The Evolution of the Hominid Brain

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Abstract

The evolution of the human brain has been a combination of reorganization of brain components and increases of brain size through both hyperplasia and hypertrophy during development, underlain by neurogenomic changes that have involved epigenetic changes largely effecting regulation of growth dynamics. While both genomics and comparative neuroanatomical studies are invaluable to understanding how brains and behavior correlate, it is paleoneurology, based on endocast studies (chapter "▶ Virtual Anthropology and Biomechanics," Vol. 1), which are the direct evidence demonstrating volume changes through time. Some convolutional details of the underlying cerebral cortex do appear on

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the endocranial surface. These details allow one to recognize reorganizational changes that include (1) a reduction of primary visual cortex and relative enlargement of posterior association cortex, (2) expanded Broca's regions, and (3) cerebral asymmetries. The size of the hominid brain increased from about 450 ml 3.5 Ma ago to our current average volume of 1,350 ml, with a slight reduction since Neolithic times. Many more data from additional fossils will be necessary to decide how and when these two changes through time occurred and whether these were gradual or punctuated.

Introduction

The evolution of the human brain has largely been a matter of integrating both increases in the size of the brain and the brain's organization through the past 3–4 myr mainly based on species of the genus *Australopithecus* and two of its species, *A. afarensis* and *A. africanus*.[1] Earlier possible hominin forms such as *Sahelanthropus* or *Ardipithecus* in the time range of 3–6 myr do not have sufficient endocranial remains to do more than estimate volumes. Three lines of evidence are used by paleoneurologists to ascertain how these events might have occurred: (a) direct evidence from the brain endocasts of fossil hominids (paleoneurology) and (b) the indirect evidence from comparative neuroscience, where variations in brain structures can be related to variations in behavior and be compared between species. This latter evidence is "indirect" because extant living animals are not ancestral to humans and have undergone their own evolutionary changes. Indeed, the last common ancestor for apes and the hominid line existed some 5–7 Ma ago. (c) Newer neurogenomics evidence also promises to provide important clues to how and when certain aspects of brain changes occurred during human evolution (e.g., Preuss 2012; Zeng et al. 2012).

Our best paleoneurological evidence suggests that the human brain evolved from an early hominid 3–4MY, *A. afarensis*, having a size of roughly 400 ml to our present average of 1,330 ml. These brain size increases, at different taxonomic levels, were mostly allometric, i.e., related to body size, but not always. Integrated with these changes in brain size was reorganization of the cerebral cortex, as well as changes in subcortical structures such as the hippocampus, amygdala, etc., to mention a few important structures that relate to aspects of social behavior but that cannot be seen on endocasts. Reorganization simply refers to both qualitative and quantitative changes through time of neural structures. Endocasts, of course, cannot provide information regarding neural variables such as subcortical volumes, cell densities, dendritic branching and connectivity, or any neurochemical or neurophysiological information. Thus from the point of view of knowing what

[1]This paper is adapted and expanded from an earlier chapter written for the Encyclopedia of Human Biology, 3rd Ed. Elsevier, In press.

exactly the data indicate regarding human brain evolution, the direct evidence of endocasts is critically important, however poor the data they contain actually may be.

At least three areas of the reorganization of the cerebral cortex were affected at different times: (a) a relative reduction of primary visual striate cortex (V1, PVC) and an attending relative increase in posterior parietal association cortex; (b) a change in Broca's region, resulting in a more humanlike pattern; and (c) increasing degrees of cortical asymmetry, as well as increases in overall brain size and number of neurons.

How exactly did the human brain evolve, and when did changes in it happen? Obviously, to answer this question fully would require a time machine and thousands of generations of observations to ascertain both the variability and direction of selection pressures in the past. We can, however, flesh out an initial understanding of how we got to be the animal *par excellence* that utilizes its brain for intelligent rationalizations, based largely on the use of arbitrary symbol systems and on behavioral adaptations involving a complementary social existence between males and females permitting prolonged infant growth and nurturance (chapters "▶ Great Ape Social Systems" and "▶ Theory of Mind: A Primatological Perspective," Vol. 2). The evidence consists of two components: (a) the "direct" evidence from the fossil record and (b) the "indirect" evidence of the comparative neuroscientific record of extant living animals, particularly those most closely related to us such as the chimpanzee and bonobo. There is also a third possibility: since the Human Genome Project has sequenced almost all of the genetic code, the future study of evolutionary neurogenomics might provide more data about the actual genetic history of our genus through time, as well as that of the great apes mentioned above (see, e.g., Hernando-Herraez et al. 2013; Gokcumen et al. 2013). As this latter possibility is little more than a gleam in our eye at present, this article will concentrate on the evidence provided by the first two components.

Lines of Evidence

Direct Evidence

The term *paleoneurology* is used to describe evidence relating to the size and morphology of the casts made from the inside of actual fossil cranial remains. Occasionally, the casts are "natural," i.e., where fine sediments have filled the inside of the cranial cavity, becoming infiltrated and compacted through time. These casts sometimes retain some of the morphological details that were imprinted on the internal table of bone of the cranium when the animal was alive. The famous australopith (*A. africanus*) Taung child's skull, described by Dart (1925), is one of the best-known examples, as are Sts 60 and SK 1585, the latter a fine example of *Australopithecus robustus*. Curiously, these "natural" endocasts are only found in the South African australopiths (chapter "▶ Analyzing Hominin Phylogeny: Cladistic Approach," Vol. 3) and date from about 3.0 myr to about 1.5 myr (see Fig. 1). Traditionally, paleoneurologists have made casts of the insides of fossil

Fig. 1 Casts of the Taung (*left*), Sts 60 (*right*), and SK 1585 (*bottom*) "natural" endocasts of Australopithecines

skulls using rubber latex, or silicone rubber, extracting these from the cranial remains. The partial cast is then sometimes reconstructed by adding plasticine (modeling clay) to the missing regions. The whole is then measured by immersion into water, and the amount of water displaced is regarded as the volume of the once-living brain. Other measurements (linear chords and arcs) and observations (convolutions and asymmetries) may be made on the original cast. More recently, "virtual" endocasts have been made from CT scans of intact or partial crania, an approach that has the advantage of being noninvasive (chapter "► Virtual Anthropology and Biomechanics," Vol. 1). As it is computer driven, there are various algorithms for deriving the size of the endocast and other metrics (chapter "► Virtual Anthropology and Biomechanics," Vol. 1; Weber et al. 2012; see also Zollikofer and Ponce de León 2013). Of course, CT scans (medical and micro) are not continuous, as is the case with actual casting materials such as silicone-based materials that flow into all the cracks, crevices, and convolutional details available.

During life, the brain is surrounded by three dural tissues (the dura mater, the arachnoid tissue and its cerebrospinal fluid, and the pia mater) that interface between the actual brain tissue (cerebral cortex, mostly) and the internal table of bone of the skull. The gyri and sulci (convolutions) of the once-pulsating cerebral cortex are thus imperfectly imprinted on the interior of the skull, and the degree of replication often varies in different regions, e.g., sometimes the frontal lobe imprints more details than the parietal lobe, as well as by age. The degree of replication also varies in different animals. Two extremely important considerations emerge from this: (a) the resulting imprints are never complete and are thus

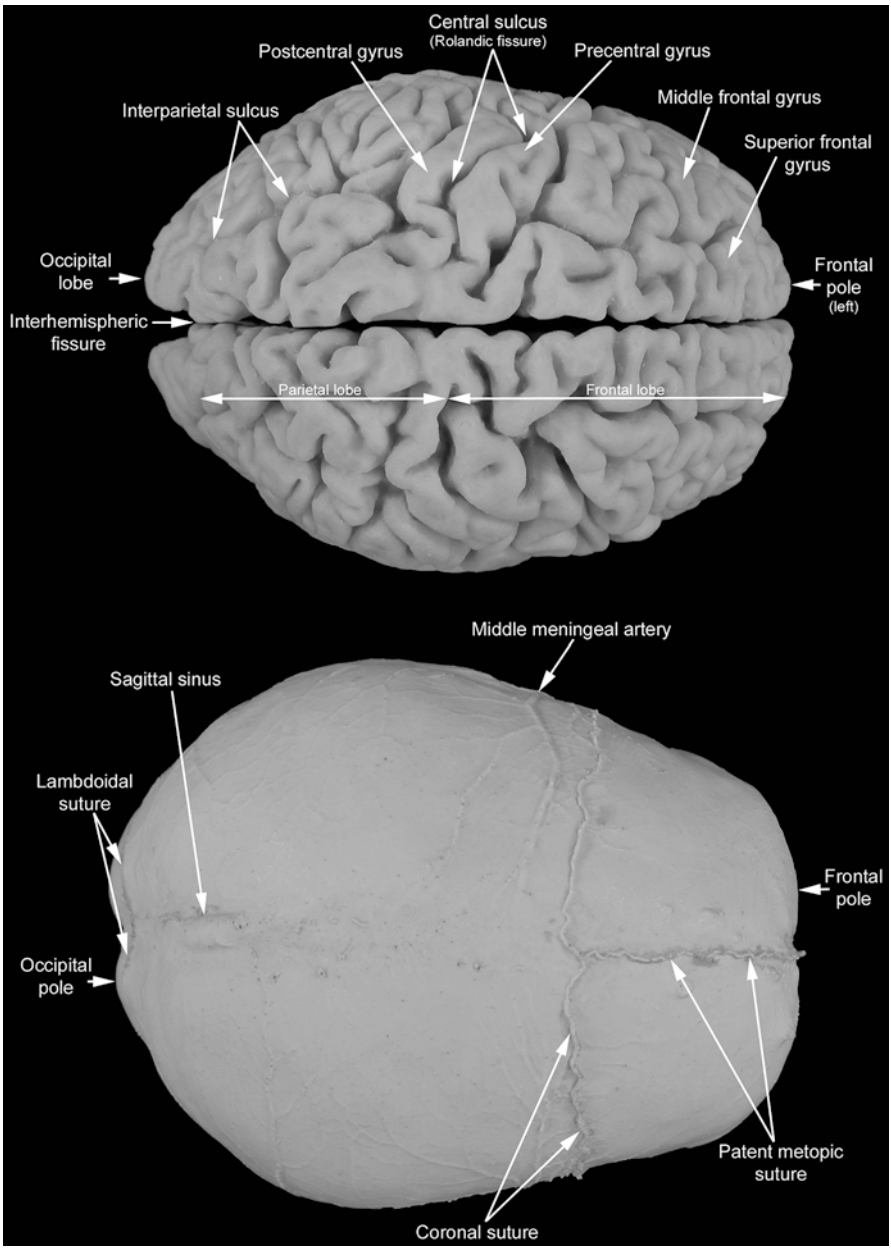

Fig. 2 (continued)

