Encyclopedia of Human Evolution and Prehistory

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Further Readings

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Brain

The human brain is the largest brain among primates but not the largest in either absolute or relative terms among the mammals. Accounting for ca. 2 percent of total body weight, the human brain consumes ca. 20 percent of our metabolic resources at any given time. By all estimates, our brain is three times as large as would be expected for a primate of our body size, and that fact alone should suggest that our brain is an organ of exceptional importance, related to our unique cultural and symbolic behavioral adaptations. The brain is not a homogeneous mass, however, but a composite of hundreds of nuclear masses and several more hundreds of interconnecting fiber tracts. Our uniqueness as a species depends both on the size of our brain and on its organization. Trying to understand the evolutionary development of the human brain is a major challenge, as we have plenty of evidence regarding the size of our ancestors' brains but little about their organization or how they were used. Perhaps it is a tribute to our species that, despite our grim problems of adapting to the world, we alone in the animal kingdom can choose to study our own evolutionary development.

The brain is an extraordinarily complex organ. It has billions of parts, if one is simply talking about nerve cells. Basically, these are either firing or not and may be excitatory or inhibitive. Thus, there is a *digital* aspect to the functioning of so many components. Whether a nerve cell will fire, however, also depends on a summation process of thousands of inhibitory or facilitative connections with other nerve cells and the surrounding neuroglial cells. This is the *analogue* aspect to the brain. To make matters more complex, the brain also has both *parallel* and *serial* organizations to its many components, so that information about the external and the internal environments of the animal are evaluated both directly and indirectly. The brain is hierarchically organized, as between its most recent acquired mantle, the grey cerebral cortex (*neopallium*), and the underlying basal ganglia, limbic system, and olfactory lobes that make up the *telencephalon,* or forebrain. This division surrounds the underlying *diencephalon,* the "between brain," which includes the thalamus, the epithalamus, the hypothalamus, and the pineal gland or body. At a lower level there is the *mesencephalon,* or "midbrain," which is behaviorally a part of the brain stem, containing the *tectum* and the *tegmentum,* consisting principally of the inferior and the superior colliculi, which are auditory and visual in function, respectively. More ancient is the next level of structures making up the *metencephalon* and the *myelencephalon,* consisting of the cerebellum, the pons, the medulla, and the third and fourth ventricles, which are integrated with the spinal cord.

While it is not strictly true that all parts of the brain are connected with each other, the combination of parallel and serial, crossed and uncrossed fiber interconnections does mean that any complex volitional act involves most, if not all, of the brain working together. No one is certain how many genes control the development of the brain and its phenotypic expressions, but a rough estimate of 40,000 genes may, in fact, be conservative. This represents an enormous amount of potential genetic variability for natural selection to work upon. Many of these genes, however, must be very conservative, for it is an awesome fact that, despite all the variation in different animal species' behavioral repertoires (species-specific behaviors), almost all mammals, if not vertebrates, have the same components in their brains. The human animal does not possess any new structures in its brain compared with most other mammals. What seems to have occurred during evolution is that certain parts of the brain have become enlarged relative to others; in the mammals, particularly the higher primates, this has involved a dramatic increase in the cerebral cortex and the underlying thalamus, with which it has two-way connections. In the human animal, the cerebral cortex accounts for ca. 76 percent of total brain weight, the highest ratio among primates. In the chimpanzee, the cortex is 72 percent of brain weight, and in the gorilla, 68 percent. The amount of cortex in humans as well as in chimpanzees and macaques is exactly what would be expected allometrically for their respective brain weights.

Thus, one of the major challenges facing any scientist trying to understand the evolution of the brain is how to account for a complex mixture of conservative and new genetic expressions involved in all of the parts of the brain and how these relate to behavior, adaptation, and evolution. Much of our current scientific explanation focuses on brain size, as this is simple to measure. The more difficult task is to quantify the organization of the brain's components and to relate this information to evolutionary histories and dynamics among species.

Lines of Evidence

Three lines of evidence exist for understanding the evolution of the human brain. The first is *direct,* derived from the study of endocasts, and is called *paleoneurology.* Data about the once-living brain are provided by either natural or human-made casts of the interiors of fossil crania. Such data include brain size (volume), convolutional details, traces of the meningeal vessels, and overall morphological patterns that include shape and asymmetries of the cerebral cortices. In life, the brain is covered by three meningeal tissues that often prevent the cortical gyri and sulci from being completely imprinted on the internal table of bone: the *pia mater,* the *arachnoid mater* (including cerebrospinal fluid), and the thick *dura mater.* It is extraordinarily rare, at least in higher primates, for the cortical convolutions to be fully preserved on endocasts, and thus the volume of the brain and possible asymmetries of the cortices constitute the most reliable evidence.

The second line of evidence is *indirect* and is provided by comparative *neuroanatomy.* This studies the brains of *living* animals, each an end product of its own line of evolutionary development. In this case, quantitative studies are made of the brains of different primates, including the neural nuclei and fibers, as well as overall brain sizes, and

these data are correlated with variations in behavior. Within this line of study, *allometry* is one of the most valuable tools of analysis.

