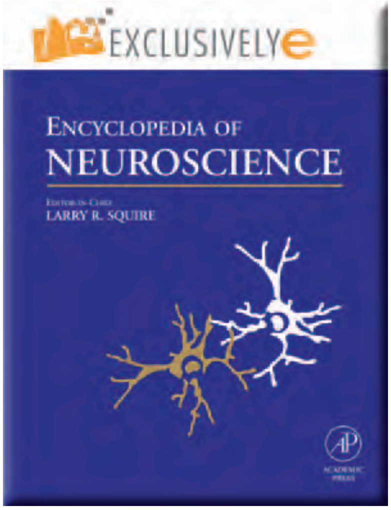

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Brain Fossils: Endocasts

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Introduction

The human brain, as any other part of our body, has an evolutionary history, no more or less remarkable than the evolutionary histories that have fashioned the nervous systems of millions of other living organisms on our planet. Yet it remains to be seen whether the trillions of potential neural states that can, through a singular human adaptation, namely, language, link with other brains of the same species and either maintain or exterminate our existence. After all, hundreds of thousands, if not millions, of species have met their terminal fates, extinction, during the past 500 or so million years. The human species, as we recognize ourselves, has had an evolutionary life span of only a few hundred thousand years, at most, whereas many animal genera have had life spans averaging 5–10 My. As a genus, we might have an ancestry of perhaps 2 My; what is left is largely up to our collective use of our brains, and another 5 My seems rather unlikely.

How did we emerge as the primate with the largest brain in absolute size and complexity? What does the fossil record tell us about the evolutionary journey our ancestors embraced during just the last 3–5 My, when we became hominids?

Evolutionary Approaches

Paleoneurology, the Direct Evidence

There are three important approaches to these questions, only one of which we will explore here in more detail. The line of evidence that is direct is paleoneurology, the study of the fossil evidence of the central nervous system, as found on the surface of endocasts. Endocasts are not fossilized brains, but rather the casts of the insides of crania of fossil animals, which in our case mean the hominids of the past 3–5 My known from Africa, Asia, and Europe. Endocasts come in three flavors: natural, artificial (or human-made), and 'virtual' (as generated by a computer from computed tomography (CT) scan data).

Some of the earliest hominid endocasts, such as those from South Africa, such as the infamous Taung child, and known as *Australopithecus africanus* and/or *robustus*, are known from natural endocasts, fashioned over thousands of years by fine sediments entering the postmortem crania, and gradually being compacted and infiltrated by calcareous solutions to become a rock-hard external replica of whatever neuroanatomical details existed on the internal table of cranial bone. Note that in this natural process, the state of the crania will determine how good the replication of surface details will be, that is, how complete the cranial portions are, and whether or not they are distorted by postmortem geological changes, fractures, and/or plastic flow. No thalami, amygdala, hippocampi, cerebellar nuclei, mirror neurons, or fiber tracts such as the corpus callosum, or arcuate fasciculus will ever be preserved. In hominids, then, and indeed, even most primates, fossil or extant, endocasts can only show the surface features of the cerebral cortex, posterior cerebellum, and some of the brain stem to the level of the foramen magnum (Figure 1).

Man-made endocasts are usually made by applying rubber latex, or silicon rubber to the internal cranial surfaces of fossil crania, and these then become the casts which are studied. More recently, because of technical advances in computer imaging and scanning techniques, 'virtual' endocasts can be made, and an endocast model literally carved out of a plastic block using the data set of scanned coordinates collected from CT scans. The same sorry set of restrictions is applicable to these endocasts. Additionally, the resolution of the scans is variable (usually between 1 and 0.5 mm); thus not all details can be collected from a 'virtual' rather than an 'actual' endocast.

So what, then, are the potential valuable insights one can derive from the direct evidence for human brain evolution if one studies endocasts?

Comparative Neurology, Indirect Evidence

Before answering this question, it is important to look at other kinds of evidence. First, there is the study of comparative neurology. It is the most important line of evidence for understanding the relationships between neural and behavioral variation. It compares the size and structures of various animal brains and attempts to relate the differences and similarities to behavior. Most importantly, however, is that the objects of study, the brains, are simply the current end products of past evolutionary events: the comparative record is not an evolutionary sequence or record. Nevertheless, monkeys, chimpanzees, rats, mice, etc., are routinely compared to modern humans as if these were in some way an evolutionary record. They are not. Nevertheless, without comparative neurology, it would be impossible to study paleoneurology (the reverse does not necessarily hold).

