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Paleoneurological Studies in Honor of Ralph L. Holloway
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THE HUMAN BRAIN EVOLVING:

Paleoneurological Studies
in Honor of Ralph L. Holloway



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FRONT COVER CAPTIONS

Center: Portrait of Ralph L. Holloway.

Upper left: A modern human brain.

Upper right: Ralph measuring landmarks on an endocast ca. 1976.

Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway).

Lower left: Ralph with an endocast of the Flores "hobbit" cranium.

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CHAPTER 1

THE HUMAN BRAIN EVOLVING: A PERSONAL RETROSPECTIVE

RALPH L. HOLLOWAY

ABSTRACT

Minor controversies notwithstanding, the evolution of the human brain has been an intermingled composite of allometric and non-allometric increases of brain volume and reorganizational events such as the reduction of primary visual cortex and a relative increase in both posterior association and (most probably) prefrontal cortex, as well as increased cerebral asymmetries, including Broca's and Wernicke's regions, with some of these changes already occurring in australopithecine times. As outlined in Holloway (1967), positive feedback ("amplification-deviation") has been a major mechanism in size increases. Exactly how this mélange of organs evolved will require many more paleontological discoveries with relatively intact crania, an unraveling of the genetic bases for both brain structures and their relationship to behaviors, and a far more complete picture of how the brain varies between male and female, and different populations throughout the world. After all, the human brain is still evolving, but for how long is quite uncertain.

INTRODUCTION

One of my goals is trying to understand how humankind evolved, and in particular, why we have become the most dangerous species on the planet. I attribute this quandary of the species to its brain, and the capacity thereby to create by means of arbitrary symbols, systems of patterned insanity, that is, delusional systems that nevertheless sustain us. This belief follows from my definition of human culture:

as that biosocial evolutionarily-derived and socially-sustained ability, possessed only by human

beings as members of societies, which organize experiences in a blend of both arbitrary and iconic symbol representations. These representations can be imposed by any level or unit of human social structure, including the individual. (Holloway 1981a; see also Holloway, 1967, 1969a, 1996).

The key element here is "imposed" meaning forced upon or done against resistance.

I recognize that this not a view shared by most people, and I could well be wrong about the patterned insanity I regard as part of human behavior (particularly religion and politics, despite what few eufunctions may attend, at least as far as I understand human history). Because the human brain is the most important constructor of experience and reality, it would be important to know how it came to its present state. Some knowledge of comparative neuroscience, the relationships between individual variation and behavior, molecular neurogenetics, and paleoneurology, or the study of the only truly direct evidence, the endocasts of our fossil ancestors, is necessary. Endocasts, i.e., the casts made of the internal table of bone of the cranium, are rather impoverished objects (the cerebrum is covered by three meningeal tissues) to achieve such an understanding, but these are all we have of the direct evolutionary history of our brains and should not be ignored. Most of my professional career has involved the study of these objects.

To cover all the evidence for human brain evolution would be an impossible task in this retrospective essay. Fortunately, a fine review of human brain evolution has been published by Annual Review of Anthropology (Schoenemann 2006), as well as by Rilling (2006), Buxhoeveden & Casanova 2002, and Preuss et al, 2003, and

these articles save me the task of restating all the evidence (see also Grimaud-Hervé 1997, Holloway et al., 2004a, Weaver 2005), and allow me to be more personal in my reflections.

BIOGRAPHICAL

Getting Out of Drexel, New Mexico, Los Angeles

My early college education started at Drexel Institute of Technology in Philadelphia, where I was enrolled in the cooperative program of metallurgical engineering. The cooperative program in the early 1950s meant half the year was spent in classes, and the other half was spent in industry, meaning some job appropriate to one's major. I was lucky enough to work at Armco Stainless Steel Co. in Baltimore, and while I never did succeed in inventing transparent stainless steel (from my boyhood science fiction fantasies), I was allowed to experiment with extreme temperatures on various alloys of stainless. Three and half years later, I had my first choice of an elective course, which could be either public speaking for engineers or reading (again) Huckleberry Finn and Tom Sawyer. I chose the former.

Family matters took me to the University of New Mexico in Albuquerque, and I was admitted on probation since my Drexel grades in calculus left something to be desired. I was thirsting for knowledge, and took a course in Anthropology and a course in Geology. These courses affected me profoundly, and I decided to become an anthropologist. My father rebelled, and to shorten this tale, I became a geologist, since it would be more likely that I could be employed in the latter pursuit than the former. Indeed, upon graduating in 1959 with experience as a roughneck in southwest Texan oil fields, and working in a geophysics lab, I was unable to get a job in geology, there being a major recession at that time. I ended up in Burbank, California working on heat resistant metals with Lockheed Aircraft. I remember going to night school and taking a course taught by Dr. Jack Prost at the University of California, Los Angeles, and a course on metal fatigue, just to keep the schizoid quality of my life in motion. A year later, I was admitted to the PhD program in Anthropology at the University of California, Berkeley; I departed Los Angeles, and gratefully moved to the Bay Area.

Getting out of Berkeley

My first mentor at Berkeley was Professor Sherwood Washburn, who was extremely kind to me in offering graduate student research support. Washburn insisted on my taking various anatomy courses until I suggested to him that I wished to take a course (then taught by Marian Diamond) in neuroanatomy. He was appalled and told me that he would no longer be my mentor if I studied neuroanatomy. I was flabbergasted: how could anyone understand how humankind evolved without un-

derstanding how the brain evolved? His response was that I would become too specialized and would not be a physical anthropologist, an argument I found entirely unconvincing. (However, if one looks at the textbooks in physical anthropology of the 1950s through the present, one will find it rare to see more than one page devoted to the brain, and what will be discussed is only the size of the organ. The recent text by Sanford et al. (2008) is an exception because one author, John Allen, is a neurobiologist who has also studied the lunate sulcus (Allen et al., 2006).

Washburn (and Irvin DeVore) had just come back from field studies in Ambolselie Game Park studying baboon behavior, and I think he wanted me to do the same. At the time, I thought primate studies were interesting, but I could not fathom using baboons as a theoretical model for understanding human evolution because I regarded each species a terminal end product of their own line of evolutionary development. Despite the warning, I took the neuroanatomy course and worked eventually with Diamond on the effects of environmental complexity on the cortex in rats. In 1966, I wrote the first paper on the effects of environmental complexity training on dendritic branching, using Golgi-Cox methods (Holloway 1966c).

