

Evolution of the Brain, in Humans – Paleoneurology

RALPH L. HOLLOWAY¹, CHET C. SHERWOOD²,
PATRICK R. HOF³, JAMES K. RILLING⁴

¹Department of Anthropology, Columbia University,
MO, USA

²Department of Anthropology and Biomedical
Sciences, Kent State University, OH, USA

³Department of Neuroscience, Mount Sinai School of
Medicine, New York, NY, USA

⁴Department of Anthropology, Emory University,
Atlanta, GA, USA

Synonyms

Paleoneurology

Definition

The evolution of the human brain from hominids existing perhaps 3–5 MYA (million years ago) to the present has been a mosaic process of size increases intercalated with episodes of ►reorganization of the cerebral cortex. The fossil evidence shows that reorganization preceded large-scale brain size increase, whether ►allometric or not, by about 2–3 MYA and again around 1 MYA, involving a reduction of primary visual cortex and cerebral asymmetries, including those within Broca's region. These changes were followed by nearly a tripling of brain size.

Characteristics

What is Paleoneurology?

►Paleoneurology is the study of the fossil evidence for brain evolution and is, at present, the only direct line of evidence as to how different animals' brains have evolved through time. Paleoneurology is not a new branch of paleontological study as earlier publications go back to those of Oken, who found petrified mud in a crocodilian skull in 1819, as mentioned by Owen in 1841. Tilly Edinger wrote a valuable monograph on the evolution of the horse brain and her 1929 [1] and 1949 [2] papers on the history of paleoneurology are an important critique of comparative neurology's mistaken

notions of human evolution. Kochetkova's [3] treatise on ►endocasts is another valuable source, both for history and methods, as well as descriptions of some of the fossil hominids.

What are Endocasts?

The objects studied are called endocasts. These are simply casts that are made from the inside table of bone of crania. It is particularly important to realize that the endocasts are just that; they are *not* casts of brains, because in life, the brain is surrounded by three meningeal layers, the dura mater, arachnoid tissue and cerebrospinal fluid and lastly the pia mater, a thin investing tissue directly overlying the brain. With death, these tissues as well as the brain dissolve, leaving a cranium that will in time fossilize.

How does Paleoneurology Differ from Comparative Neurology?

Comparative neuroscience studies the brains of living animal species and is a particularly rich source of data from a microscopic level to that of whole brains. These data are essential to the understanding of the relationships between structure, function and behavior. In other words, how the brain varies in terms of its cellular makeup, cytoarchitecture, fiber systems, neural nuclei, axons and dendrites and the supporting matrix of glial cells, neurotransmitters and neuroreceptors can hopefully be related to variability of behavior. Paleoneurology is correspondingly exceedingly poor in data, as only the surface features of the once living and pulsating brain can be observed if – and only if – they are imprinted onto the internal table of bone. The drawback of comparative studies is that each species is currently an end product of its own separate line of evolution and therefore cannot provide any real time depth to past evolutionary events that affected the brain. Nevertheless, without comparative studies, there would be no possibility of correctly identifying and interpreting those surface features of the endocast that may have changed during evolutionary time from species to species.