A third line of evidence, even more indirect, is the study of the products once made by hominins, such as stone tools and different kinds of archaeological sites that preserve patterns of hominin behavior. In addition, one can use the skeletal remains of hominins to understand locomotor adaptations, such as bipedalism, or to study bone fragments of the hands to appreciate manipulatory behavior. These provide only the most indirect clues, but major patterns of locomotor adaptation cannot evolve without some reorganization of the central nervous system controlling musculoskeletal patterns. All three lines of evidence should be used together in the attempt to enlarge our knowledge of human brain evolution, as none of them alone is sufficient for such understanding.

Paleoneurology, or the Study of Endocasts

The accompanying table (table 1) provides a partial listing of the endocranial volumes determined for many of the earlier hominins and the methods used. The brain volume in our own modern species normally varies from ca. 1,000 to 2,000 ml, with an average volume of ca. 1,350 to 1,400 ml. No convincing relationship has ever been shown between brain volume and behavior, aside from pathological cases, such as microcephaly or hydroencephaly, in which behavior is often subnormal. Microcephaly is especially interesting, as there are recorded cases of human beings having brain volumes less than those of some pongids but nevertheless using articulate language. This suggests that, while brain size is important, the organization of the brain's components is a significant contributing factor toward species-specific behavior.

This range of normal variation, without any known behavioral correlates, is about the same as the total evolutionary change in brain size from our earliest hominin ancestors, *Australopithecus afarensis* (3 Ma) to our own species, *Homo sapiens.* With the exception of the large-bodied robust australopiths, which averaged ca. 525 ml in brain volume, the earliest hominins, such as *A. afarensis* and *A. africanus,* had brain volumes ranging from 375 ml to ca. 485 ml. When the genus *Homo* appears, currently dated at ca. 2–1.8 Ma, the brain volume increases dramatically to ca. 750 ml, as represented by the KNM-ER 1470 *Homo habilis* specimen. At this time, there is certain evidence for stone-tool making, hunting, and scavenging behavioral activities, and archaeological sites suggesting complex social activities. The endocasts show three interesting developments: volume increase to ca. 750 ml (and, one supposes, an increase in relative brain size), asymmetries of the cerebral cortex suggesting right-handedness, and a more complex humanlike pattern of the third inferior convolution, which includes the famous area of Broca that helps control the motor aspects of sound production. Unfortunately, the posterior portion of the endocast, which contains Wernicke's region and is associated with receptive sound functions and intermodal associations, seldom if ever shows convolutional details that would permit one to conclude that these hominins possessed language. Some of this increase in brain volume must surely have been related to an increase in body size from the earlier smaller-bodied australopiths. Exactly how much was an allometric increase related to body size, and how much beyond that relationship, is simply unknown. From the time of *Homo erectus* on (i.e., at least 1.6 Ma), the endocasts of hominins do not show any primitive features, but rather a more or less constant growth in brain volume from ca. 800 ml to our present average of ca. 1,400 ml. This increase in brain size probably did not come about through allometry, as the body sizes of *Homo erectus,* at least as judged by the recent Nariokotome youth (KNM-WT 15000) found in Kenya, were already comparable to modern humans. Neanderthals had slightly larger brains than modern humans, but this curious fact is perhaps explained as a part of an allometric relationship to lean body mass and perhaps cold-adaptation. Thus, it appears that some of the increases in brain volume were allometric while other increases were not, and that the evolution of the human brain resulted through different selection pressures at different times, another example of complex mosaic evolution in hominin lines.

Evidence from Comparative Neuroanatomy

This line of indirect evidence is essential to our understanding of human brain evolution, a statement, incidentally, that could be made for any animal from aardvarks to zebras. While much is known about the naturalistic behavior of many species of animals, and each has a set of species-specific behavioral repertoires for adapting to its environment, the science of explaining species-specific behavior based on the structure and functioning of the brain is in its infancy. Consider the wide range of behavioral differences among living primates, such as lemurs, tarsiers, New and Old World monkeys, the chimpanzee, gorilla, orangutan, and gibbon: None of these behavioral differences can yet be related to respective brain organizations. As dog breeds are perhaps more familiar to us, it is interesting to reflect that, while enormous differences in breed behavior are known, none of the behavioral variation has been correlated with neuroanatomical differences. What are the magic variates that surely must link the two levels? Brain size, taken alone, has little explanatory power in this regard, yet it is obviously an important starting point. Indeed, considerable progress has been made through allometric studies that treat brain size as a dependent variable and in which relationships are then made to body weight, metabolism, gestation duration, longevity, and, in some cases, broad ecological domains relating to subsistence patterns such as folivory, frugivory, omnivory, and predation. But the brain is a complex organ, consisting of many different neural cell masses and interconnecting fiber tracts, many of which are differentially susceptible to hormonal secretions and environmental stimuli. Within Mammalia, it is a stark truism that all mammals have the same brain components: there are no new parts (nuclei or fiber systems) to distinguish among genera within orders or among orders. Thus, not only does brain size vary in animals, but so do the quantitative relationships among components of the brain and the ontogenetic, developmental sequences of DNA-RNA interactions that specify the development of different brain regions and