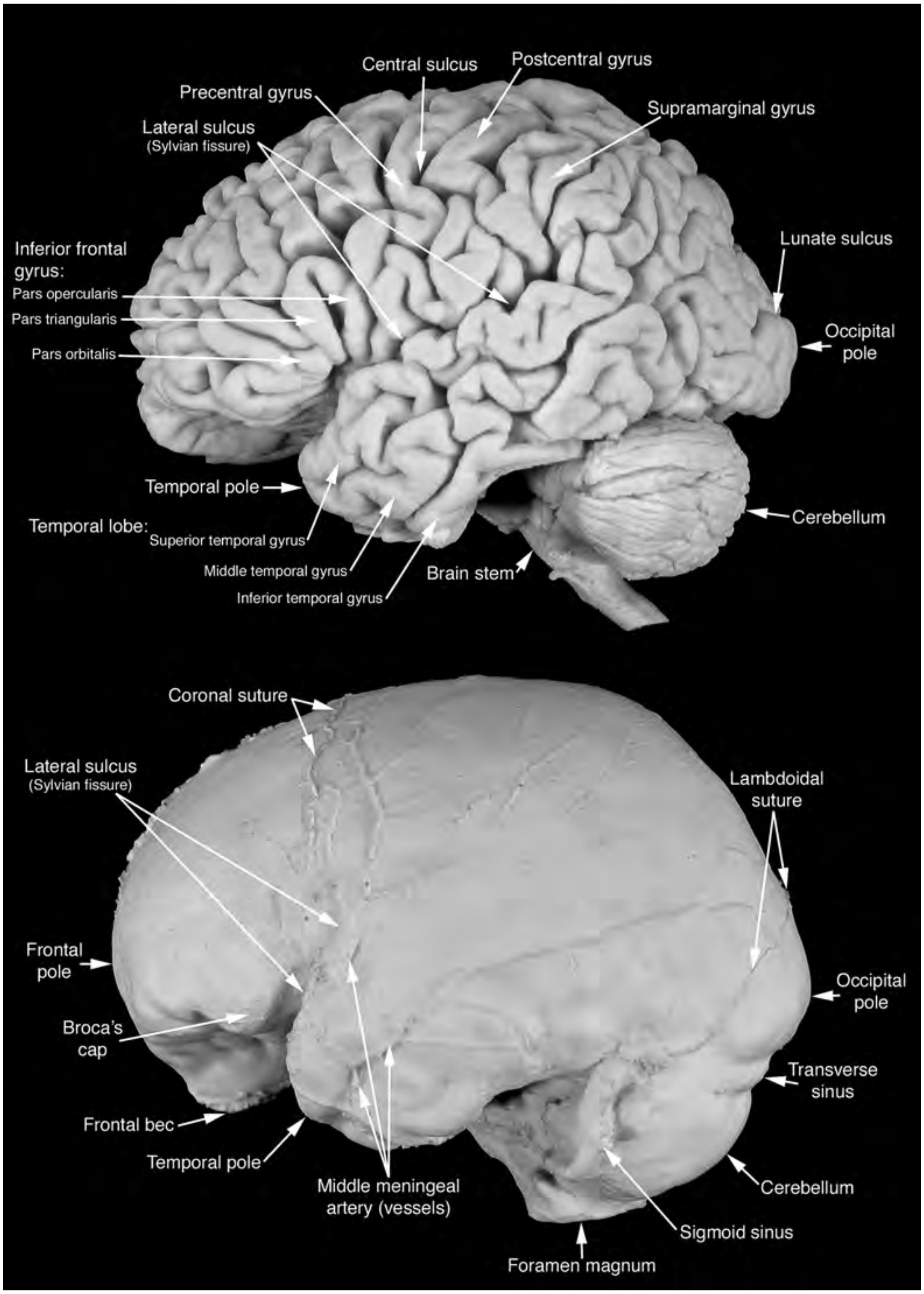

Figure 1 Lateral view of a modern human brain cast and the accompanying endocast. It is obvious that much detail is lost in the endocast.

Molecular Neurogenetics

Another source of information regarding brain evolutionary histories is so new, that little can be said, except that it could well become an important source of direct evidence regarding the evolutionary history of any living animal's brain. This source is molecular neurogenetics. Here, we are beginning to unravel not only what the genetic elements are, but which ones have been under selective pressures in the past.