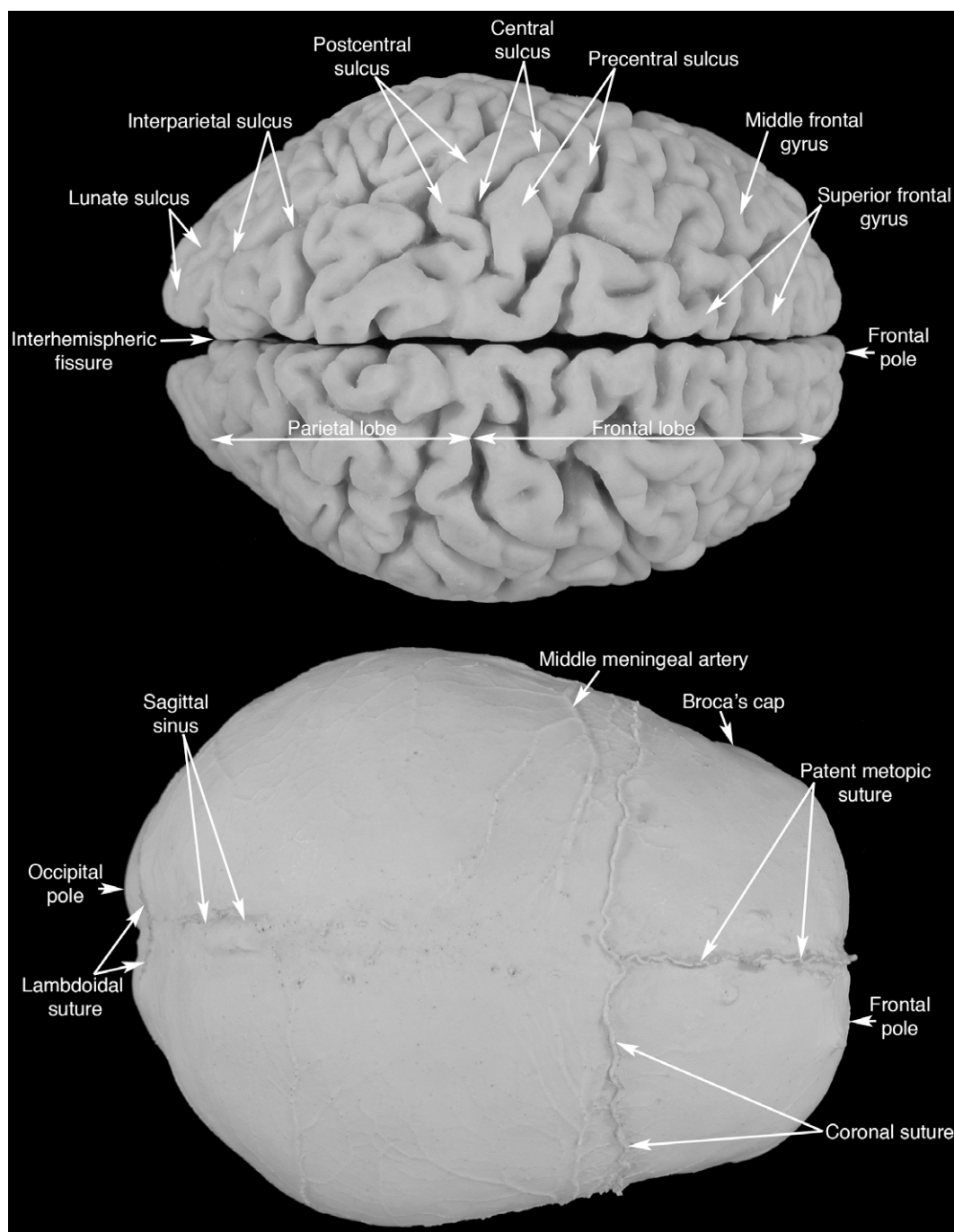
How are Endocasts Made?

First, it is necessary to appreciate that the data obtainable from endocasts depend on the completeness

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and quality of the endocast and this will be affected by how the endocast has been made. Some endocasts are natural, i.e. made by fine sediments collecting (through the foramina of the cranium) in the cranium of the deceased animal and with time being compacted and