Table 1. Endocranial (brain) volumes of reconstructed hominins

Specimen	Taxon	Region	Volume (ml)	Method	Evaluation
AL 333–45	*A. afarensis*	E. Africa	485–500	C	2
AL 162–28	"	"	375–400	est.	2
AL 333–105	"	"	310–320	C	2
L 338y–6	*A. africanus ?*	"	427	C	2
Taung	*A. africanus*	S. Africa	440*	A	1
STS 60	"	"	428	A	1
STS 71	"	"	428	C	2–3
STS 19/58	"	"	436	B	2
STS 5	"	"	485	A	1
MLD 37/38	"	"	435	D	1
MLD 1	"	"	500–520	B	3
SK 1585	*P. robustus*	"	530	A	1
KNM-WT 17000	*P. aethiopicus?*	E. Africa	410	A	1
KNM-ER 13750	*P. boisei*	"	475	A	1
OH 5	"	"	530	A	1
KNM-ER 406	"	"	525	D	2
KNM-ER 407	"	"	510	A	1
KNM-ER 732	"	"	500	A	1
KNM-ER 1805	*H. ?*	"	582	A	1
KNM-ER 1813	*H. habilis*	"	510	A	1
KNM-ER 1470	*H. rudolfensis*	"	752	A	1
OH 7	*H. habilis*	"	687	B	1
OH 13	"	"	650	A	1
OH 24	"	"	590	A	2–3
KNM-ER 3732	"	"	600–650	est.	3
OH 9	*H. erectus ?*	"	1067	A	1
KNM-ER 1590	"	"	min. 800	est.	3
KNM-ER 3733	"	"	848	A	1
KNM-ER 3883	"	"	804	A	1
KNM-WT 15000	*H. erectus*	"	900	X	1
Trinil 1(1892)	"	Indonesia	953	A	1
Sangiran 1 (1937)	"	"	815	A	1
Sangiran 4 (1938)	"	"	900	C	2–3
Sangiran [ ] (1963) Pith 6	"	"	855	A	2
Sangiran 17 (1965)	"		1059	C	1–2
Sangiran [ ] (1969) Pith 8	"	"	1004	A	1
Sambungmachan 1	"	"	1035	X	2
Modjokerto 1 (child)	"	"	est. 550–575	A	1
Lantian 2	"	China	780	X	2
Zhoukoudian II	"	"	1030	X	2
Zhoukoudian III	"	"	915	X	2
Zhoukoudian V	"	"	1140	X	2
Zhoukoudian VI	"	"	850	X	2
Zhoukoudian X	"	"	1225	X	2
Zhoukoudian XI	"	"	1015	X	2
Zhoukoudian XII	"	"	1030	X	2
Hexian	*H. erectus*	"	1025	X	3
Solo I	*H. erectus* (or? archaic *H. sap.*)	Indonesia	1172	A	1
Solo V	"	"	1250	A	1
Solo VI	"	"	1013	A	1
Solo IX	"	"	1135	X	3
Solo X	"	"	1231	A	1
Solo XI	"	"	1090	A	1
Kabwe (Rhodesian)	"Archaic *Homo sapiens?*"	S. Africa	1285	X	1

continues

Table 1. ***Continued***

Specimen	Taxon	Region	Volume (ml)	Method	Evaluation
Sale	"	N. Africa	880	A	1
Laetoli 18	"Archaic *Homo sapiens*"	E. Africa	1367	X	1
Eyasi	"	"	1285	X	3
Lake Ndutu	"	"	1100	X	1
Saldhana	"	S. Africa	1225	X	3
Narmada	"	India	1200	X	3
Dali	"	China	1120	X	2
Yinkou	"	"	1390	X	3
Vértesszöllös II	"	Europe	1325	X	3
Reilingen	"	"	1430	A	2
Steinheim	"	"	1225	X	1
Swanscombe	"	"	1325	X	2
Fontachevade	"	"	1350	X	3
Ehringsdorf	"	"	1450	X	2
Biache	"	"	1200	X	3
Petralona	"	"	1230	X	2
Arago 21	"	"	1150	A	2
Monte Circeo I	*H. sapiens neanderthalensis?*	"	1552	X	2
Saccopastore I	"	"	1200	X	2
Saccopastore II	"	"	1300	X	2
Spy I	*H. sapiens neanderthalensis*	"	1553	A	1
Spy II	"	"	1305	A	1
LaChapelle	"	"	1625	X	1
La Ferassie I	"	"	1640	X	1
Neanderthal	"	"	1525	X	1
La Quina V	"	"	1172	X	1
Le Moustier	"	"	1352	X	2
Atapuerca 4	"	"	1390	X	2
Atapuerca 5	"	"	1125	X	2
Krapina B	"	"	1450	X	3
Krapina C	"	"	1200	X	3
Krapina D	"	"	1450	X	3
Gibraltar I	"	"	1200	X	1
Ganovce	"	"	1320	X	3
Jebel Irhoud I	"	S.W. Asia	1305	A	1
Tabun I	"	"	1271	X	2
Skuhl IV	" ?	"	1554	X	2
Skuhl V	" ?	"	1520	X	1
Skuhl IX	" ?	"	1590	X	2
Amud	*H. sapiens neanderthalensis*	"	1740	X	1
Shanidar I	"	"	1600	X	1
Cro-Magnon	*H. sapiens sapiens*	"	1590	X	1
Chancelade	"	"	1530	X	2
Oberkassel	"	"	1500	X	2
Predmosti III	"	"	1580	X	2
Predmosti IV	"	"	1250	X	2
Predmosti IX	"	"	1555	X	2
Predmosti X	"	"	1452	X	2
Brno I	"	"	1600	X	2
Qafzeh VI	"	M. East	1568	X	2
Border Cave	"	S. Africa	1510	X	3
Omo II	" ?	E. Africa	1435	X	2