My next mentor was Professor Theodore McCown, who was completely open and supportive regarding my burning interests in the brain. In 1964, I completed my dissertation, after much hassle with Washburn regarding a doctoral dissertation topic, and he was not a member of my committee. My dissertation was of the library variety, a review of quantitative relations in the primate brain [Holloway 1964; the first part of which was published in *Brain Research* (Holloway 1968), but the second half was mysteriously lost between the editors in Holland and Switzerland...]. I regarded endocast studies as possibly useless, and this gave me a burning desire to do empirical research and not armchair anthropology. Ironically enough, considering my experiences in geology and engineering, 1964 was a banner year for entering the job market, and I received several offers, most notably from Columbia University and Cornell. My first wife's folks were from New York, I took the Columbia position. My father had died prior to this, so this triumph was unknown to him.

Early Columbia University

My position at Columbia was mostly as a service to sociocultural anthropology, and I taught at both undergraduate and graduate levels. At that time, we were fully committed to the four-field approach, an approach now completely rejected by the cultural anthropologists at Columbia, the majority of which appear strongly postmodern, post colonialist, feminist, and political. I suppose in the earlier days, had I been more aggressive about constructing a biological anthropology program at Columbia, my stay would have been a more pleasant experience, but I was quickly isolated and marginalized at

Columbia, and remain so. Instead, I tried to stay true to scholarship and research, and not politics. Fortunately, I was (and am) saved by my mighty tenure.

Harry Shapiro from the American Museum of Natural History was an Adjunct, and he and I shared the responsibilities of educating graduate students in the department. I tried to continue my research on the effects of environmental complexity on dendritic branching; both my children referred to me as the “man who draws spiders”, as dendritic branching was done in my darkened office, tracing the dendrites against a sheet of paper attached to the wall, while manipulating the depth of focus on the microscope, there being no joy sticks or computers in those days. My hope was to do research on the quantitative histology of the cerebral cortex of different primates including humans, but no lab facilities were available. I approached my chairman, Morton Fried at the time, and asked for his interceding with the Biology Department, in the hope that they might provide some space and histological help. The answer was brutal: Cyrus Levinthal and Eric Kandel responded to Fried somewhat as follows: “if we do not know what is happening in the brain of *Aplysia*, the sea-slug, how could we possibly learn anything from the primate brain? No.” Kandel, of course, went on to win a Nobel Prize for his research. Admittedly, this was a hard lesson for me regarding the hubris of molecular biologists, but I survived it. My early papers in those days were attempts at synthesizing hominid brain evolution (Holloway 1966a, b; 1967; 1968; 1969a,b; 1972a; 1973a), and were of the armchair variety, although I still regard certain papers [1967, 1969a,b; 1975b; 1976; these two latter papers suggested that throwing with force and accuracy selected aspects of brain evolution, well before Calvin’s (1983) book, which took this idea much further] as some of my best attempts, despite their speculative hue.

On to Paleoneurology

Indeed, the above experience led me to seek a semester’s leave, and I and my family went off to South Africa to look at australopithecines and endocasts under the guidance of Professor Phillip V. Tobias. This was in 1969, and I guess my encounters with the New York police during the 1968 student demonstrations (I experienced testicular trauma at the end of the police blackjacks...) were a sympathetic note to Tobias and the apartheid policies in South Africa that he was fighting. In any event, the experience settled my career, and I became a dedicated paleoneurologist. Ironically, my dissertation had explicitly found endocasts to be useless, particularly when I found that descriptions of *Sinanthropus* were more primitive than *Homo erectus* from Java, despite being later in time.

I met Professor Raymond Dart there, who had so kindly sent me all of his reprints when I was at Berkeley, and I became convinced that the Taung endocast needed independent study, despite the detailed work of George Schepers (Schepers 1946). My main concern at the time

was finding an accurate volumes for the hominids (Holloway 1970a,b; 1973b), and trying to find an objective method(s) for deciding whether the cortex was reorganized as Dart had previously claimed (Dart 1925, 1926, 1956). This meant trying to determine the exact location of the infamous lunate sulcus, which is almost always the anterior boundary of primary visual cortex, or area 17 of Brodmann. Was it in a typical ape anterior position as Keith (1931) figured it, or was it indeed in a posterior, more human-like position as Dart had originally claimed? Little did I realize how contentious this question would turn out to be (30+ years!), as I acquired my long-standing opponent, Dean Falk. My estimate of the Taung endocast volume came out to 404 ml, double the volume of the 202 ml hemi-endocast I had constructed under the scrutiny of both Tobias and his fabulous assistant, Alun Hughes (Holloway 1970a). This value was quite less than the 525 ml previously reported, and I was pleased that both Alun and Philip did not find fault with my reconstruction. I particularly enjoyed working on the SK 1587 endocast from Swartkrans (Holloway 1972b) at the Transvaal Museum. Of course, nothing is static in paleoneurology, and the Taung endocast volume has been recently deflated (i.e., 382 ml) by Falk & Clarke (2007) in a paper filled with questionable methods, the most grievous being that they never bothered to define a midsagittal plane, an absolute requisite when trying to mirror-image a half-portion of an endocast (R. Holloway, manuscript in preparation). Falk et al. (2000) proposed some minor deflations of other australopithecine endocast volumes, and replies will ensue in the future.

Apparently, my skills were growing, and I believe Tobias let Louis Leakey know I could be trusted with the fossils. And so in 1971-1972, my family and I spent a sabbatical year in Kenya and South Africa working on australopithecines, habilines, and *H. erectus*. (So many anecdotes, so little space, but I shall always remember Louis’ kindness to me and my family when he was in such considerable pain.)

I returned to Kenya a couple more times to work mostly on the habilines, and my visit in the late 1970s, in particular, allowed me to make an undistorted endocast of the famous KNM-ER 1470 cranium. My observations on Broca’s area were recorded in Richard Leakey’s books (where I had determined that these were of a *Homo*-like form and found a cranial capacity of 752 ml.) My method scared the dickens out of Richard, because I filled the latex coated interior of the cranium with plaster of Paris to avoid any distortion while it was still in the cranial portion. When Richard saw this, he asked how in the hell I would get it out, and I told him to come by next day. He did, and lo and behold, there sat the perfect endocast, and there sat the undistorted cranium! (Given the existing breaks in the cranium, simply dissolving the glue joints and extricating the endocast without any damage to the fossil itself was an easy task.)

