

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 some 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 of jelly, however, but a composite of hundreds of nuclear masses and several more hundreds of interconnecting fiber tracts. Our uniqueness as a species depends on both the size of our brains and its organization. Trying to understand the evolutionary development of the human brain is a challenge, as we are left mostly with 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, which are either basically firing or not and which can 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 internal environments of the animal are evaluated both directly and indirectly. The brain is hierarchically organized, as between its most recent evolutionary-derived 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, epithalamus, hypothalamus, and 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 *tegmentum*, consisting principally of the inferior and superior *colliculi*, which are auditory and visual in function, respectively. More ancient is the next level

of structures making up the *metencephalon* and *myelencephalon*, consisting of the cerebellum, pons, medulla, and 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 behavior) 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; and 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 roughly 76 percent of total brain weight, the highest ratio among primates.

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 expression 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 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 prohibit the cortical gyri

and sulci from being 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, the neural nuclei and fibers of their brains as well as their 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 hominids, such as stone tools and different kinds of archaeological sites that preserve patterns of hominid behavior. In addition one can use the skeletal remains of hominids to understand their locomotor adaptations, such as bipedalism, or 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 provides a partial listing of the endocranial volumes determined for many of the earlier hominids 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 relationship has ever been shown between brain volume and behavior, aside from pathological cases, such as microcephaly or hydrocephaly, where behavior is often subnormal. Microcephaly is especially interesting, as there are recorded cases of human beings having brain volumes less than 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

hominid ancestors, *Australopithecus afarensis* (3 m.y. ago) to our own species, *Homo sapiens*. With the exception of the large-bodied robust australopithecines, which averaged ca. 525 ml. in brain volume, the earliest hominids, 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 m.y. ago, 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 tools made to standardized patterns, hunting and scavaging 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, which helps to 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 hominids possessed language. From the time of *Homo erectus* on (i.e. at least 1.6 m.y. ago), the endocasts of hominids 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. 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.

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 the known 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 its respective brain organizations. 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 allo-

Table 1. Endocranial brain volumes of reconstructed hominids

Specimen	Taxon	Region	Endocranial Volume (ml.)	Method	Eval.
Taung	<i>A. africanus</i>	S.A.	440*	A	1
STS60	" "	"	428	A	1
STS71	" "	"	428	C	2-3
STS19/58	" "	"	436	B	2
STS5	" "	"	485	A	1
MLD37/38	" "	"	435	D	1
MLD1	" "	"	500-20	B	3
SK1585	<i>A. robustus</i>	"	530	A	1
OH5	"Z." boisei	E.A.	530	A	1
ER406	" "	"	525	D	2
ER407	" "	"	510	A	1
ER732	" "	"	500	A	1
ER1805	<i>Homo</i> ?	"	582	A	1
ER1813	" "	"	510	A	1
ER1470	<i>H. habilis</i>	"	752	A	1
OH7	" "	"	687	B	2
OH13	" "	"	650	C	2
OH24	" "	"	590	A	2-3
OH9	<i>H. erectus</i> (?)	"	1067	A	1
ER3733	" " "	"	848	A	1
ER3883	" " "	"	804	A	1
HE1 (1892)	" "	Indo.	953	A	1
HE2 (1937)	" "	"	815	A	1
HE4 (1938)	" "	"	900	C	2-3
HE6 (1963)	" "	"	855	A	2
HE7 (1965)	" "	"	1059	C	1-2
HE8 (1969)	" "	"	1004	A	1
Solo I	" "	"	1172	A	1
Solo V	" "	"	1250	A	1
Solo VI	" "	"	1013	A	1
Solo X	" "	"	1231	A	1
Solo XI	" "	"	1090	A	1
Salé	" "	Moroc.	880	A	1
Spy I	<i>H. sapiens</i> (N)	Europ.	1553	A	1
Spy II	" " "	"	1305	A	1
La Chapelle	" " "	"	1625	X	1
La Ferassie I	" " "	"	1640	X	1
Neandertal	" " "	"	1525	X	2
La Quina	" " "	"	1350	X	1
Jebel Irhoud 1	" "	Moroc.	1305	A	1
AL 333-45	<i>A. afarensis</i>	Ethiop.	485**	C	2
AL 162-28	" "	"	375-400**	est.	2
AL 333-105	" "	"	310-320**	C	2

Some selected cranial capacities for different hominids. Method A) direct water displacement of either a full or hemi-endocast 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) determination from regression formulae. X refers to previously published values, confirmed by the author. Evaluation of 1 indicates highest reliability; 3 the lowest, depending on completeness of specimen, distortion, and author's techniques. An asterisk* refers to estimated adult volume from juvenile or child's endocast. A double**, confined to the Hadar (Ethiopia) *Australopithecus afarensis* materials, refers to provisional estimates based on current research of the author. The AL 333-105 endocast is severely distorted, mostly incomplete, and that of a young child.