Data Provided by Endocasts

First, and perhaps of most importance and interest is size, meaning the endocast's volume in cubic centimeters or milliliters. This volume is of course somewhat larger than the volume of the brain, as the endocranial volume (EV) also includes meninges, cerebrospinal fluid, and cranial nerves. The EV is about 8–12% more than the actual brain volume. It is most intriguing to realize that the modern human brain varies in size from about 900 to 2000+ g (remember the old chestnut of Anatole de France at 900 and Swift and Turgenev at about 2000+?), which represent about 1000 g (or cc) which is the total evolutionary change from early australopithecines at 400 ml, to modern human average of about 1400 ml. The average brain weight for modern *Homo sapiens* is 1330 g. Intriguing or not, we now know that there is some correlative relationship between brain size and cognitive abilities at an R of about 0.3, and the fossil evidence for complex cognitive behavior surely shows an increasing complexity through the 2.6 My of hominids' tool productions and later, art works. That said, one cannot, with any degree of certainty, establish connections between selection for brain sizes in hominids and their tools. One reason is that there is a relationship between body size and brain size, and it could well have been the case that selection favored increased body size at certain times and the brain, because of its allometric relationship with body size, simply increased in size, eventually bestowing greater cognitive ability on the hominids so endowed. While rarely the case, postcranial remains are found with crania, and these can provide biological anthropologists some estimates of body size, which in turn can lead to estimates of relative brain size, and when placed within a comparative data set (say all mammals, or all primates) can lead to the calculation of encephalization coefficients (EQs). For example, *A. africanus*, which existed about 2–3 Ma, had an average brain size of about 400–450 cc, roughly the same as chimpanzees, and less than gorillas, yet their body sizes suggest slightly higher EQs than these living apes. However, when we examine these relationships in *Homo erectus* hominids, we find that their body weights were essentially the same as our own, yet their brain sizes were on the order of 750–850 cc. Clearly, there must have been selection pressures operating in the Pleistocene to increase brain size without increasing body size, thus making it reasonably clear that human brain evolution was a mosaic affair, at least as far as brain and body sizes were concerned. Furthermore, it does appear that Neandertal hominids living 200 000 to about 28 000 years ago did have, on average, larger brains than we do, but we also believe that their body sizes were also larger, with more lean muscle mass related to adaptations to colder temperatures. Table 1 provides a listing of hominid brain sizes, by taxonomic group, and their respective EQs. EQs are a relative measure of a species' degree of encephalization calculated from some known allometric data-base. For example, Martin's EQ in Table 1 is calculated from the equation, EQ Martin = brain weight of an animal/0.0991 × (body weight)$^{0.762\,37}$. The data comes from 88 species of primates where the allometric equation for this data set becomes the denominator of the above equation. The EQ Homo is based on the equation: EQ Homo = brain weight/1.0 (body weight)$^{0.649\,06}$. Since

Table 1 Hominid brain sizes, by taxonomic group, and their respective EQs

Taxa	*Mean vol. (cm^3)*	*N*	*Range (cm^3)*	*Mean (Ma)*	*Body mass (kg)*	*EQ Martin*	*EQ Homo*
A. afarensis	445	5	387–550	3.11	37.00	4.87	42.79
A. africanus	462	9	400–560	2.66	35.50	5.21	45.58
P. ethiopicus	431	4	400–490	2.09	37.60	4.66	41.01
A. garhi	450	1	450.00	2.50	NA	NA	NA
H. erectus	941	20	727–1220	0.81	57.80	7.32	67.64
H. ergaster	800	2	750–848	1.74	57.50	6.25	57.72
H. habilis	610	6	510–687	1.76	34.30	7.06	61.50
H. heidelbergensis	1265	12	1150–1450	0.27	68.70	8.64	81.30
H. rudolfensis	788	2	752–825	1.87	45.60	7.35	66.08
H. neanderthalensis	1487	28	1200–1700	0.08	64.90	10.60	99.14
H. sapiens	1330	23	1250–1730	0.01	63.50	9.63	89.90
H. soloensis	1155	7	1013–1250	0.06	NA	NA	NA
P. robustus	493	3	450–530	1.50	36.10	5.49	48.11
P. boisei	515	6	475–545	1.65	41.30	5.17	46.02
P. troglodytes	405	> 100	350–450	0.01	46.00	3.75	33.75
G. gorilla	500	> 100	400–685	0.01	105.00	2.47	24.39

N, number of specimens.

