the human brain and behavior. His research is primarily the study of fossil hominid brain endocasts, and trying to synthesize these with modern neuroscience. He has done research on sex differences in the human brain, particularly the corpus callosum.

Chapter 2
Neuroscience and Human Brain Evolution

Laura D. Reyes and Chet C. Sherwood

Abstract Evidence from comparative neurobiological studies indicates that humans differ from other primates along several different dimensions of brain organization. Differences in cytoarchitecture, connectivity, and gene expression demonstrate that substantial remodeling of brain microstructure and molecular biology occurred during human evolution, and these changes are likely associated with cognitive specializations. The paleoneurological study of brain reorganization, however, has often been considered only on a larger scale, since the evidence from endocasts is limited to brain regions that can be detected from the traces left in the fossil record. Neuroscience offers a critical perspective on paleoneurology by investigating the microstructure and genetic mechanisms that might be responsible for brain reorganization. Recent findings suggest that neural tissue differs in its anatomical structure and molecular biology across primate species and is not uniform in its processing capabilities. Connectivity patterns can differ across species, producing selective enlargement of connected brain regions. Changes in patterns of innervation for various neurotransmitters may also occur on a microscopic scale, but can produce substantial changes in brain function and cognition. Furthermore, differential regulation of various transcription factors and genes can produce variation in the size of brain structures across primate species. Although the exact nature of brain reorganization related to the evolution of cognitive processing in humans remains to be fully defined, these findings indicate that it may have occurred through a number of different pathways. Further research in both neuroscience and paleoneurology is necessary to identify areas where brain reorganization likely occurred, along with the underlying mechanisms of evolutionary change in human brain structure and function.

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Introduction

Overall brain size has increased over evolutionary time in several mammalian lineages, and especially in primates (Jerison 1973, 1979; Shultz and Dunbar 2010). Scaled to body size, however, cranial capacity in the hominin lineage has increased even more dramatically than is typical of other primates, indicating that brain size has expanded in hominins significantly more than expected based only on body size increase (Jerison 1973; Hofman 1983; Hawks et al. 2000). Modern human brain mass, which is approximately 1,400 g on average, is about three times larger than in great apes, our closest living relatives. While cranial capacity displays clear evidence of enlargement in the hominin fossil record, the issue of when brain reorganization occurred is more difficult to determine. The term brain reorganization refers to changes in the structures of the brain that account for differences in function and behavior that are independent of variation in brain size (Holloway 2008).

The notion of concerted versus mosaic evolution as a means of reorganization has been addressed in reference to brain evolution across mammals. Concerted evolution can be defined as changes in structure that occur in a coordinated manner throughout the entire brain due to constraints on neural development, while mosaic evolution is the ability for specific systems or regions to change independently of one another. Finlay and Darlington (1995) proposed that the size of brain regions in mammals enlarge predictably based on absolute brain size. This is primarily due to a conserved order of neural development in mammals, which was shown to be correlated with the relative enlargement of different brain regions as brain size increased. These results suggest that adaptations for many behaviors in evolution likely involve enlargement of the whole brain, since modification of individual regions is most easily achieved by changing the duration of the entire brain's schedule of neurogenesis.

However, there are instances in which certain systems within the brain of particular species or lineages have been shown to increase in size independently of changes in overall brain size (Barton and Harvey 2000). For example, neocortical volume in primates is disproportionately large when compared to neocortical volume in insectivores, with primate neocortical volume nearly five times that of a similarly sized insectivore brain. These results suggest that neocortical enlargement in primates is associated with adaptation toward a different ecological niche, and shows that increased neocortical volume relative to brain size may be a part of

Fig. 2.1 The lunate sulcus forming the boundary between the parietal and occipital lobes on the *left* hemisphere of a chimpanzee brain. The location of the lunate sulcus in hominin fossil endocasts has been highly debated

that adaptive grade shift. There is also evidence of an adaptive shift in primates toward a diurnal niche and increased reliance on vision, with the size of areas associated with vision negatively correlated with size of areas associated with olfaction. Hence, the evidence of brain reorganization in primates indicates that constraints may have resulted in overall concerted evolution among most brain structures, but these constraints did not preclude system-specific changes. For example, in anthropoid evolution, mosaic changes, such as the coordinated evolution of regions linked by a common system, affect neural diversity more than changes in relative brain size. Relative brain size only accounts for a small proportion of the variation seen in anthropoid brains, and underestimates the contribution made by the different neural pathways (Smaers and Soligo 2013).