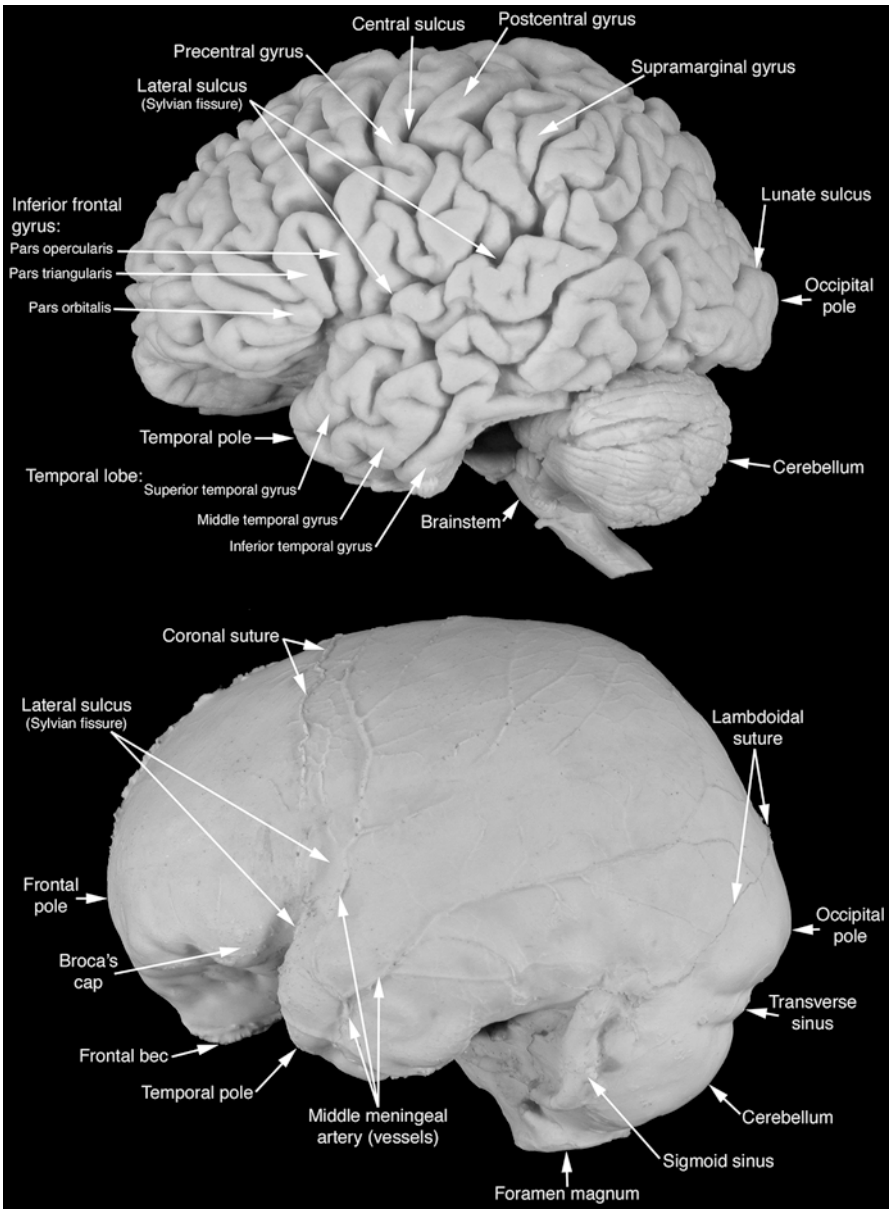

Fig. 2 Dorsal (see *previous page*) and lateral (see *above*) views of a modern human brain and the endocast to demonstrate the loss of detail on the endocast surface

in that sense "data poor," never including subcortical structures, and (b) the controversial interpretations of what the underlying brain once looked like are guaranteed (see Fig. 2). Nevertheless, endocranial casts do provide extremely important information regarding (1) overall size, (2) shape, (3) rough estimates of

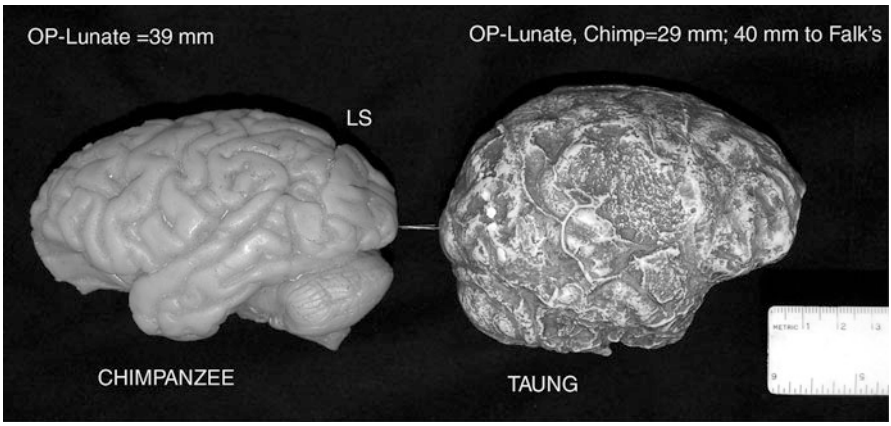

Fig. 3 Lateral view of a chimpanzee brain and the Taung *A. africanus* endocast. The lunate sulcus separates PVC from association cortex and is in an anterior position in apes. The *white dots* on the Taung endocast show where the average chimpanzee lunate sulcus would fall and that location violates the sulcal morphology on Taung. Placing it more anteriorly would be a monkey-like configuration. The Taung lunate sulcus would most probably be posterior, in a humanlike position, which is near the lambdoid suture

the lobal dimensions of the brain, and (4) cortical asymmetries that have relationships to hemispheric specializations and behavioral processes including handedness. In addition (5), if the imprints of the underlying gyri and sulci are available, they can provide important information regarding the organization of the cerebral cortex and whether the patterns of these are the same or different as in known extant primate brains. The infamous "lunate sulcus" is a good example, as it is a demarcation boundary between purely sensory primary visual striate cortex (PVC) and multimodal association cortex in both Old World monkeys and anthropoid apes. When the lunate sulcus appears in an anterior position, it is most similar to the condition known in modern apes. When it is found in a posterior position, it is in a more humanlike condition. Ascertaining its correct position is thus essential in deciding whether or not such a fossil hominid had a brain organized along human or ape lines. In modern humans, the "lunate" is only partially homologous with that found in apes and is usually fragmented (Allen et al. 2006). Hominins such as *Homo erectus*, *H. heidelbergensis*, *H. georgicus*, and *H. neanderthalensis* unfortunately do not have occipital lobes that allow clear-cut identification of the lunate sulcus if it were a singular unfragmented sulcus. Figure 3 shows a comparison between a chimpanzee brain with a lunate sulcus and that of the Taung child, *A. africanus* (See also Holloway 1984, 2000). Finally (6), meningeal arteries and veins that nourished the dura mater also imprint on the internal table of bone and sometimes show patterns that are useful for deciding taxonomic issues; these have no known relationship to behavioral functions of the brain. (See also Grimaud-Hervé in Holloway et al. 2004, for further discussion and illustrations.) Figure 4 shows that a more recent *A. africanus* specimen from Sterkfontein, S. Africa, Stw 505, shows a clear lunate