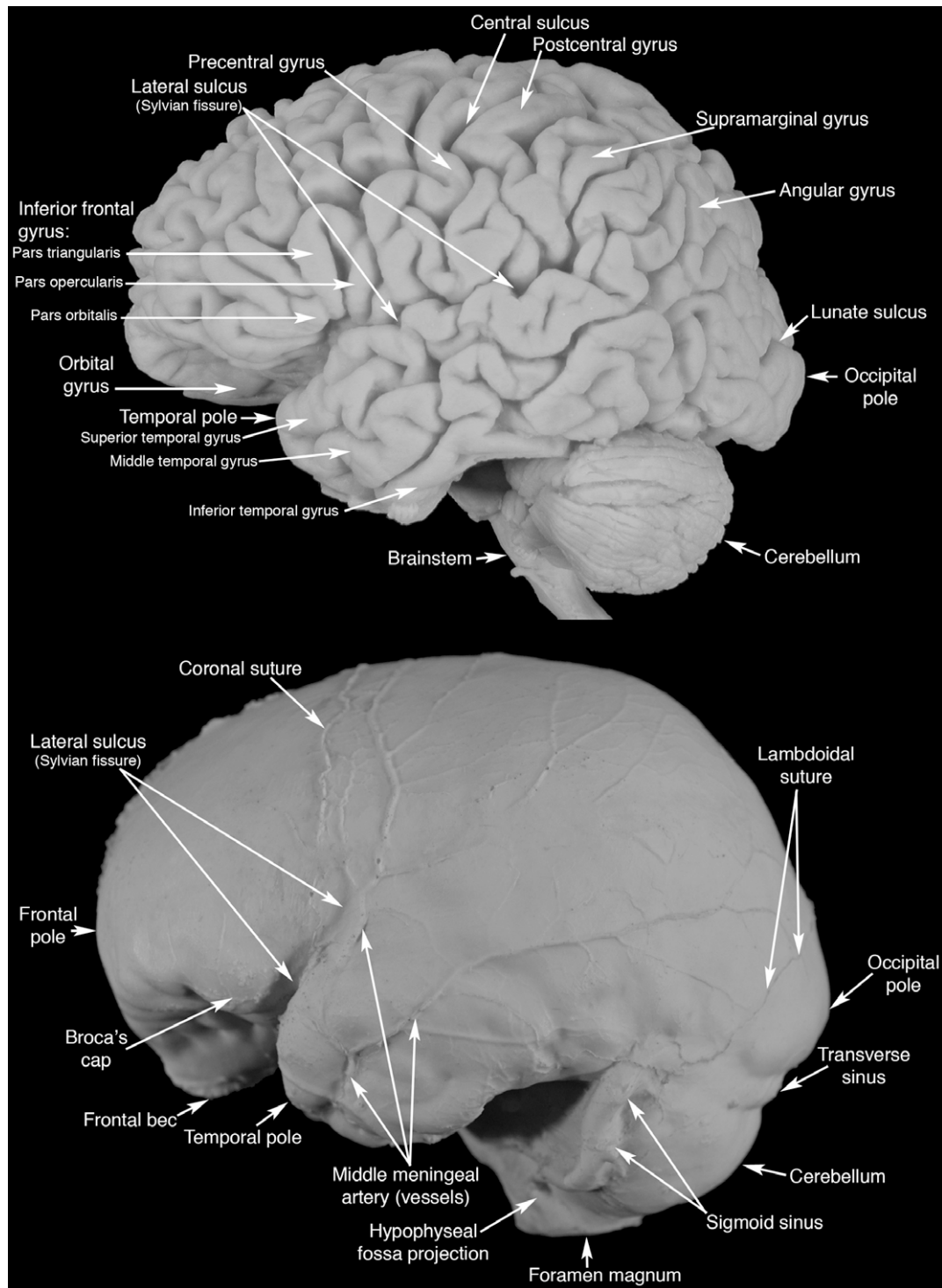
eventually turned to stone. Some of these endocasts can obtain an almost jewel-like quality. At least three endocasts of our ancestral hominid australopithecine line of 2–4 million years ago were made in this way (e.g. Taung, Sts 60, Sk 1585, Type 2; see [4] for