With respect to the hominin fossil record, the discussion of brain reorganization has centered on whether changes in the relative size of cortical regions occurred prior to major brain expansion or whether these changes were primarily linked to allometric effects of cortical enlargement, with a longstanding debate concerning the position of the lunate sulcus (Fig. 2.1). Lunate sulcus position is important because it indicates the location of the parietal cortical areas important for sensorimotor integration, object manipulation, and attention (Bruner 2010), in relation to the primary visual cortex in the occipital lobe (Holloway 2008). Comparative data from volumetric measurement across hominoid primates indicates that the modern human primary visual cortex is significantly reduced and that the position of the lunate sulcus provides a reasonable approximation of primary visual cortex size (de Sousa et al. 2010). In ape endocasts, the lunate sulcus occupies a rostral, or more anterior, position than in modern human endocasts (Falk 1980). Therefore, a more caudally positioned lunate sulcus in an endocast would signal a shift in cortical reorganization toward a more modern human-like pattern of parietal expansion and occipital reduction.

Much of the debate regarding the position of the lunate sulcus has focused on australopithecines, from approximately 4 to 2.5 million years ago, particularly the Taung endocast of *Australopithecus africanus*. Whereas Falk (1980, 1983, 1985a, b, 1989) identifies the australopithecine lunate sulcus more rostrally in an ape-like position, Holloway (1981a, 1983, 1984, 1988, 1992), Holloway and Shapiro (1992), and Holloway et al. (2004) assert that the position of the lunate sulcus is more caudal, similar to modern humans. Because australopithecines have relatively small cranial capacities in the range of great apes, a rostrally positioned lunate sulcus would suggest that reorganization had not occurred in these species, and did not occur in the hominin lineage prior to brain enlargement. A caudally positioned lunate sulcus, however, would suggest that reorganization in the parietal and occipital lobes had occurred in these relatively small-brained species prior to brain enlargement in the hominin lineage (Holloway et al. 2004).

Recent fossil discoveries have provided further evidence for the possibility of reorganization in other regions of the cerebral cortex in hominins without an increase in brain size. The discovery of *A. sediba* from about 2 million years ago suggests the possibility that cortical reorganization had occurred prior to brain size enlargement in hominins. The endocast of *A. sediba* has a relatively small endocranial volume comparable in size to earlier *Australopithecus* species. However, the morphology of its orbitofrontal region is claimed to be more similar to that seen in later *Homo* (Carlson et al. 2011). Further complicating the debate is the endocranial morphology of the *H. floresiensis* specimen LB1. The position of the lunate sulcus in the LB1 endocast of *H. floresiensis* from 94,000 to 13,000 years ago has been identified in a more posterior modern human-like position and it displays other derived morphology of the frontal and temporal lobe similar to that of *Homo erectus*, even though it has an incredibly small cranial capacity of 417 cc (Falk et al. 2009).