Cranial capacities in ml for selected hominin crania. An asterisk (*) refers to estimated adult volume from a juvenile or child's endocast. The values were obtained by one of four methods: (A) direct water displacement of either a full or a hemiendocast with minimal distortion and plasticene reconstruction; (B) partial endocast determination as described by Tobias (1971); (C) extensive plasticene reconstruction amounting to half of total endocast; (D) volume calculated from regression formula or estimated on the basis of a few measurements. X refers to previously published values, either confirmed or not by the author. The reliability of these values is evaluated on a scale of 1 to 3, where 1 indicates the highest reliability, and 3 the lowest depending on endocast completeness, distortion, and methods.

Table 2. Selected primate brain and body weights and EQs (encephalization quotients)

Taxon	Mean Body Weight (g)	Mean Brain Weight (g)	EQ1 Homocentric—As % of *Homo*	EQ2—All Primates	EQ2—As % of *Homo*
Microcebus murinus	53.0	1.81	0.138	0.887	0.299
Cheirogaleus major	417.3	6.90	0.137	0.700	0.236
Lemur catta	1780.3	21.99	0.171	0.738	0.249
Eulemur mongoz	1653.8	23.68	0.193	0.841	0.284
Daubentonia madagascarensis	2203.5	44.05	0.298	1.257	0.424
Loris tardigradus	267.1	6.67	0.178	0.951	0.321
Perodicticus potto	932.8	13.23	0.156	0.727	0.246
Galago senegalensis	161.0	4.43	0.164	0.928	0.313
Tarsius spectrum	175.0	4.65	0.163	0.915	0.309
Saguinus oedipus	302.0	9.68	0.238	1.256	0.424
Cebus capucinus	2340.0	72.51	0.472	1.976	0.667
Saimiri sciureus	446.6	22.12	0.422	2.131	0.719
Aotus trivirgatus	706.5	16.69	0.236	1.133	0.382
Callicebus moloch	669.0	15.95	0.234	1.129	0.381
Ateles geoffroyi	7944.8	108.98	0.321	1.169	0.395
Macaca fascicularis	4332.8	69.72	0.304	1.188	0.401
Macaca mulatta	5688.2	91.34	0.334	1.265	0.427
Macaca nemestrina	6567.0	103.64	0.345	1.286	0.434
Cercocebus albigena	7064.3	99.76	0.317	1.171	0.395
Papio hamadryas anubis	24780.0	196.20	0.276	0.884	0.298
Papio hamadryas hamadryas	13833.3	175.67	0.361	1.235	0.417
Papio hamadryas ursinus	18294.5	175.27	0.300	0.996	0.336
Cercopithecus aethiops	3226.6	67.69	0.357	1.444	0.487
Miopithecus talapoin	1040.3	39.70	0.437	2.007	0.677
Erythrocebus patas	5350.0	97.33	0.370	1.412	0.483
Procolobus badius	6581.2	77.33	0.257	0.958	0.323
Hylobates agilis	5890.0	90.20	0.322	1.216	0.411
Hylobates lar	5698.4	102.16	0.373	1.412	0.477
Hylobates moloch	5915.1	93.37	0.333	1.255	0.424
Hylobates syndactylus	11684.5	132.63	0.304	1.061	0.358
Pongo pygmaeus	52140.4	346.46	0.301	0.886	0.299
Pan troglodytes	41250.6	378.00	0.382	1.155	0.523
Gorilla gorilla	93095.0	454.11	0.270	0.746	0.252
Homo sapiens	62772.2	1334.41	1.000	2.962	1.000