Evolution of the Brain, in Humans – Paleoneurology. Figure 1 A dorsal view of a cast of a modern human brain and its accompanying endocast. Note that the left occipital lobe is wider and projects more posteriorly than the right side and that the right frontal lobe width is slightly larger than the left. This is typical of the torque petalial pattern associated with right-handedness.

descriptions). Endocasts can also be man-made, by directly covering the surface of the internal bony table with a casting medium, such as latex rubber or various forms of silicon rubber (Figs. 1 and 2). Endocasts can

also be made from the data collected during CT scans, which can be rendered as a “virtual” endocast on the computer. This data set, in turn, can be sent to a machine that will literally carve out an endocast from a block of



Evolution of the Brain, in Humans – Paleoneurology. Figure 2 The same brain and endocast in lateral view, showing the difference in details between a cast of the brain and its endocast.

plastic, producing what is called a stereolithographic endocast. For example, the recent “hobbit” endocast of the putative *Homo floresiensis* hominid was made this way [5], as was the virtual endocast for Saccopastore, a Neandertal from Italy [6]. Increasingly, CT scans are used for endocranial analyses.

What Data Can Endocasts Provide?

Overall Brain Volume

The most useful data gleaned from endocasts is the size of the once living brain, usually determined by either water displacement of the endocast or by a computer algorithm which simply adds sections taken from a CT scan of either the endocast or the cranium. Endocast volumes are somewhat larger, by about 8–12%, than the actual once-living brain, as the endocranial volume (ECV) includes meninges, cerebral fluid (including cisternae) and cranial nerves. Fossil hominids, of which we are the present-day terminal end products, had brain sizes varying from roughly 385 to 1,700 ml, while the average for our own species is about 1,400 ml. If the body weight is known from estimates made from measuring postcranial bones, then it is possible to calculate some derived statistics that may have some epistemological value. For example, “relative brain size” (RBS) would be the weight of the brain divided by body weight. Modern humans have an RBS of roughly 2%, and this value is neither the smallest nor largest in the animal kingdom or even in the primate order. It is also possible, when body and brain sizes are known, to calculate a statistic called the “encephalization quotient” (EQ 1 [7]). An EQ’s value depends on the database used to make the calculation. For example, equations derived from two different data sets appear

below, with the corresponding modern human value:

$$\text{EQ (1)} = \text{Brain weight (of any species)} / 0.12 \\ \times \text{Body weight}^{0.66}$$

The human value is 6.91, 4.02 for chimpanzee and 1.8 for gorilla.

$$\text{EQ (2)} = \text{Brain Weight} / 1.0 \text{Body weight}^{0.64}$$

This is the “homocentric” equation of Holloway and Post [8], which then expresses each EQ as a direct percentage of the human value, taken as 100%. The chimpanzee EQ is 39.5% and the gorilla 19.1%.

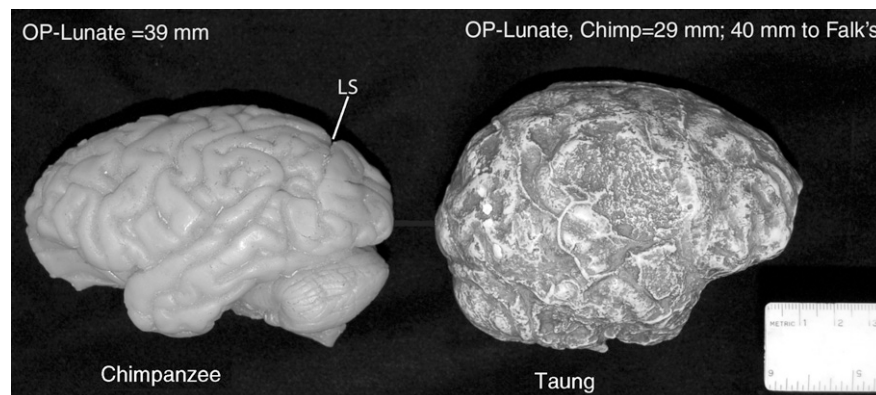
While these values appear very different, the relative position within the primate order is almost static, the rank order correlation being about 0.9 [8].