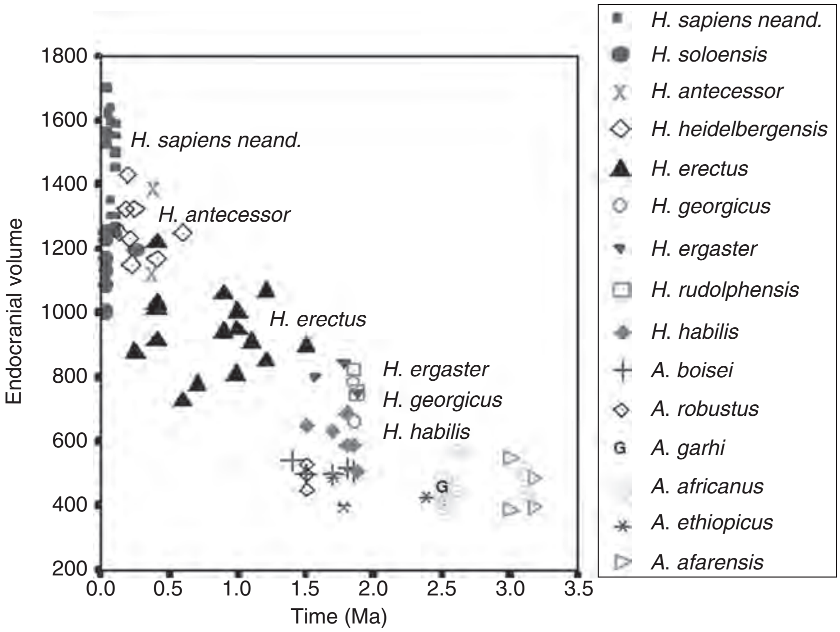

Figure 2 This chart shows the changes through time of hominid EV. It is important to realize that each point itself takes up many thousands of years, and that such a rendition can have little to suggest in terms of actual evolutionary forces and resultant brain changes.

H. sapiens has the highest EQ (whatever method or data set is used), this immediately provides an EQ for an animal as a percentage of modern *Homo*'s value, which is 1.00 or 100. (This equation is based on plotting the log 10 of modern *Homo*'s 1330 brain against his body weight of 65 000, and the intercept is 1.0, since if body weight is zero, so is the brain.)

If the brain sizes of our hominid ancestors of the last 3 My are plotted against time (Figure 2), one finds a curve that appears curvilinear, but which has so many gaps in the fossil record, that it cannot truly represent the complexity of selective forces that operated both on brain and body sizes during the Pliocene and Pleistocene. Of interest, there are data which show that brain size in modern humans has decreased over the last 10 000 years, and should the protein resources of this planet suffer severe degrading, it can be reasonably speculated that brain size would show a further decrease in those regions severely affected. What effect this would have on cognition is not certain.

Second, endocasts provide information about cerebral asymmetries. As LeMay and Galaburda *et al.* showed, cerebral petalias (projections of cerebral cortex into the surrounding cranial table of bone) correlated at roughly 90% with handedness in living modern humans. For example, a torque-like pattern of a protrusion of the left occipital cortex and a rightward greater width of the prefrontal lobe was highly concordant with right-handedness. The opposite pattern correlated with left-handedness, and both patterns could be found with ambidextrous subjects. Again, these relationships were correlations, and the relationships were clearly not 100% obligate. As we know from many neurological studies, including split-brain research, each hemisphere appears to show specializations for cognitive processing, the left hemisphere usually credited with greater analytical reasoning, the right with more holistic, gestalt-like processing. While it is true that asymmetries are found in many different animal brains, this particular pattern of a torque-growth process appears relegated to humans alone, although more research needs to be done with the chimpanzee, our closest animal relative (Figure 3).

Here is where the principle of uniformitarianism is important: if we find similar cerebral patterns on fossil hominid endocasts, are we reasonably entitled to suggest that they also had some degree of cerebral specialization and cognitive processing either very similar to, or identical to our own? Since behavior does not fossilize, it is unlikely we will ever know the full answer. Many archeologists and paleoanthropologists believe, for example, that there could not have been any hominids with language until one finds evidence for symbolic art, as found in the caves of France and Spain, dating to roughly 20 000–30 000 years ago. Others, including this author, conclude that if one finds evidence for cerebral asymmetries, including those for left/right Broca's regions, then one must consider that language could well have been present, at least by 1.8 Ma, since the fossil hominid, *Homo rudolfensis* (KNM-ER 1470, with an EV of 752 cc),