Relative sizes of the various lobes of the cerebrum have also been estimated to differ among hominin species with similar brain sizes, suggesting that changes can occur in a mosaic fashion without a change in overall brain size. Balzeau et al. (2012) examined the surface areas of the frontal, parieto-temporal, and occipital lobes relative to endocranial volume for *Homo* endocasts. Humans and Neandertals exhibited marked differences in relative lobe size despite similar endocranial capacities; Neandertals had relatively larger frontal and occipital lobes and a relatively smaller parieto-temporal lobe than humans. Evidence for parietal and cerebellar expansion in humans has also been demonstrated using geometric morphometrics techniques (GM). GM is based on the use of landmarks to define the shape of an object. Landmarks are biologically homologous loci across all specimens, and contain spatial data that can be separated according to size and shape information (Zelditch et al. 2004). The use of GM methods has transformed the field of paleoneurology, as it allows for a quantitative, rather than descriptive, study of shape changes among different specimens. Using GM, Neubauer et al. (2009) investigated the growth pattern of the endocranium throughout human development. The parietal and cerebellar regions of the cranial vault undergo pronounced expansion during early postnatal development. This pattern of globularization

during early development is not seen in chimpanzees, as humans and chimpanzees differ for their entire cranial growth trajectory (Neubauer et al. 2010). Although modern human and Neandertal crania both have relatively large endocranial capacities, they differ in both adult and developmental endocranial shape; Neandertals lack the early postnatal globularization phase seen in the human cranium, and develop along a trajectory that results in a more elongated cranial shape (Gunz et al. 2010, 2012). These results show that cranial growth trajectories have influenced the shape of the modern human brain, independently of changes in overall brain size (Bruner 2004).

Thus, there is considerable evidence to indicate that reorganization has occurred in parallel with brain expansion in hominin evolution. However, it is impossible to know the full extent of reorganizational changes in human brain evolution based solely on the fossil record. Although endocasts provide the only means of studying neural morphology of extinct hominins, the information they offer is limited to overall size differences, imprints of cerebral vasculature, the external convolutional morphology of well-preserved gyri and sulci, and changes in shape (Falk 2012). Although important information can be gained from such studies, they do not provide insight concerning changes that occurred in the microstructure, connectivity or molecular biology of the brain. Furthermore, modifications of internal structures, such as the basal ganglia, thalamus, and other deep nuclei cannot be examined from endocasts. Comparative neuroanatomical and genetic data across primates, therefore, is needed to reveal possible changes in microstructure, connectivity, and function that cannot be detected in endocasts (Fig. 2.2). The knowledge gained from such research has the potential to inform our interpretations of how the earliest hominins may have differed from the living great apes, and how later *Homo* may have evolved modern behaviors such as language.

Reorganization in Structure

Recent findings have provided a better understanding of how regions of the human cerebral cortex have changed compared to other primates in terms of size and position. The frontal lobe has been identified as a region that is noticeably enlarged and widened in Neandertals and modern humans compared to other hominins (Bruner and Holloway 2010). It is notable that the primate frontal cortex (including primary motor cortex, premotor cortex, supplementary motor area, and prefrontal cortical areas combined) hyperscales relative to the rest of the neocortex and brain, with a steeper scaling exponent than what is observed in carnivores (Bush and Allman 2004). The human brain does not differ from other primates in this respect (Bush and Allman 2004), and the total frontal lobe is as large as expected for an ape of human size (Semendeferi and Damasio 2000; Semendeferi et al. 2002; Barton and Venditti 2013). Furthermore, the human frontal cortex, though absolutely larger in humans, occupies a similar proportion of the cortex as in nonhuman primates (Semendeferi et al. 2002). Thus, humans appear to follow
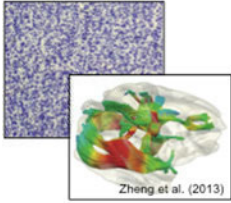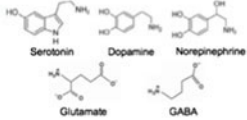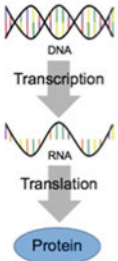
Structure

Macrostructure

Methods:
- Gross observation
- Dissection
- Magnetic Resonance Imaging (MRI)
- Geometric morphometrics
- Voxel-based morphometry

Features:
- Study of brain surface anatomy
- Shape analysis
- Gross anatomical scale
- Limited to large regions

Microstructure

Methods:
- Histology
- Diffusion Tensor Imaging (DTI)