Relative Sizes of Lobes

Endocasts provide a very rough idea of the relative sizes of the lobes of the cerebral cortex. It is rough because all the sulci on a primate endocast, particularly a hominid one, cannot be seen. It is thus not possible to find the central sulcus accurately in order to delineate the frontal lobe or to find the precentral sulcus to delineate the prefrontal lobe.

Convolution Pattern

Endocasts do provide glimpses of the underlying convolution (gyri and sulci) pattern, depending both upon the state of preservation of the endocast and the faithfulness of convolutional imprinting on the internal table of bone. Alas, this is seldom complete and such incompleteness often leads to controversy, at least within paleoanthropology. For example, the Taung endocast (natural), found with the partial cranium and jaw of *Australopithecus africanus* and described by



Evolution of the Brain, in Humans – Paleoneurology. Figure 3 Lateral views of a chimpanzee brain cast, and the hominid Taung *Australopithecus africanus* endocast. The lunate sulcus (LS) of the chimpanzee lies much farther anteriorly than on the Taung endocast. The dots on the Taung endocast show where a typical chimpanzee LS would lie, if Taung showed a typical ape-like pattern. The distance from the occipital pole (OP) to the LS is roughly 30–40 mm on chimpanzee brains. The measurement from OP to Falk’s LS line on the Taung endocast is about 40 mm. Both the typical chimpanzee LS placement and that of Falk violate the sulcus morphology on the Taung endocast.

Raymond Dart in 1925, showed a depression taken by Dart to represent the lunate sulcus or what would have been the approximate anterior limit of primary visual cortex (V1). This appeared to Dart to be in a relatively posterior position, signaling that, even in this early representative of hominids, the brain was organized differently from that of any ape and was moving toward a more human-like condition (Fig. 3). This depression was in the same region as the lambdoid suture and thus could not be definitively recognized. Putting a lunate in the position expected of an ape such as the chimpanzee or gorilla would violate the existing morphology and the placement of the lunate sulcus even anterior to this would result in a position comparable to an Old World monkey. It was not until 2005 that a description of a posteriorly-placed lunate on the Stw 505 *A. africanus* specimen was made by Holloway et al. [4], effectively settling this controversial issue as to whether the hominid brain had to enlarge before cortical reorganization took place.

Asymmetry

Endocasts, depending on completeness (both halves necessary) and relative lack of distortion, show varying degrees of asymmetry of the once throbbing cerebral hemispheres and these asymmetries become interesting for their relationship to cerebral specializations, including possible handedness and language. For example, when the endocasts show a bulging left hemispheric projection of the occipital lobe posteriorly (and often laterally), combined with a wider right frontal bulge (these bulges are called petalias), this pattern matches what we know from modern human endocasts and radiography to be the result of a torque-like growth pattern [see 9,10,11]. Modern humans also show

asymmetries in the Broca's cap regions of the third inferior convolution of the frontal cortex. These asymmetries probably differ by handedness as well as by unknown functional relationships. Such asymmetries are present in Neandertals and even earlier on some *Homo erectus* specimens (indeed they are clear on the 1.8 million year-old *Homo rudolfensis* specimen, KNM-ER 1470). They cannot prove that this or that hominid had language, but if these asymmetries are homologous to those found in modern humans, well, why not? What is curious is that scientists speculating about the origins of language never bother to look at the paleoneurological evidence [e.g. 12].

Statistical Analyses

Endocasts have shapes and are thus amenable to measurements that can be taken with calipers or from CT scans. Such data sets can then be statistically analyzed using a variety of multivariate statistical techniques.

Blood Supply Patterns

The blood supplies to the meninges show different patterns in different hominid taxa and thus might be useful, in some cases, for identifying hominid phyletic lines [13].