The regressions are based on 85 species including Homo sapiens *(data from H. Stephan). Two different approaches to EQ are used. The* homocentric *EQ1 values are calculated by using the equation,*

$$EQ_{HOMO} = \text{brain weight/body weight}^{0.64906}$$

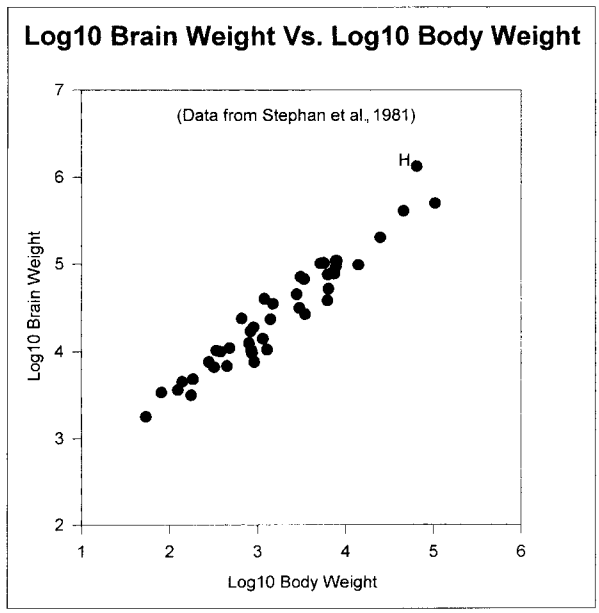
in which the animal's body weight is raised to the 0.64906 power.

This exponent is derived from drawing a line connecting the average brain and body weight values for Homo *(1330, 65,000 g) and the origin (0,0) on a log base 10 graph. This makes the coefficient 1.0, and resulting EQ is expressed as a percent of the human value, which is the highest among all mammals.*

The EQ2 values were calculated using the equation,

$$EQ2 = .0091 \times \text{brain weight/body weight}^{0.76237}$$

The column "EQ2 as % of Homo *" simply divides EQ2 by 2.962, the value for* Homo. *As can be seen, these values are sometimes very much higher than the homocentric EQ1 values. These values show that the intervals between the values are arbitrary in the case of EQ2. There is no reason to believe that the squirrel monkey* (Saimiri sciureus) *should have an EQ that is 71.9% of* Homo *'s. This illustrates well the "relativity of relative brain measures."*



A log-log (base 10) plot of the mean brain and body weights for 85 species of primates, including Homo sapiens, *from data kindly provided by Dr. Heinz Stephan, Max Planck Institute for Brain Research. The H is the human value, and the closest three are chimpanzee, gorilla, and orangutan. The correlation coefficient without* Homo *is 0.97, and the human value for the brain is about three times higher than would be predicted for a primate of its body weight. The slope of the regression line is about 0.76 without* Homo. *This value suggests a metabolic constraint between body weight and the weight of the brain. It should be remembered that the points in this figure are for a large number of primate taxa. If these data points are plotted within different taxonomic categories (i.e., prosimians alone, New World monkeys alone, etc.) each group would scale somewhat differently, usually with a slope of about 0.66. This latter exponent suggests a geometric relationship between surface area and volume (i.e., the ratio 2/3). Thus, the calculated encephalization coefficients (EQs) are "relative," as each species value depends on the allometric equation used. Courtesy of Ralph Holloway.*

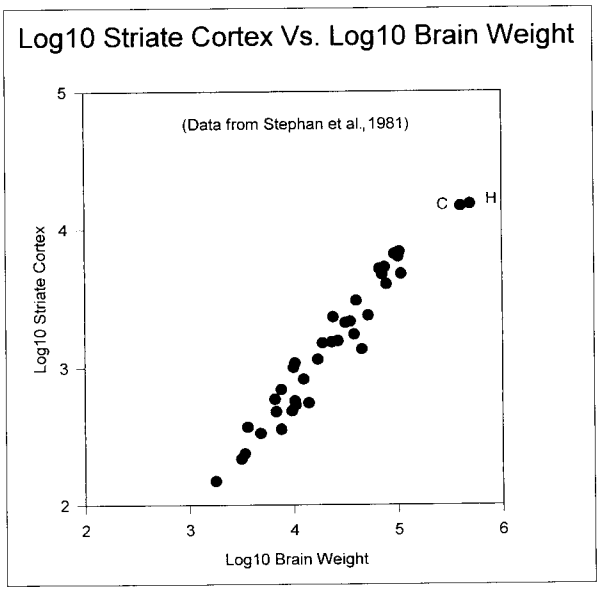
their underlying neurotransmitter substances. Humans are not the only animals that have asymmetrical brain regions: Almost all animals have asymmetries to varying degrees, and some, like certain birds, have a seasonal sensitivity to increases and reductions of certain nuclei related to song patterns. In the human case, however, it is probably both the kind and the degree of cortical asymmetries that are distinctive.

As mentioned above, in our own species the brain accounts for ca. 2 percent of our total body weight but uses close to 20 percent of our metabolism at any given moment. It is a voracious organ. Thanks to recent allometric studies, it appears that the relationship between brain and body size is constrained more strongly by metabolic factors than by surface-area/volume relationships as was once popularly believed. Thus, when the log (base 10) values of brain size and body weight are plotted together, the resulting slope is usually close to 0.75 rather than 0.66. This is for the order as a whole; in plotting the values for superfamilies or lower-level taxa (e.g., families), the slope is ca. 0.66. In general, the slope decreases as the taxonomic units become more specific, until, within a species such as ours, the slope is ca. 0.25.