I believe it was during a 1978 visit, perhaps earlier, that Richard approached me in the Center’s lab,

and asked if Dean Falk could take some impressions (“peels”) from the cranium, and I said yes, but did not know that she would later publish her observations (Falk 1983a) without either acknowledging my agreement, or even mentioning my findings, which were mentioned in Leakey’s books (Leakey and Lewin 1978, Leakey 1981). At the time, I was supposed to be preparing a full description to be included in Bernard Wood’s monographic treatment of the Kenyan discoveries (Wood 1991). My results (Holloway 1983d), in very abbreviated form, were published in the journal *Human Neurobiology*, of which Doreen Kimura was a founder, but which did not survive very long as a journal. In the latter part of 1972 I went briefly to Indonesia to make endocasts from the newly discovered *Homo erectus* crania (Sangiran 4, 10, 12, and 17) in Dr. Teuku Jacob’s lab at Jogjakarta. The hospitality was splendid, but the weather abominable.

The Armchair Stuff, Compulsive Collecting of Data, and More Controversies

Meanwhile, throughout the late 1970s and early 1980s, my interests broadened to more theoretical approaches to human brain evolution (albeit my 1967 paper in *General Systems* was a major beginning), and are reflected in my paper published in 1979, where I tried to synthesize brain size, brain reorganization, structural and regulatory genes, and allometry in the volume edited by Hahn, Jensen and Dudek (Holloway 1979, in Hahn et al. 1979) (see Figure 1). At this time I was in the midst of conceptual battles with my colleague Harry Jerison, who appeared, at least to me, to have little regard for the concept of reorganization (Holloway 1969b, 1974; see also Holloway 1966a for a critique of the extra neuron model Harry had offered in 1963). I was honored to give the James Arthur Lecture on the Evolution of the Human Brain (Holloway 1975b), in which I suggested, as I had in my earlier (Holloway 1967) paper, that selection for social behavioral complexity was what had driven the evolution of the hominid brain. (I would have been wiser to have called it “Machiavellian Intelligence,” or the evolution of the “social brain,” the current popular jargon which ignores earlier publications). The paper on relative encephalization quotients (EQ) measures (Holloway & Post 1982) was an important contribution also. My 1969 paper, “Culture: A Human Domain,” was an attempt to describe what humans did as quite different from what other primates were doing, although if I were to rewrite that paper, I would find many more areas of behavioral continuity between our symbolically mediated behavior, and theirs. At that time, I thought the basis of human language, the use of arbitrary symbols, had aspects of cognitive processes that were shared by stone tool making.

A recent paper by Stout et al. (2008) using fMRI on Nick Toth while he was making stone tools indicates a possible connection between language sites in Broca’s and Wernicke’s regions of the cerebral cortex and stone tool making, something I had suggested in the above

paper on the possible similarities, cognitively, between language and tool-making behavior.

I had, by 1978, made close to 200 latex rubber endocasts of modern humans and apes and monkeys, and compulsively collected thousands of data points on a comparative collection of these endocasts, including fossil hominids, apes, and modern humans, using a stereoplotter that was suggested to me by Dr. Alan Walker. This gadget measured the dorsal surface of the endocast every ten degrees in two planes, and took the distance from a homologous central point to the endocast surface, thus avoiding problems with allometric corrections. These results (Holloway 1981c) indicated that the region of greatest shape difference was in the posterior parietal region, which I thought was a buttress to my belief that relative expansion of the posterior parietal lobe had occurred early in hominid evolution, and was indicated on the Taung endocast, as well as the AL 162-28 specimen from Hadar, Ethiopia (Holloway 1983a, Holloway & Kimbel 1986). This was also a time in which I published my observations on the Spy Neandertal endocasts, the Omo endocast, and the Solo endocasts (Holloway 1980a,b; 1981b,d,e; 1983b; 1985b). More recently, I have been making endocasts of modern *Homo sapiens*, from sectioned crania in the bone lab at Columbia, and from the Von Lauschan collection at the American Museum of Natural History, adding roughly another 75 specimens to the growing sample size of the 15-20 that I did much earlier. Included among these latter specimens are 5-6 microcephalic endocasts (thanks go to Milford Wolpoff, who lent the crania to me) and a couple of extreme cranial deformation examples. These have all been done using “Dentsply Aquasil LV” dental impression material, which has, hopefully, a much longer shelf life than the earlier latex endocasts, many of which have deteriorated. Thanks to the efforts of Dr. Janet Monge and Dr. Tom Schoenemann, these endocasts (not the more recent human ones) have been scanned.

THE LUNATE SULCUS

Dart (1925,1926,1956) had believed that the Taung child’s endocast showed definite signs of reorganization toward a more human-like condition on the basis of his belief that the lunate sulcus, which defines the anterior boundary of primary visual striate cortex, Brodmann’s (1909) area 17, was visible on the Taung natural endocast. The cortex anterior to the lunate sulcus would be the parietal and temporal lobe association cortex, where higher cognitive functions occur. I trumpeted the concept of reorganization in my dissertation and early papers (e.g., Holloway 1966b, 1967,1979) and, indeed, still believe the concept to be of value as an additional set of quantitative changes that are not directly caused by brain size increase alone. How the brain is organized as well as its size is of great importance. (I came to this conclusion before 1964 when I made a seminar presentation in one of Washburn’s classes, demonstrating that some human