Two additional endocasts, recently made by Dr. Alan Walker of the Johns Hopkins University, are not in the above table. Through personal communication Dr. Walker suggests that the cranial capacity of a newly discovered robust form of *Australopithecus*, dated at 2.6 m.y., from the western shore of Lake Turkana (Kenya), is 410 ml. (the specimen is a robust male). A recently discovered *Homo erectus* youth discovered at Lake Turkana has a cranial capacity of 900 ml., according to Dr. Walker.

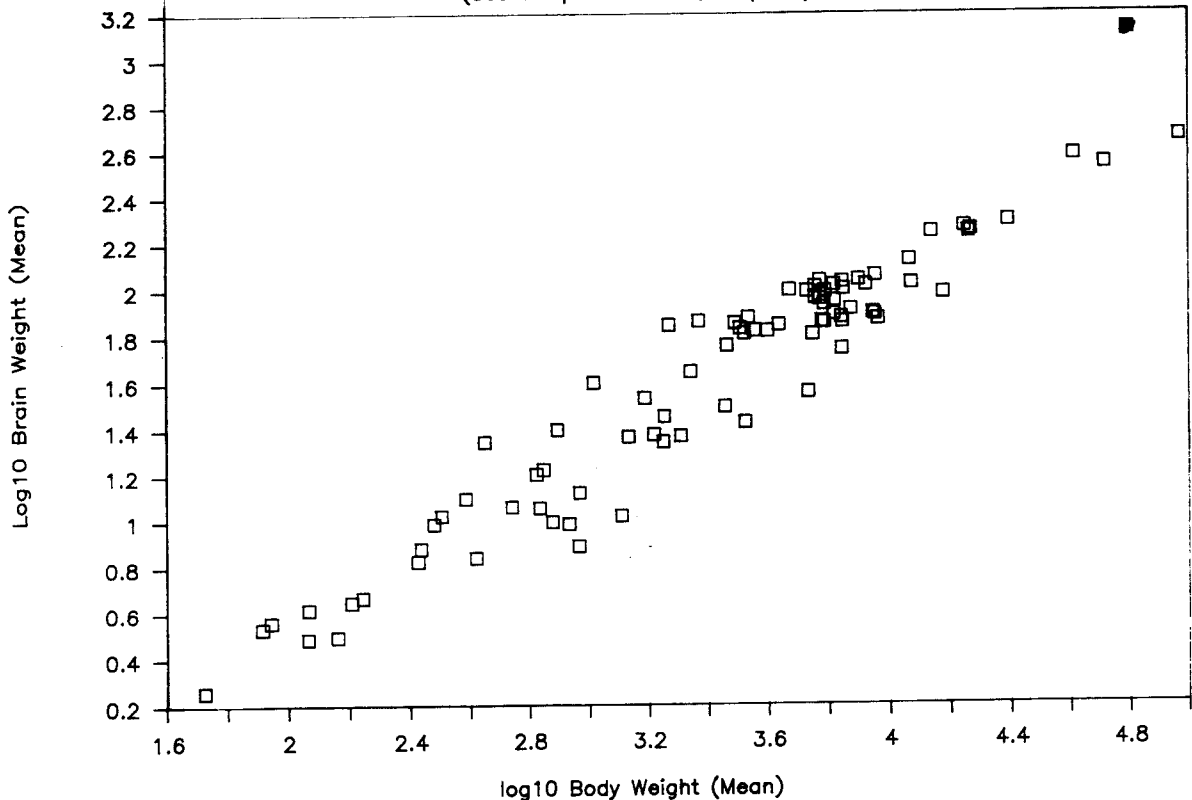
metric studies that treat brain size as a dependent variable and in which relationships are then made to body weight, metabolism, gestation duration, longevity, and in some cases broad ecological domains relating to subsistence patterns, such as folivory, frugivory, omnivory, and predation. But the brain 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 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.