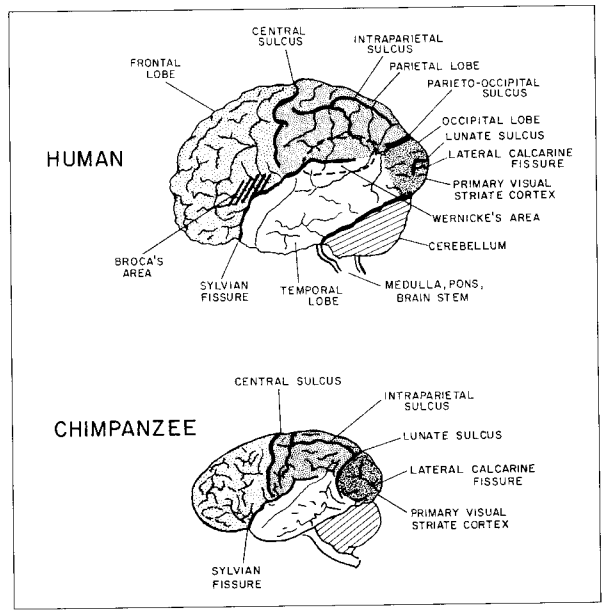
Shown here is one such plot based on 85 species of primates from data kindly supplied by Dr. Heinz Stephan. The human value is clearly an "outlier" in this plot and has a brain volume (or weight) roughly three times that expected for a primate of this body size. The gorilla value is lower than expected, and, indeed, one can go through the list of primates and find differences between predicted and observed values of greater than 100 percent. The point here is that the slope of 0.75, reflecting metabolic factors, is not a *law,* but a *constraint,* around which species vary. The picture becomes more complex when individual parts of the brain are plotted against brain weight for different species of primates, and such data provide a basis for understanding differences in brain organization among primate species.

Usually, brain components scale closely to total brain weight, and predicted and observed values differ by less than 10 percent. The cerebral cortex and the cerebellum are two good examples of this. The differences between expected and observed values are, for *Homo sapiens,* only 0.33 percent and 6.5 percent, respectively, when based on a sample of 44 primate species excluding *Homo.* There are, however, some extraordinary departures from predicted values for certain brain structures, and one of these in particular is important to a fuller understanding of human brain evolution and of the importance of certain key fossil hominin endocasts in showing *Homo*-like derived, rather than pongidlike retained, primitive characteristics. As the second plot shows, the volume of primary visual striate cortex (area 17 of Brodmann) is some 120 percent *less than expected* in the human primate with our brain size. Similarly, the lateral geniculate body of the epithalamus shows a reduction of 140 percent + from the predicted or expected volume of this nucleus based on allometry within the Anthropoidea. These deviations should make us wary that all size differences can be explained through allometry alone. Both the primary visual striate cortex and the lateral geniculate nucleus are important components of our visual system. This relative decrease in *Homo* probably meant that there was a relative *increase* in parietal association cortex during human evolution. The real question is, when did this occur?

The third figure shows a lateral view of chimpanzee and human brains. In the posterior part of the cerebral cortex is found the *lunate sulcus,* which represents the most anterior boundary of purely sensory cortex: the *primary visual striate cortex.* Anterior to this cortex is what we commonly call the *association cortex* of the parietal and temporal lobes, a region of complex intermodality association and cognitive functioning, which happens to include, at least in humans, Wernicke's area. Based on the same sample of 45 primate species, the human primary visual striate cortex subserving vision is roughly −121 percent less than expected for a primate of this brain size. This fact does not mean that our visual sense is functionally reduced but rather that there has been a compensatory increase in the relative amount of parietal and temporal-lobe association cortex. The ventricles of the brain, which in the fetal stages provide the neuroblasts that become part of the 10 billion neurons making up the adult cerebral cortex, are ca. 52 percent greater than expected on the basis of allometry. Some neural structures deviate from expected values by as much as 7,000 percent. These departures from



The figure shows the log-log (base 10) relationship between the volume of primate visual striate cortex, area 17 of Brodmann, against the mean weight of the brain for 37 species of primates, including Homo, *shown as H. The regression has a correlation coefficient of about 0.97 without the human value. The human value is over 121 percent lower than would be predicted for a primate with its brain weight. Most other differences between observed and predicted values are around 10–25 percent, and are mostly explained by statistical error from small samples. The* Homo *difference, however, is quite large and is paralleled by the same result when the volume of the lateral geniculate nucleus of the thalamus is regressed against brain weight. In this case the human value is over 140 percent lower than would be predicted. The two neuroanatomical systems are intimately related. As the human primate has no loss of vision compared to other primates, these results suggest that during evolution there was either a relative reduction in primary visual striate cortex (area 17) in the human brain or a relative increase in parietal association cortex. The major question, of course, is when did the reduction occur in the course of hominoid evolution? Courtesy of Ralph Holloway.*