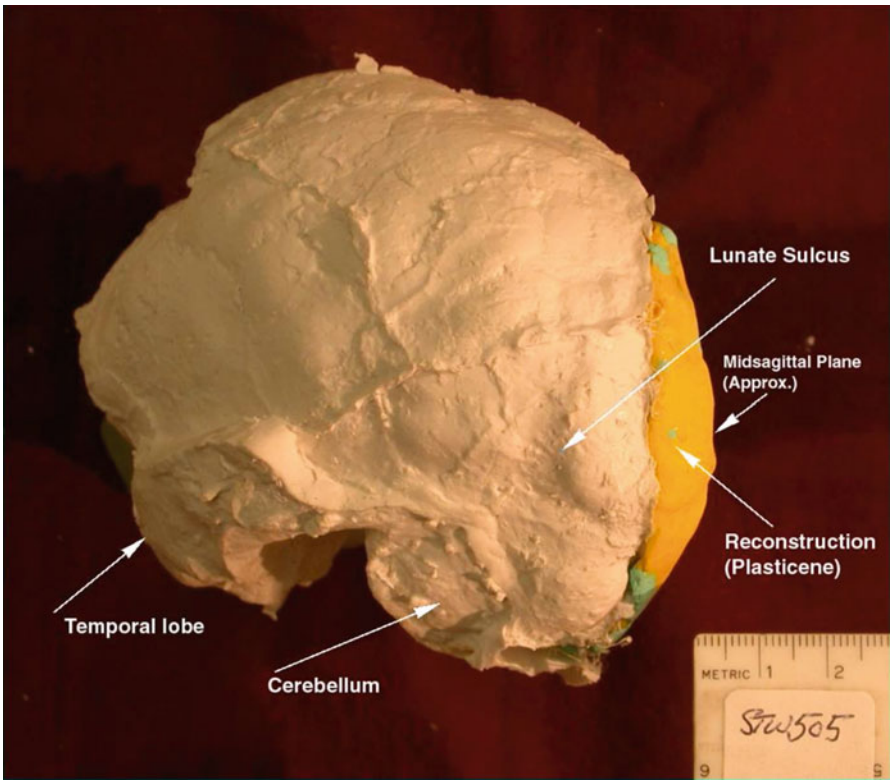

Fig. 4 Oblique view of the Stw 505 *A. africanus* specimen, showing a prominent lunate sulcus in a posterior position. This specimen makes it clear that at least some australopithecines had reduced primary visual cortices and expanded posterior parietal lobes, evidence showing that reorganization probably preceded brain size increases

sulcus in a relatively posterior position compared to chimpanzee brains. Falk (2014) has made the bizarre suggestion that is perfectly crescentic lunate sulcus is the lateral calcarine sulcus, which is not possible given the medially directed curvature of both inferior and superior ends of the depicted lunate sulcus in Stw505. When in the course of subsequent hominin evolution, the lunate sulcus changed into a more fragmented partially homologous structure as found in modern humans is unknown, as neither *Homo erectus* nor Neanderthals show detailed gyri in the occipital region (chapters "► Later Middle Pleistocene *Homo*" and "► Neanderthals and Their Contemporaries," Vol. 3).

The frontal lobe is of course a major focus of examining endocasts in the hope of understanding the evolutionary trajectories through time of the most crucial part of neuroanatomy underlining our very humanness, intelligence, and social behavior. Here, we are plagued with by the fact that very few sulcal details are available on the endocasts of early hominins, particularly the australopiths. A recent paper by Carlson et al. (2011) describes the frontal portion of an endocast of MH1 (Malapa

Hominin 1) that they have named *Australopithecus sediba* and that shows some possibility of prefrontal organization toward a more human condition.

Indirect Evidence

This line of evidence is "data rich," providing comparative neurological information on living species, such as brain size (both absolute and relative, i.e., related to body size), the actual makeup of the brain from the gross to microscopic levels, including neural nuclei, fiber systems and interconnections, and distribution of neurotransmitters and neuroreceptors. Additionally, the brain can be studied ontogenetically, and neuroscientists can actually study the relationships between how the brain varies neurologically and how these variations relate to the behavioral variation. Modern examinations including CT, MRI, fMRI, and tensor diffusion techniques can be applied, yielding different kinds of data relevant to different aspects of growth and development, genetic and epigenetic unfolding, and behavioral consequences (chapter "► Virtual Anthropology and Biomechanics," Vol. 1). Neurogenomic information will also add considerable details as to how living brains vary and operate, both within and between different species, and hopefully inform us about selection events in the evolutionary past. This richness is simply lost to the paleoneurologist. However, it is necessary to realize that the extant living species often used as comparisons to humans, e.g., bonobo, chimpanzee, and macaque (chapters "► Estimation of Basic Life History Data of Fossil Hominoids," Vol. 1, "► Evolution of the Primate Brain," and "► The Hunting Behavior and Carnivory of Wild Chimpanzees," Vol. 2), are end points of their own evolutionary lines of development and are not our ancestors, however closely related to us they may be. It is thus the blending and complementation of these two approaches which provide the best set of evidence for when and how our brains evolved. Another aspect of the comparative evidence is the question of how well we can explain species-specific behavior on the basis of what we know from comparative neurology. Considering the behavioral differences between chimpanzees and bonobos and gorillas and orangutans, there are no current explanations to explain these in terms of neuroanatomical detail.

Characteristics of the Human Brain

Brain Size, Absolute and Relative

The human animal is obsessed with size, and those who study the brain comparatively are perhaps more so than average. With a mean brain weight of 1,330 g and a body weight of 65,000 g (Tobias 1971), the human species has the largest absolute brain size within the primate order, but is actually dwarfed by elephants and some of the whales, in which brain weight can exceed 7,500 g. Of course, body weights are also very much higher in elephants and whales. But even for its body weight,

Table 1 Fossil hominid brain volumes

	Average				
Group	Number	Location	Brain volume	Range	Dating (myr)
A. afarensis	3	E. Africa	435	385–500+	3–4
A. africanus	8	S. Africa	440	420–500+	2–3
A. aethiopicus	1	E. Africa	410	na	2.5
A. garhi	1	E. Africa	Ca. 450	na	2.5
A. sediba	1	S. Africa	Ca. 420	na	2–3
A. robustus	6	E. and S. Africa	512	500–530	1.6–2.0
H. rudolfensis	2	E. Africa	775	752–800	1.8
H. habilis	6	E. Africa	612	510–687	1.7–2.0
H. georgicus	3	Georgia and Europe	677	600–775	1.7
H. ergaster	2	E. Africa	826	804–848	1.6
H. erectus	2	E. Africa	980	900–1,067	1.0–1.6
H. erectus	8	Indonesia	925	780–1,059	1.0
H. erectus	8	China	1,029	850–1,225	0.6
Archaic *H. sapiens*	6	Indonesia (Solo)	1,148	1,013–1,250	0.13
Archaic *H. sapiens*	6	Africa	1,190	880–1,367	0.125
Archaic *H. sapiens*	7	Europe	1,315	1,200–1,450	0.5–0.25
H. sapiens (Neand.)	25	Europe and M. East	1,415	1,125–1,740	0.09–0.03
H. sapiens sapiens	11	World	1,506	1,250–1,600	0.025–0.01

Source: Holloway 1997

Homo sapiens does not have the largest relative brain weight (about 2 % of body weight), being outdone by several monkeys, some rodents, and even some fish. Normal modern human brain size varies between roughly 900 and 2,000 g, although a very small number of exceptions do occur, with sizes in the 750–900 and 2,000–2,200 g range. Human populations vary, as do the sexes. In general, Arctic peoples tend to have larger brains than those living in the tropics, and the smallest brains appear to be found among Ituri forest pygmies who also display small stature. Males in all populations for which good autopsy or cranial data have been gathered show brain sizes on the average of 100–150 g greater than females, an amount roughly the same as the range of modern human racial variation. It should be pointed out that these differences, and their possible relationship to cognitive skills, are highly controversial, and simple correlations are deceptive (Holloway 1996, 2008; Nyborg 2003). Table 1 provides a listing of the major fossil hominid taxa and their respective brain sizes (See Neubauer et al. 2012 for confirmation of my australopithecine volumes). Notice that the range of values

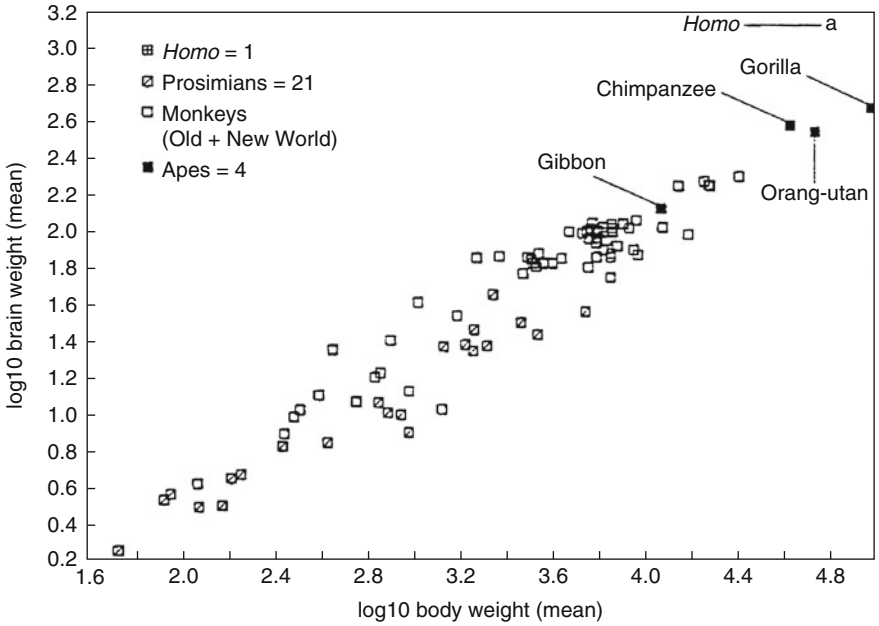

Fig. 5 Graph showing human deviation from a plot of log brain weight against log body weight for primates, with *Homo* at the extreme upper right position

from the earliest australopithecine to modern *Homo* is roughly 1,000 ml or about the same amount as the normal range of variation within our species.