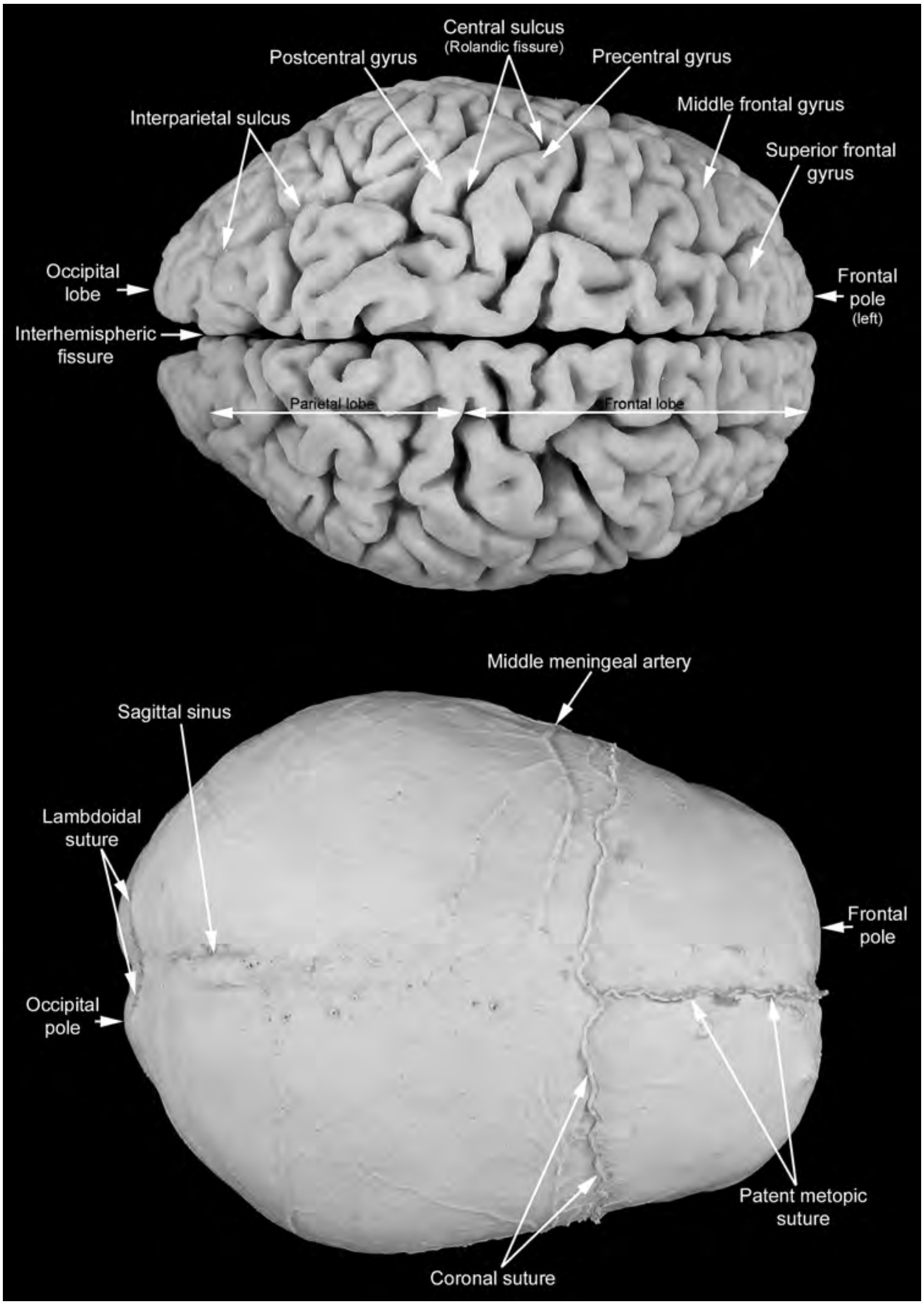

Figure 3 A dorsal view of a modern brain cast and the accompanying endocast. Note that the left occipital lobe extends further posteriorly than the right side, while the lateral width of the right frontal lobe is greater than the left. This is the typical torque-like petalial pattern associated with right-handedness.

shows such asymmetries very clearly. Similarly, such asymmetries can be found in some of the *H. erectus* specimens, and also Neandertals. No art is known for the so-called Clovis peoples of 12 000 years ago in the Americas, just beautifully fashioned spear points. Would one argue that these members of modern *H. sapiens* lacked language? Australian Aborigine stone tools are primitive, but anthropologists still struggle to understand their complex social relationships, learned by Aborigines through their languages. As the author and de LaCoste-Lareymondie showed, the petalial patterns of a combination of left-occipital and right prefrontal width were not found in a large sample of chimpanzees and gorillas, but were found in many of the fossil hominid endocasts. We conclude, that language, surely more primitive than our own, has been around for at least a million years, if not well before that.

Third, endocasts sometimes do show cerebral morphology, that is, convolutional details that suggest reorganizational changes as well as size increases of the whole brain. For example, relevant to the above suggestions regarding Broca's region, the various endocasts of australopithecines do not show a Broca's cap region (areas 44, 45, 47) that is like our own, whereas later fossil hominids, such as KNM-ER 1470, and all subsequent fossils of the genus *Homo*, do appear to have such a region like our own, at least in terms of endocast morphology. (What the actual cytoarchitecture was is anyone's guess.)

