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Emiliano Bruner *Editor*

Human Paleoneurology

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Emiliano Bruner
Editor

Human Paleoneurology

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Editor
Emiliano Bruner
National Research Center on Human
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Spain

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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, Lee 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 multidisciplinary, digital anatomy, and computed morphometrics.

Burgos, May 2014

Emiliano Bruner

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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 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

R. Holloway (✉)

Department of Anthropology, Columbia University, 1200 Amsterdam Avenue,
New York, NY 10027, USA
e-mail: rlh2@columbia.edu

studying the only really direct evidence, those sometimes ugly, seldom complete, and data-impooverished 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, Grimaud-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 researchers 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 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 than in Europeans (Klekamp et al. 1994). Holloway and Schoenemann (2014) have taken considerable