Encephalization (Encephalization Coefficient, EQ)

Nevertheless, the human animal does come out on top of the evolutionary heap when its absolute brain and body weights are considered together. When the log (base 10) of brain weight is plotted against the log10 of body weight for a group of relevant taxa, the result is usually a linear relationship, where (log10) brain weight = a + b (log10) body weight. For a large array of primate data (e.g., Stephan et al. 1981), the slope of the line (b in the equation above) is about 0.76, and the correlation coefficient is 0.98, indicating that the relationship is almost perfect (chapter "▶ Estimation of Basic Life History Data of Fossil Hominoids," Vol. 1). This relationship will naturally vary depending on the databases and the transformations used. This is known as an allometric equation, and these are used frequently in biology to assess the underlying relationships between the size of parts of the body and the whole (see Fig. 5). The slope sometimes has an interpretation suggesting functional relationships between the brain and other variables. For example, in the above example, the slope is 0.76, extremely close to 0.75 or 3/4, which often describes a metabolic relationship (Martin 1983). The slope of 0.66, or

Table 2 Some examples of encephalization quotients

Species	Brain wt. (g)	Body wt. (g)	EQ *Homo*[a]	EQ Jerison[b]	EQ Primates[c]	EQ Stephan[d]
Lemur	23.3	1,400	21	1.56 (22.6)	0.94 (32.7)	5.66 (19.6)
Baboon	201	25,000	28	1.97 (28.5)	0.90 (31.3)	7.94 (27.5)
Gorilla	465	165,000	23	1.56 (22.5)	0.61 (21.2)	6.67 (23.2)
Orang	370	55,000	31	2.15 (31.1)	0.91 (31.7)	8.90 (30.9)
Chimp	420	46,000	39	2.63 (28.1)	1.81 (41.1)	11.3 (39.3)
Human	1,330	65,000	100	6.91 (100)	2.87 (100)	28.8 (100)

Source: Holloway 1997. Note: each formula is based on a different set of data. The EQ *Homo* equation simply uses the average brain and body weight for *Homo sapiens* and assumes an intercept where both brain and body weights are zero. The value of whichever animal is calculated is then given as a direct % of modern *Homo sapiens*. EQ Jerison is based on data for almost 200 mammals, while the EQ Primates is based on Martin's (1983) data set for primates only. The EQ Stephan equation is based on insectivores only. The numbers in the parentheses are the % of the *Homo sapiens* value

[a]Formulae: EQ *Homo* = Brain wt/1.0 Body $wt^{0.64906}$

[b]EQ Jerison = Brain wt/0.12 Body $wt^{0.66}$

[c]EQ Primates = Brain wt/0.0991 Body $wt^{0.76237}$

[d]EQ Stephan = Brain wt/0.0429 Body $wt^{0.63}$

2/3, has been championed by some (e.g., Jerison 1973) as indicating an important geometric relationship between volume and surface area. It is important to realize that these slopes vary depending on the taxa examined. In general, as the taxa become more similar, the slope decreases. Species within a genus generally have a slope around 0.3; within a species, the slope is smaller yet, being about 0.2, and the correlation coefficient is also reduced (see also Martin and Isler 2010).

Just as the human animal is curious, it is also vainglorious, always trying to find a measure that places it at the top. Thus we can fabricate a device, the *Encephalization Coefficient* or EQ, which shows that relative to any database, the human animal is the most encephalized animal living. The point for *Homo sapiens* shows a clear positive residual above the expected regression line, and in fact the human value is about three times that expected for a primate with its body weight. Table 2 provides a number of different equations based on differing databases, which happily give *H. sapiens* the highest value. (Actually, young immature dolphins will provide a higher number, but when compared to an immature human, the value is higher in the latter.) Two additional points should be made: (a) EQs are relative to the databases used, and thus there is an inherent "relativity" to relative brain sizes; and (b) EQs do not evolve, only brain weight/body weight relationships do, and EQs are simply a heuristic device enabling comparisons between taxa; they have no reality outside of the database chosen, or species within a taxa, and are not designed to discuss within-species variation. For example, female humans are "more" encephalized than males, given their smaller body sizes, more body fat which is not innervated, and smaller brains, but the relationship might be simply a statistical artifact with no known gross behavioral manifestation given the sexes equal overall intelligence. It is more likely that small differences in

neural reorganization might be related to behavioral differences such as language ability or math and spatio-visual manipulation rather than brain size or EQ.

I will discuss later how the processes of hypertrophy and hyperplasia have been positively selected for in the course of the last 2–3 myr of hominid evolution. (Hypertrophy refers to increases in size of the neural components, e.g., neurons, dendritic branching, nuclei, and fiber tracts; hyperplasia refers to increased production of cells through mitotic division.) It is most probably the case that these processes are controlled by regulatory genes, and one of the major differences between ourselves and our closest nonhuman primate relative, the chimpanzee (brain size = ca. 385 g), relates to the schedules by which hyperplasia and hypertrophy are turned on and off during ontogenetic development (Holloway 1980, 1995; Miller et al. 2012).

Brain Organization and Reorganization

It is well known that the brains of most animals are extremely similar to each other in terms of their overall organization, by which are meant neural nuclei and fiber systems. The human animal does not appear to show any different structures when compared to Old World monkeys such as the macaque or the great apes, including bonobo, chimpanzee, gorilla, and orangutan. Even the neural fiber tracts that are involved in human language appear in these primates (Deacon 1997). One might ask, then, given the obvious species-specific repertoires that exist in all animals, how can these behaviors differ without differences in the underlying nervous systems? This is one of the major challenges of studying brain evolution and in particular understanding what neural organizations account for the specificity of, say, human behavior, the ability to use language composed of arbitrary symbols. In other words, all mammals have a cerebral cortex, a thalamus, cerebellum, hypothalamus, etc., and basically these structures possess almost identical divisions of nuclei and do the same neural tasks. Clearly, brain size alone will never explain species-specific behavior, and the relationships between neural nuclei and fiber tracts will only go so far in explaining behavioral differences.

Allometric equations showing the relationship between individual bodily components and the whole are instructive here. If we were to plot the logs (base 10) of primary visual cortex (PVC) against brain volume, we would find that the human PVC is 121 % *less* than predicted, and similarly, the lateral geniculate nucleus of the thalamus is about 144 % *less* than expected for a primate of our brain size (see Fig. 6). In contrast, if one plots the amount of cerebral cortex against brain weight the result is a straight line, and the human point lies almost exactly on the line. In short, the human cerebral cortex is as large as would be expected for a primate of its brain size. But do portions of the cerebral cortex vary in size between different primates? In humans, the residuals mentioned above suggest that compared to chimpanzees, the amount of PVC is significantly smaller in humans, or alternatively put, the posterior association cortex of the parietal and temporal lobes is relatively larger in humans. Since there are no essential differences between

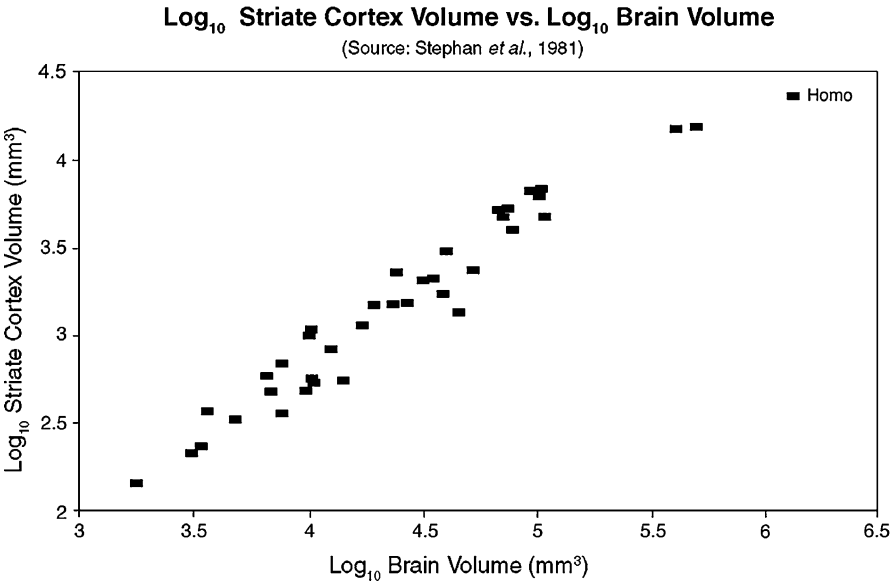

Fig. 6 Graph showing log striate cortex (area 17) versus log brain volume, where the value for *Homo sapiens* (*upper right*) is 121% less than expected from the log-log regression (see also Table 3, which shows other departures between actual and predicted values for different brain structures)

Table 3 Human brain structure residuals[a]

Dependent variable	Independent variable	Number species	Correl. coeff. (R)	Actual value (A)	Expected value (E)	(A)/(E) ratio	%Diff. (A)/(E) homo
Striate cortex	Brain weight (C)	37	0.971	22,866	50,598	0.45	−121.30
		19	0.977		38,097	0.60	−66.60
Lateral geniculate	Brain weight (C)	37	0.978	416	1,026	0.41	−146.60
		19	0.982		857	0.49	−106.00
Cerebellum	Brain weight (C)	44	0.990	137,421	128,932	1.07	6.20
		26	0.994		150,535	0.91	−9.50
Dienceph.	Brain weight (C)	44	0.995	33,319	51,512	0.65	−54.60
		26	0.998		47,899	0.70	−43.70
Septum	Brain weight (C)	44	0.983	2,610	2,085	1.25	20.10
		26	0.991		2,201	1.19	15.70
Amygdala	Brain weight (C)	16	0.990	3,015	4,633	0.65	−53.70
		7	0.985		3,753	0.80	−24.50
Lateral geniculate	Thalamus	21	0.979	416	731	0.57	−75.72
		10	0.988	416	636	0.65	−52.88