Another important landmark, at least in primate neuroanatomical terms, is the lunate sulcus, which in great apes (as well as all anthropoids) is a sulcus delimiting the anterior extent of primary visual striate cortex (PVC), area 17 of Brodmann from adjacent parietal association cortex. As we know from allometric studies, the modern human PVC is about 120% less in volume than would be expected for a primate of its brain size, and the lateral geniculate body is about 144% less. The question is, when did this reduction take place, and what part of the cortex had to expand relatively to make up for the lost PVC volume? The answer to the latter is evident, and that is that parietal association cortex probably expanded relatively in hominids. The first question, however, has been largely controversial. When Dart published his epochal paper in *Nature* (1925), part of his reasoning for naming the small natural endocast, and fossil crania and mandible as *A. africanus*, was that the endocast showed a lunate sulcus in a relatively posterior position compared to apes, that is, more of a human-like posterior position. This led Dart, a student of Grafton Elliot Smith, the neuroanatomist who helped define the lunate sulcus, to conclude that even a couple of million years ago, the hominid brain had undergone some cerebral reorganization from an ape-like ancestor. Modern humans seldom show a complete lunate sulcus, and, when present, it is mostly fragmented, and is not a completely perfect delimiter of PVC, although it does occur in a relatively posterior position (Figures 4 and 5).

As mentioned earlier, not all convolutions impress onto the internal table of cranial bone, and reading some of the dim imprints can be very challenging, and controversial. The sulcus in question is not without ambiguity, but the placement of the lunate sulcus in more anterior positions either converts the Taung hominid to a monkey, or violates the remaining morphology. As we showed in several publications, placing the lunate in a typical chimpanzee position violates the remaining morphology. Nevertheless, these two examples, Broca's regions and the lunate sulcus, demonstrate that the hominid brain became reorganized to a human-like pattern early in hominid evolution, and well before the final enlargement of the cerebral cortex as in modern *H. sapiens*.

Fourth, one can measure the endocasts using CT scans or plain calipers, rendering large data sets with chord and arc measurements, and then apply sophisticated multivariate analyses to the data sets, in the hope that combinations of measurements might reflect some taxonomic shape differences that might

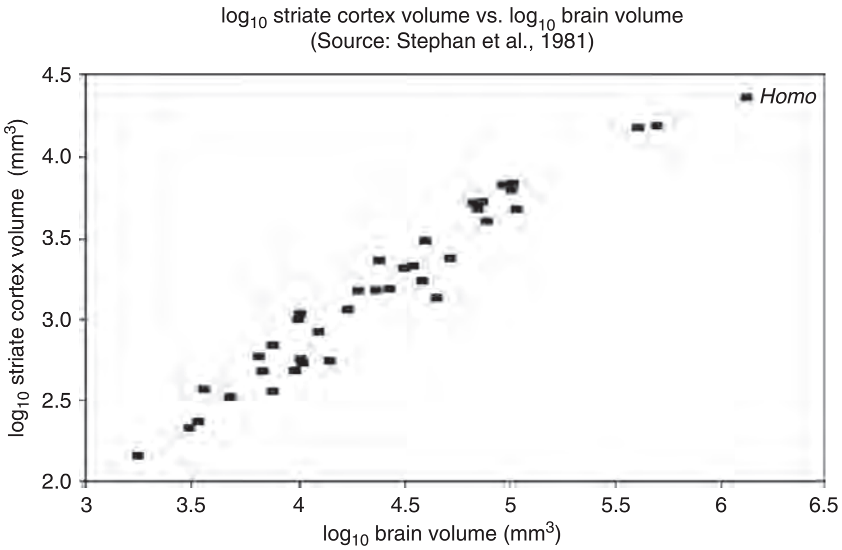

Figure 4 This shows a typical allometric relationship between total brain size and a part of the brain, primary visual striate cortex (area 17 of Brodmann). The log–log relationship is obviously linear, and the human point is about 121% lower than would be expected based on the rest of the primate data.