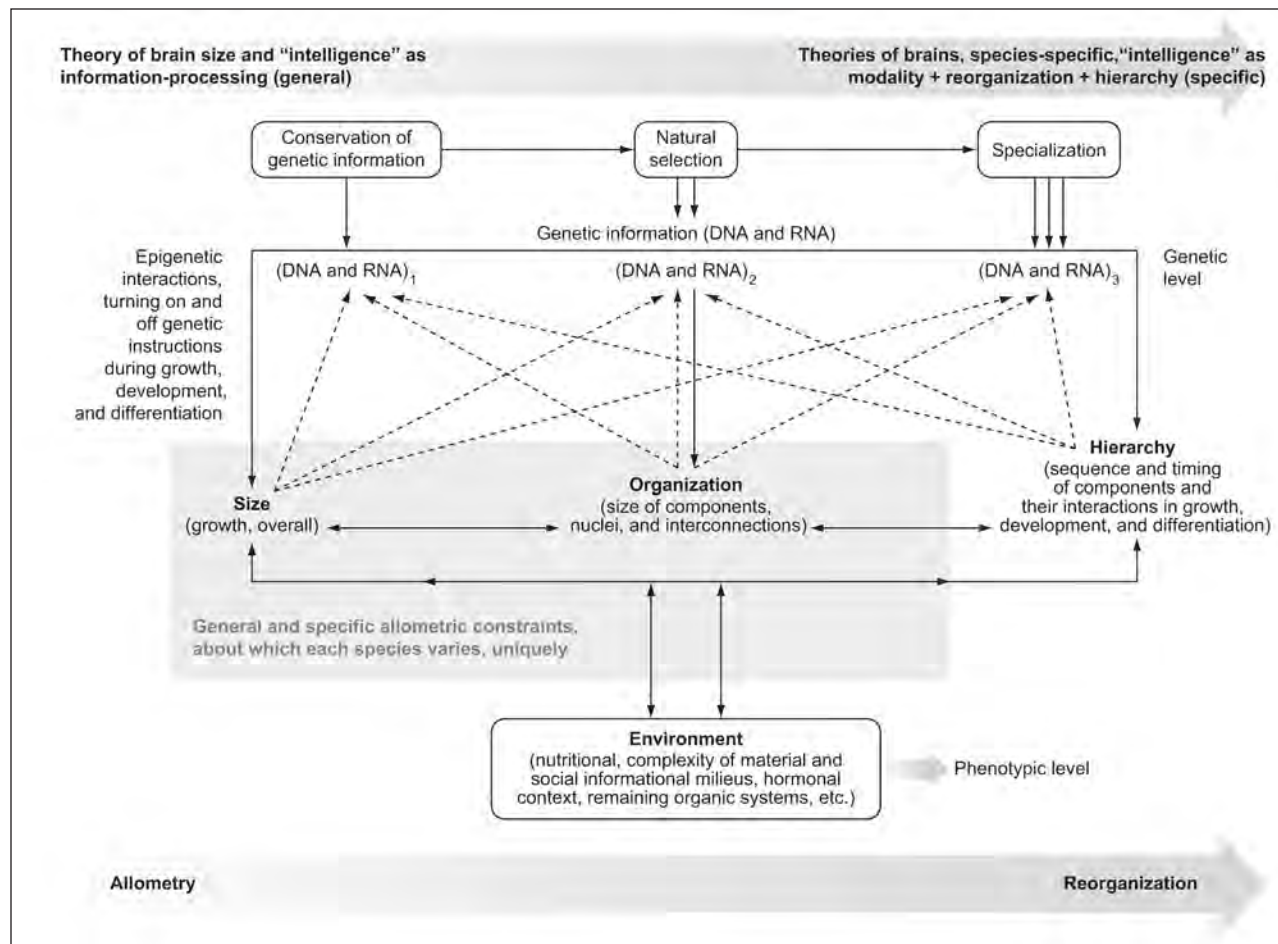


Figure 1 The brain is a composite of size, organization, and hierarchy, which is acted on at the phenotype level by natural selection throughout the life of the organism. Mathematical formulations and prediction tests are so far applied only to the shaded box containing size and organization. This model conceives of natural selection variously acting on three subsets of genetic information (DNA+RNA123), which also interact with each other and the developing and differentiating organism in epigenetic fashion. Allometrists and brain mass theorists are almost totally working within the framework of the left-hand side of the diagram.

microcephalics with brain sizes that some gorillas might deride as diminutive were nevertheless able to talk. That meant to me that something in their brains was organized differently than in the great apes.) Most biological anthropologists ignore organization and cathect on brain size, which is a bit unscholarly. Dart, after all, had studied under Grafton Elliot Smith (see Smith 1904), the major claimant and champion of the lunate sulcus, and Dart himself wrote his dissertation on the evolution of the turtle brain, which of course has no lunate sulcus. This history was covered (Holloway 1985a; see also Holloway 1988a,b; Holloway et al. 2001a,b; 2003; 2004b) because Dean Falk had previously restudied the Taung endocast and decided that the lunate was represented by a small dimple placed well anterior of the lambdoid suture, and even more anteriorly than would be found in almost all chimpanzees, gorillas and orangutans all without any measurements based on a comparative sample (Falk 1980;1983a,b,c; 1985; 1989). It was, however, the question of a possible lunate sulcus in the Hadar AL 162-28 A. afarensis that received the most unwelcome

confrontation with Falk. She (Falk 1983b) incorrectly oriented the Hadar specimen so that the cerebellar hemispheres protruded beyond the cerebral cortices. Further, the depression along the lambdoid suture region, which she regarded as the lunate sulcus, was placed in an anterior, ape-like position, which simply reflected her own bias. She had apparently accepted my earlier (Holloway 1983c) identification of the posterior end of the interparietal sulcus (IP), which usually abuts the lunate sulcus. I was reluctant to accept the depression as a true lunate sulcus because I had found many of my Pan endocasts had a distinct "sulcus" just immediately anterior to the lambdoid suture, which I name the "prelambdoid pseudosulcus", and which is actually caused by the posterior and inferior lip of the parietal bone. Clark et al. (1936) showed this artifact very clearly when they rubbed off the charcoal soot from the endocast surface and compared the endocast to the actual brain. Later, Bill Kimbel and I (Holloway & Kimbel 1986) tried to set the matter straight by pointing out Falk's error of orientation and the fact that the distance between her purported lunate

Table 1 Changes in the reorganization of the hominid brain based on endocasts (After Holloway et al. 2004a)

Brain changes (reorganization)	Taxa	Time (mya)	Endocast evidence
Reduction of primary visual striate cortex, area 17, and relative increase in posterior parietal cortex	<i>A. afarensis</i>	3.5 to 3.0	AL 162–28 endocast
	<i>A. africanus</i>	3.0 to 2.0	Taung child, Stw 505 endocast
	<i>A. robustus</i>	~2.0	SK 1585 endocast
Reorganization of frontal lobe (third inferior frontal convolution, Broca's area, widening prefrontal)	<i>Homo rudolfensis</i>	2.0 to 1.8	KNM-ER 1470 endocast
	<i>Homo habilis</i>		Indonesian endocasts
	<i>Homo erectus</i>		
Cerebral asymmetries, left occipital, right-frontal petalias	<i>H. rudolfensis</i>	2.0 to 1.8	KNM-ER 1470 endocast
	<i>H. habilis</i> , <i>H. erectus</i>		Indonesian endocasts
Refinements in cortical organization to a modern <i>Homo</i> pattern	<i>H. erectus</i> to present?	1.5 to 0.10	<i>Homo</i> endocasts (<i>erectus</i> , <i>neanderthalensis</i> , <i>sapiens</i>)

Table 2 Major cortical regions involved in early hominid evolution (with major emphasis on the evolution of social behavior and adapting to expanding environments) (After Holloway et al. 2004a)