Human Brain Evolution as Seen from Paleoneurology

It is important to keep in mind that roughly 4 MY of evolutionary time has existed for hominid evolution to date and that the number of brain endocasts for hominids that provide reliable data either for size or cerebral organization is very small, numbering no more than about 160, including modern *Homo sapiens* from the end of the Pleistocene (see Holloway et al. [4])

Evolution of the Brain, in Humans – Paleoneurology. Table 1 Reorganizational changes based on the paleoneurological record of hominid endocasts (after Holloway et al. [4])

Brain changes (reorganization)	Taxa	Time (MYA)	Endocast evidence
Reduction of primary visual striate cortex, area 17, and relative increase in posterior parietal cortex	<i>A. afarensis</i>	3.5–3.0	AL 162–28 endocast
	<i>A. africanus</i>	3.0–2.0	Taung child, Stw 505 Endocast
	<i>A. robustus</i>	ca. 2.0	SK 1585 endocast
Reorganization of frontal lobe (Third inferior frontal convolution, Broca's area, widening prefrontal)	<i>Homo rudolfensis</i>	2.0–1.8	KNM-ER 1470 endocast
	<i>Homo habilis</i>	Indonesian endocasts	
	<i>Homo erectus</i>		
Cerebral asymmetries, left occipital, right-frontal petalias	<i>Homo rudolfensis</i>		KNM-ER 1470 endocast
	<i>H. habilis, H. erectus</i>	Indonesian endocasts	
Refinements in cortical organization to a modern <i>Homo</i> pattern	? <i>Homo erectus</i> to Present ?	1.5–10	<i>Homo</i> endocasts (<i>erectus</i> , <i>neanderthalensis</i> , <i>sapiens</i>)

Appendix, for a complete listing up to that date). In essence, there is one brain endocast for every 235,000+ years of evolutionary time. Nevertheless, we believe we can perceive a mosaic of brain evolutionary events that involve size increases interspersed with elements of cerebral organization, as shown in Tables 1–3. At least two important reorganizational events occurred rather early in hominid evolution, (1) a reduction in the relative volume of primary visual striate cortex (PVC, area 17 of Brodmann), which occurred early in australopithecine taxa, perhaps as early as 3.5 MYA

and (2) a configuration of Broca’s region (Brodmann areas 44, 45, and 47) that appears human-like rather than ape-like by about 1.8 MYA. At roughly this same time, cerebral asymmetries, as discussed above, are clearly present in early *Homo* taxa, starting with KNM-ER 1470, *Homo rudolfensis*.

The first change suggests that the relative reduction in PVC was accompanied by a relative increase, most likely in the inferior parietal and posterior temporal lobes. Exactly what selective forces led to this shift can only be guessed, but following the archaeological record of stone

Evolution of the Brain, in Humans – Paleoneurology. Table 2 Major allometric and non-allometric increases in brain size based on the hominid endocasts (after Holloway et al. [4])

Brain changes	Taxa	Time (MYA)	Evidence
Small increase, allometric ^a	<i>A. afarensis</i> to <i>A. africanus</i>	3.0–2.5	Brain size increases from 400 to 450 ml, 500+ ml.
Major increase, rapid, both allometric and non-allometric	<i>A. africanus</i> to <i>Homo habilis</i>	2.5–1.8	KNM-1470, 752 ml (Ca. 300 ml)
Small allometric increase in brain size to 800–1,000 ml (assumes <i>habilis</i> was KNM 1470-like)	<i>Homo habilis</i> to <i>Homo erectus</i>	1.8–0.5	<i>Homo erectus</i> Brain endocasts and postcranial bones, e.g., KNM-ER 17,000
Gradual and modest size increase to archaic <i>Homo sapiens</i> , mostly non-Allometric	<i>Homo erectus</i> to <i>Homo sapiens neanderthalensis</i>	0.5–0.10	Archaic <i>Homo</i> and neandertal endocasts 1,200–1,700+ ml
Small reduction in brain size among modern <i>Homo sapiens</i> , which was allometric	<i>Homo s. sapiens</i>	0.015 to present	Modern endocranial capacities