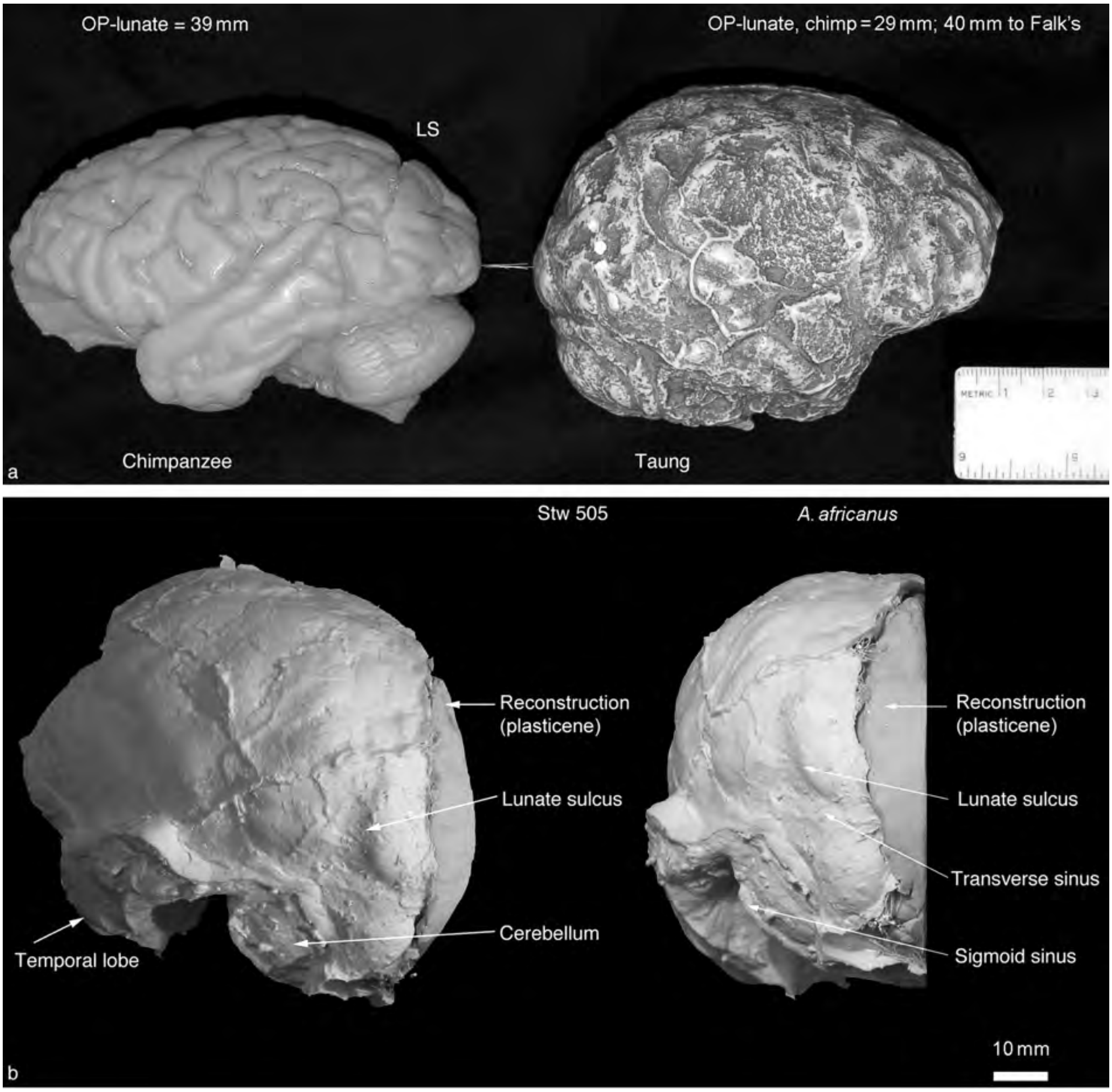

Figure 5 (a) This shows the contrast between a typical chimpanzee (*Pan troglodytes*) brain and that of the natural endocast of the Taung fossil (*Australopithecus africanus*) from South Africa. When the typical chimp position for the lunate sulcus (LS) is placed on the Taung endocast, it violates the sulcal morphology, indicating that the lunate was not in a typical ape position on the Taung child. Placing the LS more anteriorly reduces the Taung child to a monkey status, which is clearly wrong. (b) Views (oblique, occipital) of the new Stw 505 *A. africanus* endocast, showing a true lunate sulcus in a relatively posterior position, thus indicating reorganization of the cortex prior to any significant brain enlargement.

be in turn related to function. Alas, this is not the case. All of the measures and the resulting indices largely, if not completely, reflect the fact that the measurements are completely correlated to the endocasts' volumes. Still, to the extent that endocast shape might have some taxonomic value, or help with reconstructions of missing regions, these measurements do have value.

Fifth, the meningeal patterns of blood supply to the meninges through the middle meningeal artery (mostly) do show variability between hominid groups. In general, as the brain enlarged, the pattern of meningeal imprints on hominid endocasts shows an increase in complexity. Unfortunately, these patterns have no known association with behavioral variables.