Cortical regions	Brodman's areas	Functions
Primary visual striate cortex	17	Primary visual
Posterior parietal and anterior occipital (peri- and parastriate cortex)	18, 19	Secondary and tertiary visual integration with area 17
Posterior parietal, superior lobule	5, 7	Secondary somatosensory
Posterior parietal, inferior lobule (mostly right side. Left side processes symbolic-analytical)	39	Angular gyrus perception of spatial relations among objects, face recognition
Posterior parietal, inferior lobule (mostly right side. See above)	40	Supramarginal gyrus spatial ability
Posterior superior temporal cortex	22	Wernicke's area, posterior superior temporal gyrus, comprehension of language
Posterior inferior temporal	37	Polymodal integration, vision, auditory input. Perception and memory of objects' qualities
Lateral prefrontal cortex (including mirror neurons)	44, 45, 47 (also 8, 9, 10, 13, 46)	Broca's area (Broca's Cap), motor control of vocalization, language
		Complex cognitive functioning memory, inhibition of impulse, foresight, etc.

Table 3 Major size changes in human brain evolution (After Holloway et al. 2004a) aAllometric means related to body size increase or decrease, whereas nonallometric refers to brain size increase without a concomitant body-size increase.

Brain changes	Taxa	Time (mya)	Evidence
Small increase, allometric ^a	<i>A. afarensis</i> to <i>A. africanus</i>	3.0 to 2.5	Brain size increases from 400 ml to 450 ml, 500+ ml
Major increase, rapid, both allometric and nonallometric	<i>A. africanus</i> to <i>Homo habilis</i>	2.5 to 1.8	KNM-1470, 752 ml (Ca 300 ml)
Small allometric increase in brain size to 800 ml–1000 ml (Assumes <i>habilis</i> was KNM 1470-like)	<i>Homo habilis</i> to <i>Homo erectus</i>	1.8 to 0.5	<i>Homo erectus</i> brain endocasts and postcranial bones, e.g., KNM-ER 17000
Gradual and modest size increase to archaic <i>Homo sapiens</i> mostly nonallometric	<i>Homo erectus</i> to <i>Homo sapiens neanderthalensis</i>	0.5 to 0.10	Archaic <i>Homo</i> and neandertal endocasts 1200 to 1700+ ml
Small reduction in brain size among modern <i>Homo sapiens</i> , which was allometric	<i>Homo s. sapiens</i>	0.015 to present	Modern endocranial capacities

sulcus and the occipital pole was only 15 mm, roughly half the distance that occurs normally in chimpanzee brains of roughly the same volume, i.e., 385-400 ml. Measuring the distance between the occipital pole (the most posterior point on the occipital lobe) and the lunate sulcus on ~80 chimpanzee hemispheres, suggested that the Hadar A. afarensis AL 162-28 specimen was almost 3 standard deviations outside of the mean chimp value, which varied between 25 and 30+ mm. (Holloway et al. 2001a,b, 2003, 2004b).

This brouhaha was part of a larger theoretical issue, i.e., whether an increase in brain size must necessarily precede any organizational shift in brain components, or a reduced primary visual cortex relative to the size of the brain. Jerison (1990), Falk (1983b), and Armstrong et al. (1991) appeared to take the position that the brain did not reorganize until there was an increase in brain size, and I was taking the position, as had Dart before me, that reorganization took place prior to the increase in brain volume. I believed then and remain convinced today that the earliest hominids, i.e., *Australopithecus africanus*, *A. afarensis* and *A. garhi*, had brains definitely different than any ape's, despite their small size, and that natural selection had worked on more complex social behaviors (Holloway 1967, 1975b), as would be expected if the relative reduction in the primary visual cortex (PVC) signaled a relative increase in parietal association cortex.

Hopefully, the newer *A. africanus* brain endocast of Stw505 (from Sterkfontein, South Africa), with its clear-cut posterior location of a lunate sulcus (Holloway et al. 2004b) will convince most skeptics that, indeed, the australopithecine hominids had reorganized brains despite their overlapping in size with ape brains. Whether biological anthropology textbooks will recognize this possibility is another matter. As near as I can determine, many of the textbooks in biological anthropology only discuss brain volume in hominids (Sanford et al. 2008 being an exception).

In 1990, I had the honor of being a participant in the Fifth Interdisciplinary Fyssen Symposium, in which I presented a paper "Toward a synthetic theory of human brain evolution", eventually published in 1995 (Changeux and Chavaillon, 1995). This was the first time I tried to present a framework where brain size increases were interspersed with reorganizational changes. The point here was to suggest that different selection pressures occurred at different times regarding both size and organization. Falk, in her usual sarcastic manner characterized the paper as the same old stuff (Falk, 1997) even though this was truly a newer synthesis. If she has disagreed with my premises and outlines, I would have been pleased and would have regarded such as a positive step in our skirmishes, but instead it was just an opportunity to denigrate and ignore my ideas without ever providing counter-evidence, or discussing what was wrong with the data presented.

Tables 1, 2, and 3 (updated from Holloway et al. 2004a) present my recent synopsis of the evidence I pre-

sented then.

Another major brouhaha with Falk and her colleagues emerged after White & Falk (1999) asserted that the Omo L338y-6 australopithecine from Ethiopia had an occipital-marginal sinus drainage pattern that allied the specimen to robust australopithecines. Having studied and described the original specimen (Holloway 1981b), and not a cast of a cast, I was amazed to see this publication and hear these claims. I examined my original endocast reconstruction and, as I clearly remembered, could find no trace of such a sinus. Tim White and his colleagues were kind enough to secure a new mold of the posterior section of the newly cleaned Omo specimen and serially sectioned it through the purported region claimed by White & Falk. There was absolutely no sign of a marginal sinus on this specimen (Holloway et al. 2002). The presentation of these findings at an American Association of Physical Anthropology meeting caused an extremely emotionally charged encounter between me and David DeGusta on the one side and Falk and White on the other, each armed with their own endocast copies. (Fortunately, at 430 ml, the endocasts could not do much damage even if thrown, despite being made of plaster.)