The brains of chimpanzee (below) and human in lateral view. Although the human brain is some three to four times heavier than the chimpanzee brain, there is considerable similarity between the two species with regard to the convolutional details. The human brain has more convolutions and considerable variation of its gyri (hills) and sulci (valleys), particularly in the parietal and frontal lobes, but the primary and secondary gyri and sulci are the same between the two species. Of considerable interest to those studying the paleoneurology of our fossil ancestors are the sulci labeled the lunate, *the* intraparietal, *the* sylvian, *and the* lateral calcarine. *In apes, such as the chimpanzee, the lunate sulcus is always present and is the anterior boundary of the primary visual striate cortex, which subserves visual functions. The intraparietal sulcus, in its posterior part, always terminates against the lunate sulcus and divides the parietal portion of the cerebral cortex into superior and inferior lobules. The calcarine fissure always runs medial to lateral but terminates before it reaches the lunate sulcus. When a lunate sulcus appears in the human brain, it is in a very posterior position, relative to where it can be found in other apes. As the figures for the volume of visual striate cortex discussed in the text indicate, the human brain has relatively less of this cortex making up its cerebrum than does the ape brain. This means that the relative amount of parietal "association" cortex has increased in the human species. The challenge is to document when such change took place in hominid evolution. Unfortunately endocasts seldom show the convolutions that existed in the brain. The central sulcus divides the frontal from the parietal lobe and functionally marks the separation between the mainly motor anterior gyrus and the posterior sensory gyrus. Both the inferior third frontal convolution (with Broca's area) and the posterior temporal and middle parietal lobes (containing Wernicke's area) appear more convoluted in the human species and have important relationships to both the motor and sensory (receptive) aspects of communication by language. These particular regions are seldom well preserved on fossil endocasts and are areas of considerable interpretive controversy among paleoneurologists. Courtesy of Ralph Holloway.*

allometric expectations could very well provide interesting clues about which structures in the human brain might have undergone significant evolutionary change.

Comparative studies of the brain provide other clues about the evolution of our major organ of adaptation, of which three can be briefly mentioned: encephalization, asymmetries of cortical hemispheres, and sexual dimorphism of the brain.

Encephalization has two meanings in comparative neurology. First, it refers to evidence that in the course of evolution the cerebral cortex has taken on more functions and that the organization of the cortex is more susceptible to debilitating damage through injuries. A second, more recent meaning of encephalization refers to a ratio in which an animal's brain weight is divided by an allometric equation derived from a particular taxon. For example, the equation

$$EQ = .0991 \times \text{brain weight}/(\text{body weight})^{0.76237}$$

provides an *encephalization quotient* (EQ), in which the denominator is the allometric equation based on 88 species of primates. In this case, using an average brain weight for *Homo sapiens* of 1,300 gm, the EQ is 2.87. For the chimpanzee and the gorilla, the EQs are 1.14 and 0.75, respectively. If an allometric equation for insectivores were used, the human, chimpanzee, and gorilla EQs would be 28.8, 11.3, and 6.67, respectively. The important points here are twofold: first, the human animal always has the highest EQ regardless of the denominator; second, the EQ values and their relative values among species can vary by as much as 20 percent. When these equations are applied to fossil hominins, their relative closeness to modern humans or to our ape cousins, such as chimpanzees, will vary depending on the basal equation chosen. This is known as the *relativity* of relative brain measures.

Since the human animal apparently has the highest EQ value among mammals, we can use a *homocentric* equation, in which *Homo sapiens* has the highest value of 1.0, or 100 percent. This equation appears as follows:

$$EQ_{HOMO} = \text{brain weight/body weight}^{0.64906}$$

This equation is derived by drawing a line through the average log (base 10) values of modern *Homo* to the origin point of zero brain and body weights. The advantage of this equation is that all other animal EQs are expressed as a direct percentage of the human value. For example, the chimpanzee EQ is 0.39 (39 percent) and the gorilla value 0.23 (23 percent). Unfortunately, it is a matter of taste as to which EQ equation one selects, or which groups or taxa one wishes to compare and discuss. To work out the EQs for particular hominin fossils requires an accurate knowledge of both brain and body weights, and the latter values must necessarily be guessed. A single EQ value for a particular fossil hominin tells us nothing about how the EQ varied within the species. In general, australopiths show slightly higher EQ values than do chimpanzees, but not by very much.

Asymmetries of the cerebral cortex, while existing in animals other than humans, do not show the *pattern* that is most often expressed in our own species. Humans are mostly right-handed (numbering up to ca. 87–90 percent of most populations), and both the motor and the sensory regions involved in symbolic language are dominant on the left side of the cerebral cortex. Evidence from the neurosciences shows that the left hemisphere controls symbolic parsing and cognitive tasks mediated by symbols. The right hemisphere appears to have more control over gestalt appreciation of visuospatial relationships, facial recognition, and emotions. While only sophisticated neurological examinations of the working brain show this, it is well known that the gross appearance of the cerebral hemispheres is highly correlated with handedness and thus with cerebral dominance. *Petalias* are extensions of parts of the cerebral cortex extending beyond their counterparts on the other side of the brain. For example, in most right-handers the classical petalial pattern is for a longer left occipital pole, a broader left parietal region, and a broader right frontal width. True left-handers and many mixed-handers show the opposite pattern. While other primates, particularly the gorilla, do show some asymmetries, they rarely show the combined torquelike petalial pattern described above for humans. There is also a lack of any clear-cut data demonstrating handedness (rather than preference) for other primates. It is thus an intriguing fact that fossil hominins show overwhelmingly the human petalial pattern, and N. Toth has discovered that many of the early stone tools were apparently made by right-handers. Some of the australopith fossil endocasts show a petalial pattern that suggests right-handedness, despite their pongidlike brain sizes. It is possible that the brain evolved some modernlike human patterns of organization early in hominin evolution before the great expansion of brain size, although this is a controversial area.