These five sets of data are what one can find by studying endocasts. As animals differ more, say between mammals, reptiles, amphibians, birds, and fish, brain endocasts show very different patterns of neurological structures, and the interested reader will

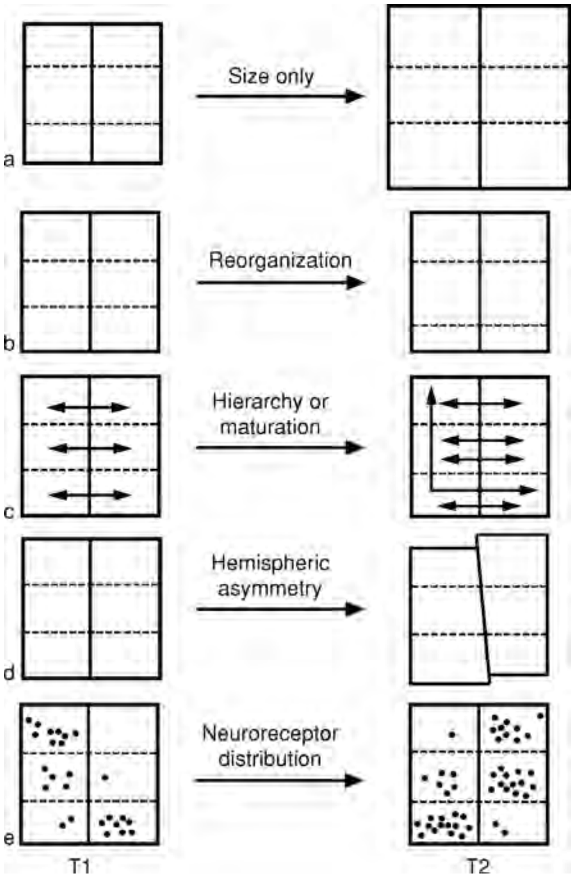

Figure 6 These boxes represent some possible scenarios of brain changes from 'time 1' to 'time 2'. Scenarios (b–e) suggest reorganizational changes that may not be visible on endocasts, although (b) and (d) are variably present on endocasts. (b), For example, symbolizes a reduction of primary visual striate cortex, with a posteriorly placed lunate sulcus, and (d) shows the typical torque-petalial pattern we associate with right-handedness. Neither (c) or (e) are likely to show details on the cortical surface, as the changes could be related to fiber connections, or to subcortical structures not appearing on endocasts.

find a rich literature of comparative neuroanatomy covering these and many invertebrate species (Figure 6).

Conclusions

Clearly, with so few fossil remains discovered thus far, and these spanning a time period of perhaps 5 My, our understanding of how our brains evolved must be incomplete, and largely speculative. In the past, and continuing today, it is brain size that appears to capture most scientists' minds. The direct paleoneurological evidence tells us, however, that our brain evolution picture had to have been far more complex, as we have clear evidence of reorganizational changes interspersed with brain size changes, some of which were absolute, and some relative, that is, dependent on body size increases or decreases. The picture, most importantly, is not a lineal one, but one in which the rates of change were not constant but shifting with selection pressures, immigration, genetic drift, mutations, and environmental challenges involving a most complex interplay of climates, ecologies, prey and predators, as well as social and material interactions within and between groups. Brain evolution in hominids was a mosaic of mosaics. Measuring the size of brain endocasts is the least difficult task in unraveling the evolutionary changes through time. Far more difficult, yet equally important, is discovering the organizational changes that occurred, and when these occurred. The picture starts out with brain sizes within the range of our closest relative, the common chimpanzee, *Pan troglodytes*, with an average brain size of about 385–400 cc. This is apparent in australopithecine hominids, starting with *Australopithecus afarensis* at about 3–3.5 Ma. However, one of these endocasts shows a lunate sulcus in a posterior position quite different than the anterior position found in apes, including the Miocene *Proconsul africanus* fossil. The frontal lobes of this australopithecine, as well as the later derived *A. africanus* group, are narrow, and the Broca's region is not human like. That reorganizational change occurs much later, being present in *Homo* lineages (such as *H. erectus*, *H. ergaster*, *H. antecessor*, *H. habilis*, *H. rudolphensis*, *H. georgicus*, *H. heidelbergensis*, and *H. sapiens neandertalensis*) at about 1.8 Ma, with a brain size of 752 cc. Thus, two critical reorganizational changes took place before the major increase in brain and body size occurred. The author believes that those changes relate to social skills including primitive language being evolved, setting a positive feedback pattern, in which behavioral complexity and brain size are inextricably linked. After ~1 Ma, brain sizes increase to modern values, while the body size remains similar to our own, and the archeological records suggest increasing social and material (stone tools, etc.) behavioral complexity occurring through this time. Perhaps other reorganizational changes in the brain, refinements of cortical structures, acquisition of specific socially relevant behavioral modules accompanied these size increases. What these were cannot at this time be gleaned from the direct endocast evidence. On these questions, the evidence is mute and perhaps forever moot.

See also: Allometric Analysis of Brain Size; Brain Asymmetry: Evolution; Brain Development: The Generation of Large Brains; Brain Modules: Mosaic Evolution; Brain Scaling Laws; Brains of Primitive Chordates; Evolution of Vertebrate Brains; Social Brain: Evolution.

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