One last example might be of interest: in *Braindance*, (Falk 2004, pp. 165-66) discusses her "radiator hypothesis" (Falk 1990) as a proven hypothesis and then provides a partial quote from my critique which appeared in *Brain and Behavioral Sciences* (Holloway 1990a), focusing on my belief that her hypothesis had the structure of a simple just-so story and was unduly speculative. What Falk then left out were my eight points regarding the lack of any empirical demonstration that show an increase in blood cooling associated with cranial capacity increase, upon which the fossil evidence is simply mute. Nor did she ever bother to respond in any detail to Kimbel's (1984) paper and (1990) critique. My paper (Holloway 1980c) on a re-analysis of the Pakkenberg & Voigt (1964) data on Danish brain weights which showed very clearly on p. 113 that body size alone could not explain the difference in male/female brain weights, a result she also finds in her 2004 edition of *Braindance*. Our work (de Lacoste-Utamsing & Holloway 1982; Holloway 1990b; Holloway et al. 1993) on the corpus callosum was not mentioned in her discussions of sexual dimorphism, nor our work on cerebral asymmetries (Holloway & de Lacoste-Lareymondie 1982).

On a more positive note, I was honored in 2007 with a two-day conference ("The Human Brain Evolving: Papers in Honor of Ralph L. Holloway") held on my behalf in Bloomington, Indiana, where 20+ colleagues came together to give papers on various aspects of brain evolution. This conference was sponsored by the Stone Age Institute and Indiana University under the leadership of Drs. Nick Toth and Kathy Schick and also organized by two former students, Drs. M.S. Yuan and D.C. Broadfield. I take this as a validation of my research.

A Brief Aside on What Constitutes Evidence for Hominid Brain Evolution

This little battle, however, brings forth an interesting question about how valuable paleoneurology and comparative neuroanatomy are in discussing hominid evolution. As I have tried to point out in several places (e.g., Holloway et al. 2004a), the only direct evidence for hominid brain evolution is paleoneurology, the study of endocasts, despite the paucity of that information. Perhaps, in the future, molecular neurogenetics might be able to provide more details regarding what elements of the brain (neurotransmitters to gross neuroanatomy, i.e., gyri, sulci, fiber tracts, overall size; see, for example, Sherwood et al. 2003 regarding Broca's homologue in chimpanzees) have changed during hominid evolution. At the moment, however, such data are not available, and comparative neuroanatomy remains the study of extant (not extinct) animal brains, each of which have undergone their own separate evolutionary path development to their present condition, whatever that may be.

Give these questions some serious thought: Is today's chimpanzee brain (against which we do so many comparisons, whether in terms of size or structure) the same as that of the last common ancestor of hominids and chimps? Has the chimpanzee brain evolved during the past 5-7 million years? If so, are our comparisons with the present day chimpanzee on target? Should the same questions be asked of other areas of comparative primate comparisons, e.g., dentition, locomotion, behavior? The incomplete brain endocast of *Proconsul africanus*, of roughly 12 mya, appears to show an anthropoid pattern of having the lunate sulcus in an anterior position (which all extant anthropoids share) (Radinsky 1974, 1975, 1979). So perhaps with this characteristic, the derived condition (lunate sulcus in a posterior position, indeed an autapomorphy) for *Homo* is a reasonable conclusion that can be translated into functional (i.e., behavioral) terms, such as what we know about the role of posterior parietal association cortex in perception of objects, their position, recognition of faces, social behavior, and aspects of language reception. Herein lies the great value of comparative neuroanatomy: It is the essential link between neurobiological and behavioral variation writ both large and small. Still, where are the studies that link what we know of species-specific behavioral patterns and neuroanatomy in the primates? Where is the research that explains, neurologically, the behavioral differences between chimpanzee, gorilla, and orangutan. Even trying to describe the behavioral differences between *Pan troglodytes* and *Homo sapiens* is difficult, despite clear-cut differences in brain anatomy that have been described. I ask these questions not to detract from comparative studies, but simply in the hope of sharpening our analytic abilities and to caution against the wholesale use of extant species' morphology in trying to understand human brain evolution. So much of the primate behavior I have read and the speculation that follows regarding hominid

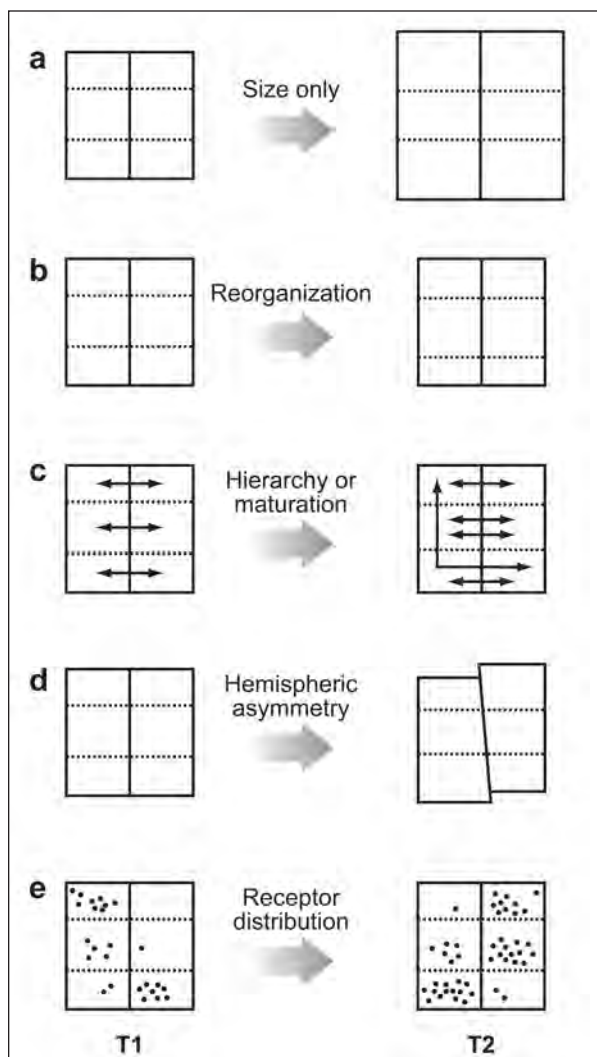


Figure 2 Figure 2 shows several different scenarios where it is possible to reorganize the brain without any apparent increase in size, from T1 (time 1) to T2 (some time after an arbitrary interval of evolution). The horizontal dashed lines represent the central sulcus and lunate sulcus, respectively, with the frontal lobe facing upward. The vertical line divides the two cerebral hemispheres. Thus in part (a), Time 1 to Time 2 involves an increase in size without changing any parts of the brain. In part (b), the lunate sulcus moves posteriorly, but brain size remains constant from T1 to T2. In part (c), different fiber tracts mature at different times and differentially increase or decrease. In part (d), the two hemispheres are asymmetric (left-occipital and right-frontal width petalias), but overall brain size remains constant. In part (e), brain size is constant, but neuroreceptors are differently distributed between T1 and T2 (*Praire* and mountain voles, and oxytocin receptors come to mind.). Needless to say, some of these scenarios cannot be detected on endocasts (parts c and e, and sometimes b). These are a few alternative ways to reorganize a brain without increasing its size.

evolution seem to be based on the premise that the chimpanzee has had no further evolution since our split with Pan-like hominoids roughly 7 MYA.