[a]Based on Stephan et al. (1981) data

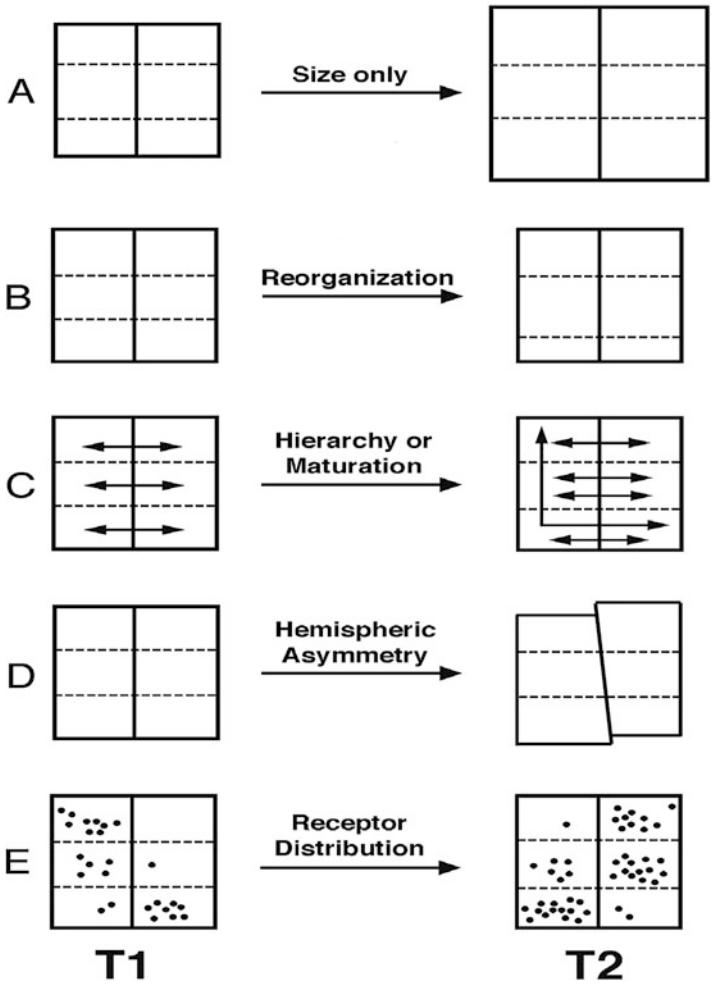

Fig. 7 Types of reorganization without necessary brain size increase. The *dashed lines* represent boundaries between frontal, parietal, and occipital lobes, which if changed in relative positions from T1 to T2 would suggest reorganization

chimpanzees and humans in their visual abilities and competencies, these differences most probably reflect selection for expanded functioning of the association cortex in humans. This is precisely what is meant by "reorganization" (Table 3).

When used in a comparative or evolutionary context, reorganization means changes in the sizes and proportions thereof of neural nuclei and their fiber tracts (see Fig. 7). Given that chimpanzees and hominids had a last common ancestor some 5–7 myr and that chimpanzees appear to have large PVC cortices, we infer that one aspect of human brain evolution has been some reorganization of the

cerebral cortex, namely, an increase in posterior association cortex (or, equally, a reduction in PVC) involved in polymodal cognitive tasks, where visual, auditory, and motor information are brought together in a synthetic whole. The trick, of course, is to demonstrate objectively when, where, and why these changes took place. This example of PVC has been purposefully chosen because one of the sulcal landmarks of the cortex that defines the anterior border of PVC is the "lunate" sulcus, named for its crescentic shape, and there is some hope of identifying its position on some of the early hominid brain endocasts. In this regard, endocasts are most often frustratingly mute on other convolutional details.

Neuroanatomists have been trying for many decades to demonstrate the major differences between us and other primates, and aside from gross brain size, very little else of significance has been shown as most of the differences can be explained as allometric scaling. The frontal lobe, and particularly its prefrontal portion, has been a favorite target, and indeed, Brodmann (1909) claimed it was proportionally larger in humans, a view most recently championed by Deacon (1997). Unfortunately, other work has shown that the human brain has just as much frontal lobe as would be expected for a primate of its brain weight (von Bonin 1937, 1948; Semendeferi et al. 1997; Uylings and van Eden 1990), although the picture regarding prefrontal cortex has yet to be determined objectively using cytoarchitectonic criteria, which is how prefrontal cortex is differentiated from the pure motor cortex behind it (Schenker et al. 2010; Sherwood et al. 2003; Rilling et al. 2008). Hominid brain endocasts do not, alas, provide any sulcal landmarks with enough reliability to determine the boundaries of prefrontal cortex, which is so important to impulse control, and higher cognitive functions such as planning and abstraction and recognition of social actors and behavioral elements suggesting "theory of mind" abilities. Thus, these regions cannot be accurately measured in a phylogenetic sequence. However, given the apparent closeness between us and the great apes in terms of percentage of prefrontal cortex, it strikes this writer as extremely doubtful that there could be any major quantitative differences in prefrontal relative volume among the various hominin taxa. The Neanderthals, living from about 300,000 to about 28,000 years ago, have frequently been described as having smaller frontal lobes; this is not based on objective measurements, but rather a perception that the large brow ridges on these humans were constraining frontal lobe development. Studying the Neanderthal brain endocasts and comparing them to modern humans, I have failed to see any significant difference between these two groups, and Bookstein et al. (1999) showed that their prefrontal profiles were practically indistinguishable. More recently, Pearce et al. (2013) have suggested that Neanderthal orbital size meant they had larger visual cortices and thus less parietotemporal association cortex and were thus less intelligent than modern *H. sapiens*. Unfortunately, these authors did not control for facial size which is larger in Neanderthals, nor did they bother to take into account the large degree of occipital lobe variation in those Neanderthal endocasts providing such details. There is nothing in the external morphology of Neanderthal endocasts that can pinpoint any primitive characteristics in cortical morphology; and yes, their brains *were* on average larger than ours today, but not necessarily than Upper Pleistocene

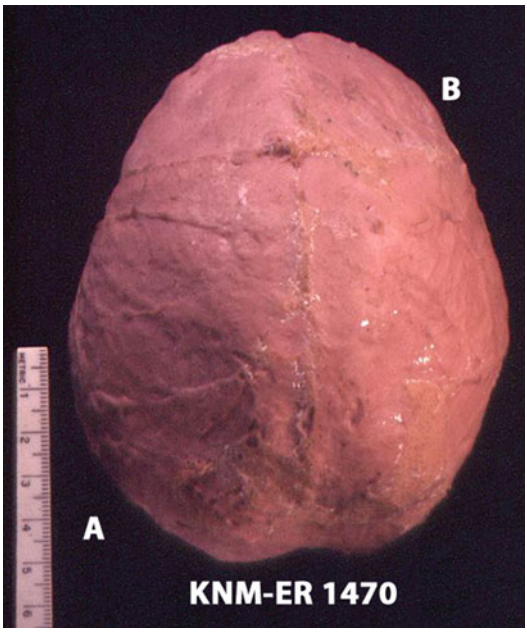

Fig. 8 Dorsal view of KNM-ER 1470, *Homo rudolfensis* (1.8 myr), showing a typical *Homo* pattern of petalias, the left occipital projecting more posterior and being wider than the right side (*A*) and the right frontal being wider than the left (*B*)

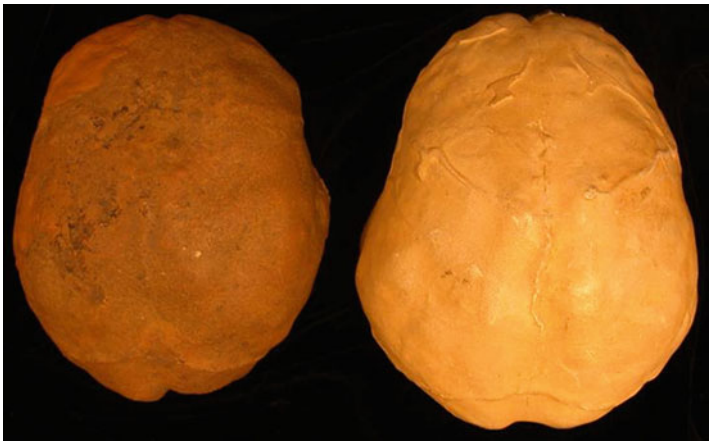

Fig. 9 Neanderthal cerebral asymmetries. *Left* is Monte Circeo and *right* is La Ferrassie. Both show a larger width of the right-frontal lobe and a larger left-occipital region (as in Fig. 8)

anatomical modern humans. Their bodies, being larger in terms of lean body mass, might have required larger brains.

Similarly, regions such as "Broca's and Wernicke's areas," anterior and posterior association cortical regions involved in motor (Broca's) and receptive (Wernicke's) aspects of speech, are determinable on most fossil endocasts, and

we can determine, for example, that Broca's region is more humanlike on one brain cast of an early *Homo*, some 1.8 Ma. This is the famous KNM-ER 1470 endocast of *Homo rudolfensis* from Kenya, which had a brain volume of 752 ml. It may not be a direct ancestor to our own line of *Homo*, but it does show cerebral asymmetries similar to those found in modern *Homo* (Fig. 8, KNM-ER 1470). We know that Broca's regions in modern *Homo* are asymmetrical both in overall size and cytoarchitectonic divisions between areas 44, 45, and 47 of Brodmann (Amunts et al. 2010; Schenker et al. 2010). Interestingly, Neanderthal endocasts show similar asymmetry to modern humans in Broca's region (Fig. 9).