^aAllometric means related to body size increase or decrease, while non-allometric refers to brain size increase without a concomitant body-size increase

Evolution of the Brain, in Humans – Paleoneurology. Table 3 Major cortical areas (Brodmann’s) involved in reorganization changes (With major emphasis on the evolution of social behavior, and adapting to expanding environments) (after Holloway et al. [4])

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

tool development at roughly 2.6 MYA, these changes are perhaps best explained as a response to an expanding ecological niche, where scavenging, some small game hunting and a vegetarian food base necessitated a more complex appreciation of environmental resources, as well as social behavioral stimuli within foraging hominid groups. A positive feedback model for these and other interacting variables was suggested by Holloway [15,16].

Certainly, the second reorganizational pattern, involving Broca's region, cerebral asymmetries of a modern human type and perhaps prefrontal lobe enlargement, strongly suggests selection operating on a more cohesive and cooperative social behavioral repertoire, with primitive language a clear possibility. By *Homo erectus* times, ca. 1.6–1.7 MYA, the body plan is essentially that of modern *Homo sapiens* – perhaps somewhat more lean-muscled bodies but statures and body weights within the modern human range. This finding indicates that relative brain size was not yet at the modern human peak and also indicates that not all of hominid brain evolution was a simple allometric exercise. Again, this pattern reflects the mosaic nature of human brain evolution. Neandertals were present at least 200,000 years ago, and those known from Western Europe, Eastern Europe and the Middle East have brain volumes that on average exceeded those of modern man, yet with bodies that appear more massive (lean body mass). The only difference between Neandertal and modern human endocasts is that the former are larger and more flattened. Most importantly, the Neandertal prefrontal lobe does not appear more primitive. Table 4 provides a brief statistical description of the major hominid taxa

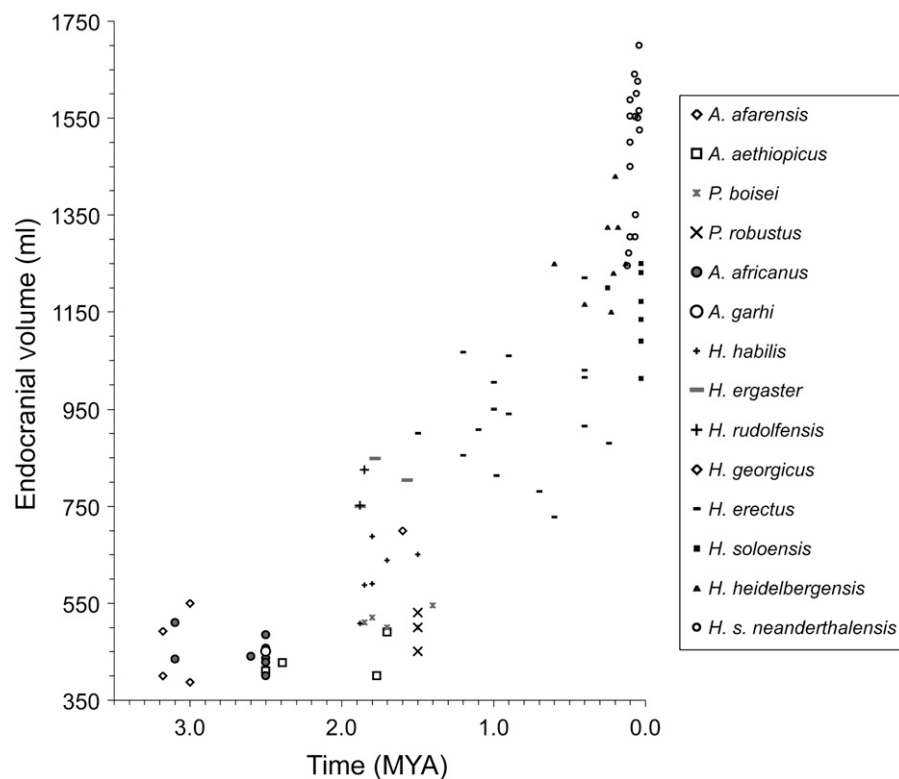
and their respective sample sizes, endocranial volumetric means and ranges. The EQ values that accompany this Table were calculated using Holloway and Post's [8] homocentric equation (see Holloway et al. [4], pp. 13–14 for a more detailed explanation) as well as Martin's EQ's based on a mammalian sample. Figure 4 presents a plot of endocranial volumes against time.