Enter the “Hobbit”, *Homo floresiensis*: an ongoing tango

In the above context, a parallel problem exists with respect to comparing modern-day human pathology with ancient hominid discoveries. The recent controversy over the “hobbit” *Homo floresiensis*, whether or not it is a true new species of hominid (see Brown et al. 2004 for original claim and description) or a case of pathology, has not been settled (e.g., Henneberg & Thorne, 2004; Hershkovitz et al. 2007; see also Richards 2006). I have spent more than two years studying the endocast of this creature and am still sitting on the fence as to whether or not it is a case of microcephaly or some other pathology, or a new species (Holloway et al. 2006). As cogent as the arguments of Jacob et al. (2006) and Martin et al. (2006a,b) might appear, I agree with the depictions in Falk et al. (2005) of the virtual endocast compared to modern *Homo sapiens*, *Homo erectus*, chimpanzee, and microcephalic *H. sapiens* [an unfortunate choice of one extremely small microcephalic (278 ml)], and the observation that there are no microcephalic brains yet published that show the suite of features found on the “hobbit” endocast, although the example by Martin’s et al. (2006b) of the Indian microcephalic comes very close. What I see are : (a) extreme platycephaly, (b) extremely thin and protuberant gyri recti of the prefrontal lobe, (c) appearance of a smallish prefrontal lobe and temporal lobes as seen on the undistorted left side, (d) unusually spread cerebellar lobes, and (e) a peculiar triangular-shaped occipital sinus. These observations leave me sitting on the proverbial fence regarding a new species or pathology argument. The point here is that modern pathology (e.g., primary microcephaly) may not match what appears to be a possible pathology 13-18 thousand years ago. The full spectrum of microcephaly and other pathological conditions affecting the brain has not been available to study or illustrated in recent articles. My consultations with several pediatric neurologists suggest that they see it (the “hobbit”) as pathological, but it does not match what they’ve seen in cases of true primary microcephaly. The original “virtual endocast” published by Falk et al. (2005) shows that they selected the damaged and inferiorly deflected right temporal lobe as a model for their “virtual endocast” when it is the left temporal lobe that was intact, and which, incidentally, appears rather small in comparison to the total size of the endocast. Their 417 ml volume is more likely to be 400 ml. In any event, this tango will not end until more of these creatures are discovered and described.

Having been kindly provided with an endocast made from the stereolith of the LB1 cranium by Peter Brown, I have never once been asked to referee any papers on the LB1 endocast. At the time of these writings Dean Falk and I are among a small number of practicing

paleoneurologists (actually, so are Emiliano Bruner and Dominique Grimaud-Herve, and Anne Weaver) to have worked on these endocasts. Promises made by Mike Morwood to receive the CT scan data so that I could make an independent study of the endocast have never materialized, and I strongly argue that independent study is sorely needed. But this tango is a common occurrence in paleoanthropology, where access to fossil specimens tends to be rigorously guarded (e.g., Atapuerca, Dmanisi, etc.)

Brain Variation and Tottering on the Edge of Political Incorrectness

The 1980s became a period of intensive data collecting. One of the first steps was requesting from Pakkenberg in Denmark the data from their study of Danish autopsies (Pakkenberg & Voigt 1964). These authors kindly sent me the data which I reanalyzed in 1980 (Holloway 1980c) because I was interested in exploring ranges of variation within a species of derived neuronal statistics such as extra numbers of neurons, EQs (encephalization quotients), and relative brain size. I was intrigued by techniques such as partial correlations, and was getting interested in possible sex differences in loss of brain weight with age and EQs, and indeed was able to show that the difference between male and female brain weights could not be fully explained by differences in body size. I was surprised to find that in males, the brain correlated significantly with stature, but the same effect did not hold for females.

At this time I had a brilliant graduate student, Christine de Lacoste-Lareymondie who was doing her dissertation on the distribution of fibers in the human corpus callosum. I remember approving and encouraging this project but insisted that she had to find out as much as possible about the variation of the corpus callosum, including variation by sex. From a small sample she had collected, Kitty discovered that females appeared to have larger corpus callosa relative to brain size than did males and that the splenium in particular seemed more bulbous in females than in males. We thought this was a very intriguing find and sent a manuscript to Science. Science then asked for the data because, indeed, our sample was very small. They accepted the paper (de Lacoste-Utamsing & Holloway 1982), and this created a minor cottage industry for the next couple of decades as to whether or not the corpus callosum was indeed relatively larger in females. Many people argued that it was equal, but seldom used our methods or seemed to understand we were talking about a relative size (Holloway et al. 1993). Blistering commentary depicting us as sexist and worse came [e.g., Fausto-Sterling’s (1985) “Myths of Gender”; Bishop and Wahlsten (1997)]. We also were unaware that Bean (1906) had earlier made a similar finding, and his being a well-known racist provided these authors with the necessary guilt by association, which social scientists so savor. Finally, thanks to the sophisticated analytic paper by Richard Smith (2005)

in Current Anthropology, a case to legitimate ratio data was proven. In those days, sex differences in the brain were really politically incorrect, particularly as a vast sea of feminist literature was being produced. Today, sex differences in the human brain are commonly accepted (e.g., Gur et al. 2002; Kimura 2003; Haier et al. 2005; Narr et al. 2007). These experiences were not pleasant, however, and I found myself sort of a pariah in one realm and a hero in another, and it had a lasting effect on my quest for truth, replication, and letting data trump emotional biases. I am afraid the same principles apply to possible ethnic (“racial”) differences in the brain, because without knowing how the brain varies in the human species, it is impossible to understand fully how this organ evolved. Furthermore, given the sensitivity of the brain to environmental insult from conception on, sound knowledge of such variation, whether in overall size, maturation schedules, neuroreceptor sites, etc., is required to determine the most efficient therapeutic measures to take to ensure proper nutrition and other nurturance for the developing brain. A full understanding of the respective roles and interplay of nature and nurture particularly with respect to worldwide distributions on intelligence tests scores is impossible without knowledge of how the human brain varies and why it does so. It would be nice if human variation could be celebrated as our most precious evolutionary heritage and hope instead of prohibiting the study of our variation.