Features:
- Finer anatomical scale
- Reveals underlying cellular structure of brain regions
- Can show connectivity between regions

Zheng et al. (2013)

Molecular biology

Neurotransmitters, receptors and other molecules

Methods:
- Immunohistochemistry
- Western blotting
- Proteomics

Features:
- Use antibodies to stain neurons or glia
- Identify specific cell types
- Can identify cells that use specific neurotransmitters

Serotonin Dopamine Norepinephrine

Glutamate GABA

Genetics

DNA
Transcription
RNA
Translation
Protein

Methods:
- Comparative genomics
- RNA-seq
- PCR
- Microarray
- Transgenic/knockout organisms

Features:
- Allow for comparison of genetic material across species
- Can show changes in gene expression
- Reveals molecular differences in development

Fig. 2.2 Different levels of examining brain reorganization, with a description of methods discussed in this chapter. Macrostructure includes large, visible structures of the brain. Macrostructure is the only level that can be investigated in endocasts. Microstructure is the next level, and allows for the analysis of cytoarchitecture and connectivity between different brain regions. Molecular biology refers to neurotransmitters, receptors, genes, and other molecular components of the brain

an expected pattern of total frontal cortex enlargement for a primate of our brain size. More uncertainty surrounds the question of prefrontal cortex enlargement in human evolution. The granular prefrontal cortex of humans contains regions that are important for language, social cognition, abstract thinking, long-term planning, and other executive functions. The frontal pole region (area 10) has been measured based on cytoarchitecture across hominoid species and has been shown to be both absolutely and relatively larger compared to the rest of the brain in humans than in other apes (Semendeferi et al. 2001), though human area 10 is only approximately 6 % larger than expected for an ape of human size (Holloway 2002). Other studies of the whole prefrontal cortex have concluded that it is larger than expected by allometry in humans for both grey and white matter (Schoenemann et al. 2005a; Smaers et al. 2011; Sherwood and Smaers 2013).

Less is known about how reorganization may have affected other brain regions. The temporal lobe in humans is larger than expected for an ape brain of human size (Semendeferi and Damasio 2000; Rilling and Seligman 2002). Humans also have larger than expected temporal lobe surface area and white matter (Rilling and Seligman 2002). Enlargement of the temporal lobe may be due to adaptations for language, as it contains the auditory cortex and Wernicke's area, two regions important for language processing, along with other regions such as the middle and inferior temporal gyri that are active in phonological and lexical-semantic functions (Binder et al. 1997). The parietal lobe has been difficult to differentiate from other regions, as its boundaries are not easily identified. Semendeferi and Damasio (2000) showed that the occipito-parietal sector, which is the combined volume of the parietal and occipital lobe, is as large as expected for an ape brain of human size. Although the total volume of the occipito-parietal sector is not larger than expected in humans, more fine-grained reorganization in this region is evident in modern humans; the size of the parietal lobe appears to have become more rounded in modern humans compared to Neandertals (Bruner 2004, 2008; Bruner et al. 2011), while a comparative study including humans and apes showed that the size of the adjacent primary visual cortex in the occipital lobe is reduced in modern humans compared to hominoids (de Sousa et al. 2010).

In sum, reorganization of neocortical regions of the human brain beyond what is expected by allometry appears to be relatively subtle for most regions. Many additional significant reorganizational differences are seen in the microstructure and molecular biology of the human brain. Microstructure consists of smaller components that form the larger, visible structures of the brain, and includes cytoarchitecture and connectivity. Cytoarchitecture refers to the organization of neurons and glia within neural tissue. Connectivity involves the structure and pathways of white matter tracts that traverse the brain and connect different regions. These can be large pathways, such as the corpus callosum, or smaller ones that connect neighboring regions of tissue, such as the "U-fibers" that connect adjacent gyri in the neocortex. Brain microstructure is an important component of brain function and studies of comparative neuroanatomy have revealed key differences at this microscopic level between humans and nonhuman primates that may have resulted in unique aspects of human cognition.