While the concept of reorganization has a heuristic value in directing our attention to changing quantitative relationships between different neural nuclei and fiber tracts, we cannot yet ascribe behavioral differences between closely related animals such as chimpanzee, gorilla, and orangutans or different species of the genus *Macaca* or indeed different breeds of dogs or cats with their different temperaments, aptitudes, and sociality to particular brain conformations. We simply do not know what magic level of neural description is necessary to describe species-specific behavior. Recent research on prairie and mountain voles suggests that the difference in the females' ability to retrieve pups back to the nest depends on the distribution and number of neuroreceptors for the hormone oxytocin found in several nuclei of the brain, particularly the thalamus. Otherwise, their brains appear identical (Insel and Shapiro 1992). In addition, it is necessary to remember that the brain possesses aspects of plasticity that we did not appreciate except within the past decade and that as the brain's organization unfolds ontogenetically, interactions with environmental stimuli are always occurring, and the brain builds its organization partly through its plasticity. It is difficult enough to study and understand such patterns in laboratory animals, let alone in our fossil ancestors! While the above suggests a somewhat pessimistic tone, we should remember that advances in noninvasive technology such as MRI, fMRI, PET, and tensor diffusion scanning have enormously increased our understanding of how the brain works and how neural systems integrate and dissect data from the environment, always providing us with newer paradigms for further exploration about our brains and behavior. In time, they will do the same for those of our closest relatives, the apes, in particular the bonobo and chimpanzee (see in particular Semendeferi et al. 2010).

Human Brain Asymmetry

The cerebral cortices of the human brain are usually asymmetrical and tend to grow in a torqued manner, reflecting minor differences in maturation rates. The hemispheres are seldom, if ever, equipotential in terms of functioning. Our left hemisphere is often characterized as "analytic" and involved with language tasks, while our right hemisphere appears most competent in visuospatial integration and is often thought of as the "intuitive" or "gestalt" hemisphere. These characterizations,

while crude, hold up fairly accurately for right-handers and many ambidextrals. From radiographic studies, it was possible for LeMay (1976) to ascertain different petalia patterns for right- and left-handed humans with a high degree of precision. These petalias are small extensions of cerebral cortex that extend farther in one part of a hemisphere than on the other side. For example, we speak of a left-occipital right-frontal torque pattern of petalias as occurring with high frequency in right-handed individuals. This means that the left-occipital lobe bulges somewhat more posteriorly on the left hemisphere, while the right hemisphere is somewhat broader in width in the frontal lobe. In true left-handers, who make up about 8–10 % of human populations, the pattern is reversed, meaning they exhibit a right-occipital left-frontal pattern. Petalia patterns for a large collection of apes indicated that while chimpanzees, gorillas, and orangutans sometimes demonstrated asymmetries, they did not show the particular torque pattern described above *as frequently*. The gorilla, incidentally, was the most asymmetrical of the apes (Holloway and de LaCoste-Lareymondie 1982). On the other hand, brain asymmetries, particularly in the planum temporale (temporal cortex) of the chimpanzee, show a strong left-hemispheric size difference compared to the right (Gannon et al. 1998). This is simply puzzling as we do not have any evidence that chimpanzees use this structure in communication as do humans, and the fact that we share this difference with chimpanzees suggests that brain organizational features relating to complex cognitive functioning has been around for at least 5–7 myr. As our noninvasive scanning techniques become more sophisticated, we can expect to learn how these asymmetries function in animals other than ourselves. In fact, asymmetries appear in many animals and are hardly unique to primates (Hopkins and his colleagues have been in the forefront in demonstrating chimpanzee asymmetries and possible handedness: Hopkins and Nir 2010, Gomez-Robles et al. 2013, and references). It is probably the degree of asymmetry which is important in distinguishing humans from other primates (Balzeau and Gilissen 2010; Balzeau et al. 2012). Wey et al. (2013) have recently shown that intrinsic connectivity networks are more complex with regard to asymmetry of frontoparietal connectivity in humans compared to nonhuman primates. These connections probably, in part at least, account for the usual petalial asymmetries that appear more frequently in human brains.

Hominid brain endocasts, when complete for both sides (unfortunately, this is very rare), allow the paleoneurologist to assess the cerebral asymmetries, and indeed, even australopithecines appear to show beginnings of the right-handed torque pattern found in humans, and, as one progresses through time, the petalia patterns become more accentuated in the modern human direction. If we add to these observations those of Toth's (1985) studies on the early stone tools (chapters "► Overview of Paleolithic Archaeology," Vol. 3 and "► Modeling the Past: Archaeology," Vol. 1) of about 2 myr, which strongly suggest right-handedness, this underlines the fact that our early ancestors' brains, despite their small sizes (sometimes within extant apes ranges), were reorganized and that they probably had some modes of cognition very similar to our own (chapters "► Overview of Paleolithic Archaeology," Vol. 3 and "► Modeling the Past: Archaeology," Vol. 1).

Synthesis: Putting Together Size, Organization, and Asymmetry During Human Evolution

As mentioned earlier, human brain evolution has clearly been a process of integrating neurogenomic processes that led to increased size of the brain (hyperplasia and hypertrophy), and these neurogenomic changes also played roles in the reorganization (quantitative shifts) of neural nuclei, fiber tracts, and cortical cytoarchitectonics. In addition, it is probable that other changes occurred at the neurochemical level, involving neurotransmitters and receptor sites, but these are not well known from the comparative record, let alone the fossil one. This integration was sometimes gradual, sometimes "punctuated," at least based on the fossil hominid record currently available. The only reliable evidence from paleoneurology suggests that Brodmann area 17 (PVC) was reduced early in hominid evolution, signs of the reduction being clear in *A. afarensis* some 3–3.5 myr. While this would have meant a relative increase in posterior parietal cortex (area 39) and peri- and parastriate cortex (areas 18 and 19, respectively), the faithfulness of sulcal impressions does not allow for unambiguous definition of these areas. Similarly, it is not possible at this time to measure and delineate remaining areas of the temporal cortex and superior parietal lobule unambiguously. What is suggested, however, is that visuospatial abilities were most probably cognitively enhanced early in hominid evolution. It is not until we come to *H. rudolfensis* ca. 1.8 Ma that a case can be made for some frontal lobe reorganization in the third inferior frontal convolution, Broca's area. Thus, it would appear there was a gradient of cerebral reorganizational changes starting posteriorly and progressing anteriorly. Table 4 outlines these changes.

More recently, Falk et al. (2012) have argued that the Taung *A. africanus* specimen possessed an open metopic suture that allowed the prefrontal lobe to expand and widen despite the pelvic constraints thought to exist for this species in relation to bipedal locomotion. These authors then expanded this idea to several of

Table 4 Summary of reorganizational changes in the evolution of the human brain

Brain changes, reorganizational	Taxon
1. Reduction of primary visual striate cortex, area 17, and a relative increase in posterior parietal and temporal cortex, Brodmann areas 37, 39, 40, as well as 5 and 7	*Australopithecus afarensis* and *Australopithecus africanus*
2. Reorganization of frontal lobe (3rd inferior frontal convolution, Broca's areas 44,45, 47)	*Homo rudolfensis* and early *Homo*
3. Cerebral asymmetries, left-occipital right-frontal petalias	Australopithecines and early *Homo*
4. Refinements in cortical organization to a modern *Homo sapiens* pattern	*Homo erectus* to present

Source: Holloway 1997. Note: (4) is inferred, as brain endocasts cannot provide that level of detail necessary to demonstrate the refinements in cortical organization from surface features alone. Areas 18 and 19 are peri- and parastriate cortex just anterior to area 17 and are included in posterior association cortex here

Table 5 Brain size changes in hominid evolution

Brain changes	Taxon	Time (myr)	Evidence
1. Small increase, allometric[a]	*A. afarensis* to *A. africanus*	3.5–2.5	Brain endocast increase from ca. 400 to 450 + ml
2. Major increase, rapid, both allometric and non-allometric	*A. africanus* to *H. habilis*, *H. rudolfensis*	2.5–1.8	KNM–1470, 752 ml (300 ml increase)
3. Modest allometric increase in brain size to 800–1,000 ml	*H. habilis* to *H. erectus*	1.8–0.5	*H. erectus* brain endocasts and postcranial bones
4. Gradual and modest size increase to archaic non-allometric FOXP2	*H. erectus* to *H. sapiens neanderthalensis*	0.5–0.075	Archaic *H. sapiens*, Neanderthal endocasts 1,200–1,700 + ml
5. Small reduction in brain size among modern allometric	*H. sapiens* *H. sapiens sapiens*	0.015–present	Modern endocranial volumes

Source: Holloway 1997 and more recent endocast data Holloway et al. 2004
[a]Related to increase in body size only

the specimens regarded as early *Homo*, without providing any detailed evidence. Unfortunately, a newer study using micro-CT scanning (rather than medical CT scans) failed to show any evidence of a metopic suture except for a possible small portion just superior to nasion (Holloway et al. 2013), strongly suggesting that the infant metopic suture had already fused from nasion to bregma.