In the late 1970s and early 1980s I collected autopsy data from the Pathology department at Columbia’s College of Physicians and Surgeons (now CUMS). I was interested in age, sex, and ethnic effects on brain size changes through time as might be found in cross-sectional data. Roughly 2000 cases were collected, without personal identifications, and all cases of brain pathology were culled out of the data set. The results, unpublished, were roughly the same as found in Ho et al. (1980, 1981) work on a sample from Milwaukee, which indicated that African American brains were statistically significantly lower in weight than were European American brains, that is, of course referring to the mean values. Ho et al. (1980) concluded that cultural effects were the reason behind the difference. Interestingly, Lieberman (2005) in his review of Rushton’s (2000, 2002) claims regarding ethnic (racial) differences in brain sizes and behaviors ignored this work by Ho et al. Needless to say, Tobias’s oft-cited paper on brain weight collecting methods (Tobias 1970) was cited to claim that autopsy data on brain weights are useless. Unfortunately, however problematic such data are, one tends to forget that autopsies are not done discriminately. Once the body is on the morgue slab, the autopsy is conducted in exactly the same fashion irrespective of the cadaver’s race, and thus comparisons of such data collected by the same pathologist or medical examiner are surely valid, depending on which variables are being compared. Comparing data collected by different examiners may of course be difficult, and perhaps statistical meta-analyses would be in order. To

my knowledge, none exists.

Simply put, this research area remains an intensely political and near-suicidal enterprise. (Indeed, one colleague suggested I should incinerate the data; another suggested this kind of study had led to his relatives perishing in the Nazi concentration camps.) The continuing gap in African American and European-descent test scores on various cognitive tests (particularly IQ) throughout the US and the world (Lynn & Vanhanen 2006) is a source of tremendous concern and acrimonious debate. Indeed, Jon Marks claimed he “outed” me as a “racist” (Marks 2000; see Holloway 2000 for reply) in his biological section of the American Anthropologist Newsletter, because I had the temerity to defend Arthur Jensen against Loring Brace’s assertion that Jensen was a bigot. I had read a lot of this literature (e.g., Jensen 1998) including Jensen’s infamous 1969 piece in the Harvard Law Review, and did not find him a racist. I remain appalled at our discipline which regards him as such and which invented the appellation “Jensenism” to tar and feather him. I remain interested in the possibility that different populations have variation both in their brains and behavior, but the issue is so politically incorrect that one cannot even approach such a study with anything but trepidation. (For example, the Annual Review article by Freedman & DeBoer, 1979, was declared by socio-cultural students at Columbia as racist, and therefore not to be read!) If one disbelieves there are populational differences in the weight and/or structure of the brain, they should examine the papers by Klekamp and his colleagues, particularly regarding the finding that the primary visual striate cortex of Australian aborigines is significantly larger than in brains from people of European descent (Klekamp et al. 1994). This paper is, to my knowledge, the only paper published since the 1930’s demonstrating a real difference in brain morphology between modern populations (the last compilation of some of these earlier studies on brain morphology differences between different populations can be found in C.J. Connolly’s 1950 book, *External Morphology of the Primate Brain*, which is a sort of bible for most people working in paleoneurology. See also Kochetkova 1978.) Of course, there is Gould’s *Mismeasure of Man*, another bible of sorts, but which should be read along with Michael’s (1988) Current Anthropology paper which found that Morton’s rankings were correct and which Gould ignored in his later editions of the same book. There is certainly no evidence that Paul Broca used his elbow on the scales when measuring brains of peoples of European descent!

Additional autopsy data sets await my attention, including some 5,000 cases from Hong Kong collected by my colleague Philip Beh, and ~7,500 cases from Singapore, the latter of multiple ethnicities. I hope to get to these data sets when I retire.

POSTSCRIPT AND ACKNOWLEDGMENTS

On November 27, 2007, the science section of the New York Times ran a profile of me and my work (Balter 2007). While grateful that I could make it within the New York Times, I wish more had been said of my other interests in brain research. Thus far, neither my colleagues in the Anthropology department nor the Columbia University Administration have acknowledged the article or the previously mentioned conference.

I am very grateful to the many colleagues who mentioned the honor, and to the many students I have encountered over the decades that have truly rewarded me with their intelligence, wit, and support as well as the temerity to disagree. In particular, I mention Michael Yuan, Douglas Broadfield, Chet Sherwood, Francys Subiaul, Sam Marquez, Lynn Copes, and Jill Shapiro, who read earlier versions of this paper and who offered many useful corrections, as well as former students Christine de Lacoste-Azziz, Peter Heilbronner, Jeffrey Schwartz, Este Armstrong, Joan Witkin, Jason Kaufman, and Peter Post. My special thanks go to Nick Toth and Kathy Schick for their interest in my work and their friendship, and for hosting the conference at the Stone Age Institute. I am grateful to Carole Traviz-Henikof for her role in that honor. The encouragement and friendship of the late Clark Howell are sorely missed. My colleagues Janet Monge, Alan Mann, Jason Lewis, Robert D. Martin, Alan Walker, Dominique Grimaud-Hervé, Emiliano Bruner, James Rilling, Tom Schoenenmann, Patrick Gannon, Daniel Buxhoeveden, John Allen, Katerina Semendeferi, Milford Wolpoff, John Hawks, Anne Weaver, and Carol MacLoed deserve special mention. To Peter Brown goes a special thanks for allowing me to study the LB1 endocast, regardless of whether I agree with him! I would not have been able to make any contributions to paleoneurology without the cooperation and hospitality I received from the Leakey family in Nairobi, Kenya, and the staff at the Center. I owe a similar debt to the late Raymond Dart, Phillip V. Tobias, Bob Brain, the late Alun Hughes, the late Teuku Jacob and Ralph von Koenigswald, A. Leguebe, Roger Saban, Yves Coppens, Ian Tattersall, Eric Delson, Gary Sawyer of the AMNH, and Theya Molleson of the BMNH. I continue to enjoy the collegiality and support of Tim White, Bill Kimbel, Yoel Rak, Gen Suwa, Berhane Asfaw, W. Henry Gilbert, Scott Simpson, and all their colleagues in Ethiopia, and I look forward to continuing studies on more hominid endocasts from there. To Chuck McAlexander and Dr. Graham Kavanagh go special thanks for their support. Lastly, my wife, Dr. Daisy Dwyer, has given me so much and put up with it all.

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