Concluding Comments

Comparative neurology provides neuroscientists with the basic understanding of neural structural variation and correlated behavioral patterns [17]. Paleoneurology provides the direct evidence for hominid brain evolution but is extremely constrained in its evidentiary details, largely thanks to the meninges that surround the surface of the cerebral cortex. In time, growing understanding of molecular neural genetics may help to pinpoint more of the evolutionary differences between modern man and other primates and may even reliably date some of the key organizational and size changes that occurred in mosaic fashion in the human line. It seems that the most essential aspects of human behavior – strong cooperative (and competitive) social behavioral adaptation, far in advance of any ape, centered within and controlled by language and cognitive abilities involving multi-way interactions between predictive prefrontal and analytic parietal/temporal lobes – emerged relatively early in hominid evolution, setting the stage for positive feedback relationships between growing cerebral size and behavioral complexity, which involved a complex interaction between regulatory gene events and changes in the genes themselves.

Evolution of the Brain, in Humans – Paleoneurology. Table 4 Average statistics for different hominid taxa, based on Holloway et al. [4]

Taxon	Mean volume	Number	Range	Mean (MYA)	Body mass	Eqmartin	EQHOMO
<i>A. afarensis</i>	445.80	5	387–550	3.11	37	4.87	42.79
<i>A. africanus</i>	462.33	9	400–560	2.66	35.50	5.21	45.58
<i>P. ethiopicus</i>	431.75	4	400–490	2.09	37.60	4.66	41.01
<i>A. garhi</i>	450	1	450	2.50	NA	NA	NA
<i>H. erectus</i>	941.44	20	727–1220	0.81	57.80	7.32	67.64
<i>H. ergaster</i>	800.67	2	750–848	1.74	57.50	6.25	57.72
<i>H. habilis</i>	610	6	510–687	1.76	34.30	7.06	61.50
<i>H. heidelbergensis</i>	1,265.75	12	1150–1450	0.27	68.70	8.64	81.30
<i>H. rudolfensis</i>	788.50	2	752–825	1.87	45.60	7.35	66.08
<i>H. neanderthalensis</i>	1,487.50	28	1200–1700	0.08	64.90	10.60	99.14
<i>H. sapiens</i>	1,330	23	1250–1730	0.01	63.50	9.63	89.90
<i>H. soloensis</i>	1,155.86	7	1013–1250	0.06	NA	NA	NA
<i>P. robustus</i>	493.33	3	450–530	1.50	36.10	5.49	48.11
<i>P. boisei</i>	515	6	475–545	1.65	41.30	5.17	46.02
<i>P. troglodytes</i>	405	350–450	NA	0.01	46	3.75	33.75
<i>G. gorilla</i>	500	400–685	NA	0.01	105	2.47	24.39



Evolution of the Brain, in Humans – Paleoneurology. Figure 4 Graph showing increase in brain size during the past 3 million years from the fossil hominid endocranial casts available. While the graph appears smooth and continuous, it should be remembered that each symbol represents several thousand years, and such a graph cannot accurately portray all of the details of brain size changes with time, particularly given the incompleteness of the fossil record. After Holloway et al. [14].

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