Table 5 outlines the major size changes in the human brain during its evolutionary odyssey. Paleoneurological data simply are not detailed enough to integrate the two tables of size and reorganizational changes into one holistic sequence of events. Basically, the paleontological record supports an early reorganizational change resulting in an increase in posterior cortex associated with visuospatial processing, perhaps accompanied by a relative small allometric increase in brain size from *A. afarensis* to *A. africanus*. This would correlate well with geological and paleontological evidence that shows that early hominids were expanding their ecological niches (chapter "► The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1) and becoming more diverse in their subsistence patterns in mixed habitats. We know this based on the fact that stone tool types are becoming standardized in form, tool inventories grow larger, and right-handedness is highly probable. With the advent of *Homo*, we find strong evidence for a major increase in brain size, both allometric (related to body size) and non-allometric, and a reorganized frontal lobe, broader and showing a more modern humanlike Broca's area. This suggests that there had indeed been some strong and dramatic selection pressures for a somewhat different style of sociality, one perhaps based on a primitive proto-language that had some arbitrary symboling elements, as suggested by the standardization of stone tools (e.g., Acheulean hand axes) (chapter "► Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Vol. 3) that suggest social cohesion and control mediated through symbolically

based communication (Holloway 1981). Needless to say, this is only one speculative account of the evidence. But from about 1.8 to roughly 0.5 myr, we think there were minor allometric brain size increases to the earliest *Homo erectus* hominids of Indonesia and China, where brain sizes ranged from 750 to 1,250 ml in volume. We have very little evidence for body sizes, but we believe, on the basis of the KNM-WT 15,000 Nariokotome youth from Kenya at ca. 1.6 myr, that these did not differ significantly from our own.

This is also a time during which cerebral asymmetries are becoming more strongly pronounced. With the advent of Archaic *H. sapiens*, about 0.15–0.2 myr, we find brain sizes well within modern human values and no evidence for further allometric increases, except possibly for the Neanderthals, in which it can be argued that larger brain and body sizes (lean body mass: bone and muscle) were adaptations to colder conditions. If further changes took place in cerebral and/or subcortical organization, they are simply not apparent from a paleoneurological perspective. Yet the Upper Paleolithic is the time when cave art makes its appearance, and one cannot help but wonder whether the explicit use of art involving symbolization might not also have been the time for the emergence of full language (see, e.g., Klein 2009). However, there is nothing in the direct fossil evidence, and in particular paleoneurology, to provide any evidence for such views. Claims for a single mutation are extremely speculative, and while some genes have been identified (chapters "► Genetics and Paleoanthropology," Vol. 1 and "► *Homo ergaster* and Its Contemporaries," Vol. 3) such as the FOXP2 (also in Neanderthals), these also involve more general aspects of cognition. It is more likely that stone tool making and its underlying cognitive elements are very similar to language, if not partially homologous (Holloway 1969, 1981, 2012; Stout 2006). Finally, it would appear that there has actually been a small reduction in brain size, probably allometric in nature, from about 0.015 myr to the present (Henneberg 1988; Hawks 2012).

The totality of evidence shows that the brain has always been evolving during our evolutionary journey, with myriad changes taking place at different tempos during different times. As suggested recently (Holloway 1997, p. 200):

> In sum, the major underlying selectional pressures for the evolution of the human brain were mostly social. It was an extraordinary evolutionary 'decision' to go with an animal that would take longer to mature, reach sexual maturity later, and be dependent for its food and safety upon its caretakers (parents?) for a longer period of time. The benefits for the animal were many, including a longer learning period, a more advanced, larger, and longer-growing brain, and an increasing dependence on social cohesion and tool making and tool using to cope with the environments that they encountered. Needless to say, language abilities using arbitrary symbol systems were an important ingredient in this evolution.
>
> The fossil record shows us that there was a feedback between the complexity of stone tools (which must be seen as a part of social behavior) and increasing brain size and the expansion of ecological niches. The 'initial kick,' however, the process that got the ball rolling, was a neuroendocrinological change affecting regulatory genes and target tissue-hormonal interactions that caused delayed maturation of the brain and a longer growing period, during which learning became one of our most important adaptations.

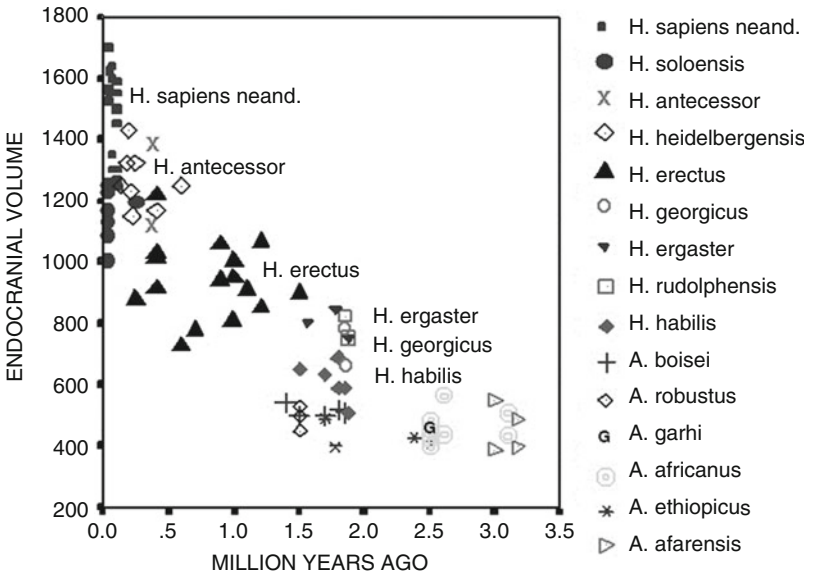

Fig. 10 Endocranial volume plotted against time, showing an accelerated change in volume from *Homo erectus* on to anatomically modern *Homo* in the late Pleistocene. This figure cannot include times of reorganization events, changes in neurogenomic elements, or any of the finer-grained differences in morphology of the endocasts. It is important to observe overlap of endocranial volumes, as well as their variation within taxa

These ideas have been detailed elsewhere (Holloway 1967, 1969, 1980, 1996, 2010), where more details may be found.

Finally, Fig. 10 provides the often-seen relationship between time and endocranial volume, and as should be apparent, there is considerable overlap between fossil groups and considerable variation within each taxon (e.g., *H. erectus*). Needless to say, such depictions cannot reveal the complex interactions between phases of reorganization, size increases through hypertrophy and hyperplasia, asymmetries in between left and right sides, different distributions of neuroreceptors and neurotransmitters, and the intricate interactions between natural selection, environmental challenges, mutation, drift, sensorimotor adaptations (think of the challenges of becoming fully bipedal), social behavior, communication skills, emotions, etc., all of which were operating during the whole of hominid brain evolution, each having some necessary relationship to neural reorganization, both cortical and subcortical. I hope the point is obvious that while we have learned much over the last century from the fossil, comparative, and neurogenomic evidence, we remain almost totally ignorant of how it really happened.

And to the Future?

There appear to be two common presumptions about our future brain evolution. One is that our biological evolution has stopped. The second is that our brains will continue to grow in size, with bulging frontal lobes, to handle our growing dependence on technology. What we have witnessed from the past fossil record is that our brains and bodies work largely in allometric fashion, and given the high metabolic cost of operating bigger brains (about 20–25 % of our metabolic resources go to supporting our brains, which constitute only 2 % of our total body weight), the second scenario seems highly unlikely. To demonstrate the first scenario would require vast amounts of information from each generation of many living populations: feasible perhaps, but not currently being collected. Furthermore, it is quite controversial whether brain size has any close relationship to intelligence; however, intelligence is actually defined and measured. Recent research based on MRI determinations of brain volume and selected batteries of cognitive tests have shown correlations between test scores and brain volume ranging from 0.4 to 0.6 (Andreasen et al. 1993; Anderson 2003; Davies et al. 2011). Most recently, Burgaleta et al. (2013) have found significant relationships between Full Scale, Performance, and Verbal IQ scores and cortical thickness in their study of cortical thickness development in children and adolescents. As more sophisticated imaging and neurogenomic advances are made, it would appear that our genes and epigenomic processes have much to do with brain biology and function. But if protein resources were to nosedive throughout the world for a significant period of time, selection would probably favor smaller body sizes in our species, and that could result in smaller brains, given an allometric relationship of roughly 0.3 between stature and brain size, at least in males (Holloway 1980). While genetic engineering may well provide some respite from the correlation between the ever-increasing mass of humanity and ecological and nutritive degradation, this too is likely to be nothing more than short-term fending off of the unstoppable future. These degradations are part and parcel of the human brain's capacity to ignore warnings that should properly curtail greed and stupidity. The paleontological record for most mammals suggests that genera (such as *Pan*, *Homo*, *Canis*, *Notocherus*, etc.) typically span approximately 5–10 Ma. Our genus has thus far a duration of about 2 myr. We, as a genus, despite our largish highly encephalized brains, have another 3 myr to go if we wish to be as successful in the paleontological longevity game.

Conclusions

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 among different populations throughout the world. After all, the human brain is still evolving, but for how long is quite uncertain.