Sexual dimorphism of the human brain can be found in the anterior hypothalamus and in the corpus callosum, through which pass most of the fiber tracts that interconnect the two cerebral hemispheres. Females show a larger splenial portion (which integrates the two occipital, parietal, and temporal regions of the cortices) than do males, when both are corrected for brain size. The corpus callosum is the only brain structure to show a very different pattern between male and female brains. Almost all structures of the brain (i.e., the cerebellum, the septum, the hippocampus, the striatum, etc.) are larger in males than in females, and significantly so. The corpus callosum, however, is roughly equal in absolute size between the sexes. When these structures are related to brain weight, however, there are no significant differences between males and females, *except* in the corpus callosum, which is *relatively* larger in females, and the differences are usually statistically significant. Given the cultural variability of most modern societies, this small anatomical difference probably does not have much significance in different cognitive-task abilities between our two sexes. It is more interesting to consider these differences (which are apparent by 26 weeks prenatal) as evolutionary residua from past selection pressures that may have favored a complementary behavioral adaptation between males and females for the increased period of social and maternal nurturance of longer-growing offspring.

Summary

Summarizing all of the changes that may have taken place over 3–4 Myr of human brain evolution is a speculative matter. Table 3 provides but an outline of how these changes might have interdigitated. The earliest australopiths (e.g., Taung and the Hadar 162–28 *A. afarensis*) already show evidence for cerebral reorganization in that the lunate sulcus is in a posterior position, suggesting that the posterior parietal association cortex had increased beyond the ape level. Cerebral asymmetries are also present, but these are more strongly represented in early *Homo,* whose appearance coincides with a major expansion of brain size (to ca. 750 ml from 450 ml) at ca. 2 Ma. Coincident with these patterns are stone tools and evidence for hunting and scavenging. The remaining doubling of size, to ca. 1,400 ml, is perhaps best explained through a combination of allometric and nonallometric processes in which natural selection favored increased body size, longer periods of childhood growth, and, one assumes, more sophisticated brains capable of more sophisticated social behavior. While this basic scenario fits well within our popular conceptions of mosaic evolution, it would be wise to remember that there were mosaics within the mosaic, and the brain has always been an important part of human adaptation whatever its size at various phases of hominid evolution. It is pointless to say that bipedalism evolved first, then brains. A complex musculoskeletal set of such adjustments as attend bipedalism could not evolve in a nervous vacuum, nor does the structural adaptation hold much meaning without reference to behavioral function. Thus, the evolution of the brain can only be understood not just in the context of its size, the reorganization of its components, and its asymmetries but in the context of the total range of the ecological and behavioral record that is associated with the actual fossil hominin discoveries.

Table 3. Summary of reorganizational and size changes in the evolution of the hominin brain

Brain Changes, Specimens	Taxa	Time
(1) Reduction of volume of area 17, primary visual striate cortex; relative increase in posterior parietal association cortex. AL 162–28 has a posterior position of the lunate sulcus.	*A. afarensis*	by 3.5–3 Ma
(2) Small increase in brain size, probably allometric, to 400–450 ml.	*A. africanus*	3–2.5 Ma
(3)Reorganization of frontal lobe, increase in cerebral asymmetries. Major increase in brain size of 250–300 ml. KNM-ER 1470.	*H. habilis/ rudolfensis*	2.5–1.9 Ma
(4) Modest allometric increase in brain size, to 750–900 ml, and increase in cerebral asymmetries. *H. erectus* brain casts, incl. KNM-WT 15000 youth.	*H. erectus*	1.9–1.6 Ma
(5) Modest increase in brain size, 300 ml, *neanderthalensis* to 1200–1700 ml, and refinements in cortical organization to a modern *Homo* pattern. Archaic *Homo* endocasts.	*H. sapiens*	200–100 Ka
(6) Small allometric reduction in brain size among modern *Homo sapiens.* Modern range of cranial capacities.	*H. sapiens sapiens*	after 100 Ka

See also Allometry; Anthropoidea; Archaic Homo sapiens; Australopithecus; Hominoidea; Homo; Homo erectus; Homo sapiens; Neanderthals; Primates; Skull; Speech (Origins of). [R.L.H.]

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Branisellinae

Extinct subfamily of cebid platyrrhine monkeys including *Branisella boliviana* and *Szalatavus attricuspis* (if the latter is a