References

Allen JS et al (2006) Looking for the Lunate Sulcus: A magnetic resonance imaging study in modern humans. The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology 288A(8):867–876

Amunts K et al (2010) Broca's region: novel organizational principles and multiple receptor mapping. PLoS Biol 8(9):e1000489

Anderson B (2003) Brain imaging and g. In: Nyborg H (ed) The scientific study of general intelligence: tribute to Arthur R. Jensen. Pergamon, New York, pp 29–40

Andreasen NC, Flaum M, Swayze HV, O'Leary DS, Alliger R, Cohen G, Ehrhardt N, Yuh WTC (1993) Intelligence and brain structure in normal individuals. Am J Psychiatry 150:130–134

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

Balzeau A, Gilissen E, Grimaud-Hervé D (2012) Shared pattern of endocranial shape asymmetries among great apes, anatomically modern humans, and fossil hominins. PLoS One 7:e29581

Bookstein F, Schäfer K, Prossinger H et al. (1999) Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. Anat Rec 6:217–224

Brodmann K (1909) Vergleichende Lokalizationslehre der Großhirnrinde. In ihren Prinzipien dargestellt auf Grund des Zellenbaues. J.A. Barth, Leipzig

Burgaleta M, Johnson W, Waber DP et al. (2013) Cognitive ability changes and dynamics of cortical thickness development in healthy children and adolescents. Neuroimage 84:810–819

Carlson KJ, Stout D, Jashashvili T et al. (2011) The endocast of MH1, *Australopithecus sediba*. Science 333:1402–1407

Dart R (1925) *Australopithecus africanus*: the man-ape of South Africa. Nature 115:195–199

Davies G, Tenesa A, Payton A et al. (2011) Genome-wide association studies establish that human intelligence is highly heritable and polygenic. Mol Psychiatry 16:996–1005

Deacon T (1997) The symbolic species: the co-evolution of language and the brain. Norton, New York

Falk D, Zollikofer CPE, Morimoto N, Ponce de León MS (2012) Metopic suture of Taung (*Australopithecus africanus*) and its implications for hominin brain evolution. PNAS 1119752109

Falk D (2014) Interpreting sulci on hominin endocasts: old hypotheses and new findings. Frontiers in Human Neuroscience 8:134

Gannon PJ, Holloway RL, Broadfield DC, Braun AR (1998) Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area homolog. Science 279:220–222

Gokcumen O, Tischler V, Tica J et al. (2013) Primate genome architecture influences structural variation mechanisms and function consequences. Proc Natl Acad Sci U S A 110:15764–15769

Gomez-Robles A, Hopkins WD, Sherwood CC (2013) Increases morphological asymmetry, evolvability and plasticity in human brain evolution. Proc R Soc B 280:20130575

Hawks J (2012) Selection for smaller brains in Holocene human evolution. arXiv:1102.5604

Henneberg M (1988) Decrease of human skull size in the Holocene. Hum Biol 60:395–405

Hernando-Herraez J (2013) Dynamics of DNA methylation in recent human and great ape evolution. PLoS Genet 9(13):1–12

Holloway RL (1967) The evolution of the human brain: some notes toward a synthesis between neural structure and the evolution of complex behavior. Gen Syst 12:3–19
Holloway RL (1969) Culture: a human domain. Curr Anthropol 10:395–412
Holloway RL (1979) Brain size, allometry, and reorganization: toward a synthesis. In: Hahn ME, Jensen C, Dudek BC (eds) Development and evolution of brain size: Behavioral implications. Academic Press, New York, pp 59–88
Holloway RL (1980) Within – species brain-body weight variability: a re-examination of the Danish data and other primate species. Am J Phys Anthropol 53:109–121
Holloway RL (1981) Culture, symbols, and human brain evolution. Dialect Anthropol 5:287–303
Holloway RL (1984) The Taung endocast and the lunate sulcus: a rejection of the hypothesis of its anterior position. Am J Phys Anthropol 64:285–287
Holloway RL (1995) Toward a synthetic theory of human brain evolution. In: Changeux JP, Chavaillon J (eds) Origins of the human brain. Clarendon, Oxford, pp 42–54
Holloway RL (1996) Evolution of the human brain. In: Lock A, Peters C (eds) Handbook of human symbolic evolution. Oxford University Press, New York, pp 74–116, Chap. 4
Holloway RL (1997) Brain evolution. In: Dulbecco R (ed) Encyclopedia of human biology, vol 2. Academic, New York, pp 189–200
Holloway RL (2000) Brain. In: Delson E, Tattersall I, Van Couvering J, Brooks AS (eds) Encyclopedia of human evolution and prehistory, 2nd edn., pp 141–149
Holloway RL (2008) The human brain evolving: a personal retrospective. Annu Rev Anthropol 37:1–19
Holloway RL (2010) Human brain endocasts, Taung, and the LB1 Hobbit brain. In: Broadfield D, Yuan M, Schick KD et al. (eds) The human brain evolving: paleoneurological studies in honor of Ralph L. Holloway. Stone Age Institute, Gosport
Holloway RL (2012) Language and tool making are similar cognitive processes. Behav Brain Sci 35(04):326
Holloway RL, de LaCoste-Lareymondie MC (1982) Brain endocast asymmetry in pongids and hominids: some preliminary findings on the paleontology of cerebral dominance. Am J Phys Anthropol 58:101–110
Holloway RL, Broadfield DC, Yuan MS (2004) In: Schwartz JH, Tattersall I (eds) The human fossil record. volume 3: brain endocasts: the paleoneurological evidence. Wiley, New York
Holloway RL, Broadfield DC, Carlson K (2013) Metopism and early human brain evolution. Am J Phys Anthro 150(S56):150–151
Hopkins WD, Nir TM (2010) Planum temporale surface area and grey matter asymmetries in chimpanzees (*Pan troglodytes*): the effect of handedness and comparison with findings in humans. Behav Brain Res 208:436–443
Insel T, Shapiro LE (1992) Oxytocin receptors and maternal behavior. Ann N Y Acad Sci 652:448–451
Jerison HJ (1973) Evolution of brain and intelligence. Academic, New York
Klein RG (2009) The human career. Human biological and cultural origins, 3rd edn. University of Chicago Press, Chicago
LeMay M (1976) Morphological cerebral asymmetries of modern man, fossil man, and nonhuman primates. Ann N Y Acad Sci 280:349–366
Martin RD (1983) Human evolution in an ecological context. American Museum of Natural History James Arthur lecture, New York, 1982
Martin RD, Isler K (2010) The maternal energy hypothesis of brain evolution: an update. In: Broadfield DC et al (eds) The human brain evolving: paleoneurological studies in honor of Ralph L. Holloway. Stone Age Institute, Gosport
Miller DJ, Duka T, Stimpson CD et al. (2012) Prolonged myelination in human neocortical evolution. Proc Natl Acad Sci U S A 109(41):16480–16485
Neubauer S, Gunz P, Weber GW 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

Nyborg H (ed) (2003) The scientific study of general intelligence: tribute to Arthur R. Jensen. Pergamon, Amsterdam

Pearce E, Stringer C, Dunbar RIM (2013) New insights into differences in brain organiztion between Neanderthals and anatomically modern humans. Proc Roy Soc B Biol Sci 280:1758

Preuss TD (2012) Human brain evolution: from gene discovery to phenotypic discovery. Proc Natl Acad Sci U S A 109(Suppl 1):10709–10716

Rilling JK, Glasser MF, Preuss TM et al. (2008) The evolution of the arcuate fasciculus revealed with comparative DTI. Nat Neurosci 11:382–384

Schenker NM, Hopkins WD, Spocter MA et al. (2010) Broca's area homologue in chimpanzees (*Pan troglodytes*): probabilistic mapping, asymmetry, and comparison to humans. Cereb Cortex 20:730–742

Semendeferi K, Damasio H, Frank R, Van Hoesen GW (1997) The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. J Hum Evol 32:375–388

Semendeferi K, Barger N, Schenker N (2010) Brain reorganization in humans and apes. In: Broadfield DC, Yuan M, Schick KD et al. (eds) The human brain evolving: paleoneurological studies in honor of Ralph L. Holloway. Stone Age Institute, Gosport

Sherwood CC, Broadfield DC, Holloway RL et al. (2003) Variability in Broca's area homologue in African great apes: implications for language evolution. Anat Rec 271A:276–285

Stephan H, Frahm H, Baron G (1981) New and revised data on volumes of brain structures in insectivores and primates. Folia Primatol 35:1–29

Stout D (2006) Oldowan tool making and hominin brain evolution: theory and research using positron emission tomography (PET). In: Toth N, Schick K (eds) The Oldowan: case studies into the earliest Stone Age. Stone Age Institute, Gosport

Tobias PV (1971) The brain in hominid evolution. Columbia University Press, New York

Toth N (1985) Archaeological evidence for preferential right-handedness in lower and middle Pleistocene, and its behavioral implications. J Hum Evol 14:607–614

Uylings HBM, van Eden CG (1990) Qualitative and quantitative comparison of the prefrontal cortex in rats and primates, including humans. Prog Brain Res 85:31–62

von Bonin G (1937) Brain weight and body weight in mammals. Journal of General Psychology 16:379–389

von Bonin G (1948) The frontal of primates: Cytoarchitectural studies. Research Publicartion - Association for Research in Nervous and Mental Disease 27:67–83

Weber GW, Gunz P, Neubauer S, Mitteroecker P, Bookstein FL (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. Cambridge University Press, New York, pp 298–316

Wey H-Y, Phillips KA, McKay DR et al. (2013) Multi-region hemispheric specialization differentiates human from nonhuman primate brain function. Brain Struct Funct

Zeng I, Konopka G, Hunt BG et al. (2012) Divergent whole-genome methylation maps of human and chimpanzee brains reveal epigenetic basis of human regulatory evolution. Am J Hum Genet 91:455–465

Zollikofer CPE, Ponce de León MS (2013) Pandora's growing box: inferring the evolution and development of hominin brains from endocasts. Evol Anthropol 22:20–23