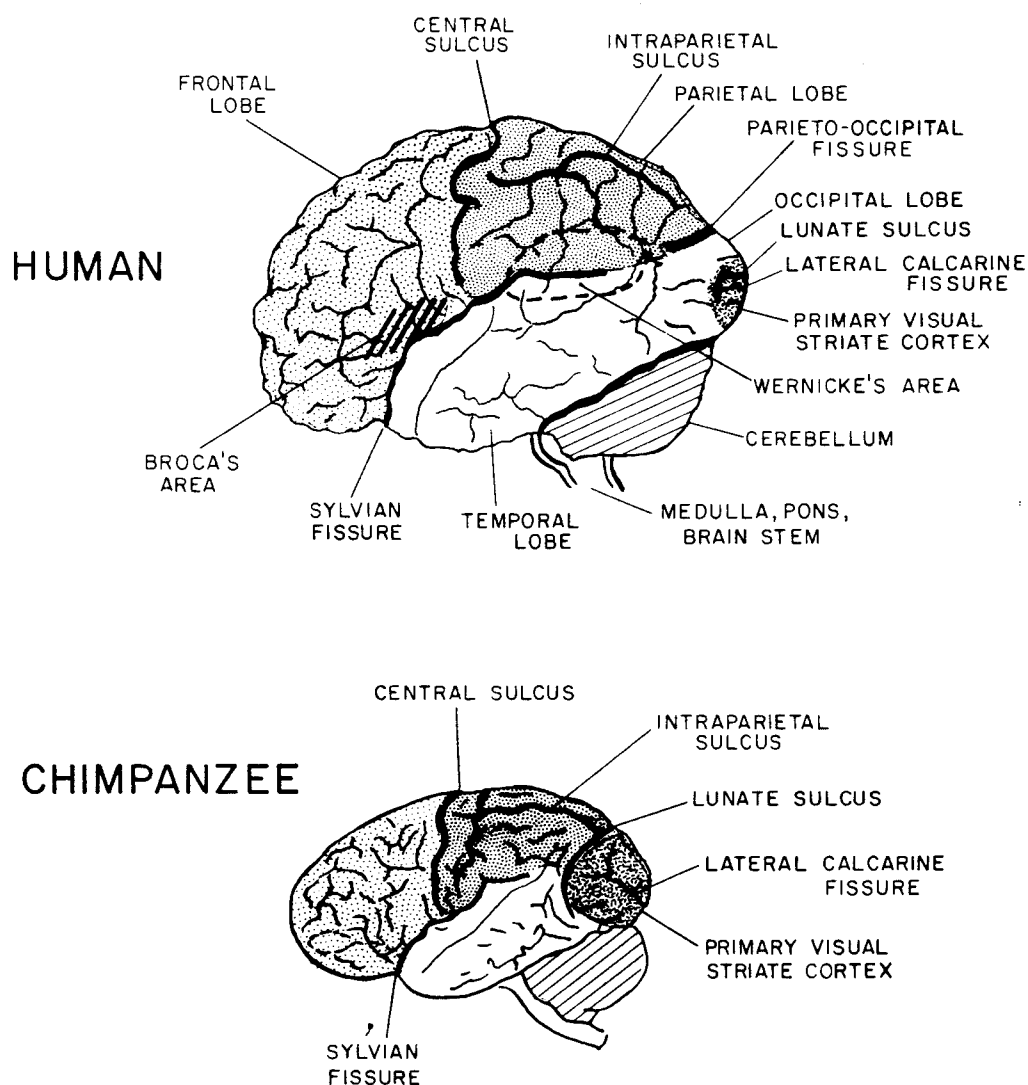
As mentioned above, in our own species the brain accounts for approximately 2 percent of our total body weight but uses close to 20 percent of our metabolism at any given moment. It is a voracious organ. Thanks to more recent allometric studies it

Log10 Brain vs. Body Weights (Mean)

(Source=pers. comm., Stephan)



A log-log (base 10) plot of the mean brain and body weights for 85 species of primates, including our own species, *Homo sapiens*. The *Homo* value is in the extreme upper-right-hand corner of the figure. The closest three rectangles are the pongids, gorilla, chimpanzee, and orangutan. The correlation coefficient is about 0.97, without the *Homo* value, which is about three times higher than its predicted value based on body weight. The slope of the regression line, without the *Homo* value, is ca. 0.76, a number strongly suggestive of 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 combination of prosimians, New and Old World monkeys, as well as the pongids and the human species. If the points are plotted *within* different taxonomic categories (i.e. prosimians alone, New World cebids alone, Old World monkeys, etc.), each group scales somewhat differently, with an average slope of ca. 0.66. This latter exponent suggests a geometric relationship between surface area and volume (i.e. the ratio 2/3). It is for this reason that encephalization quotients (E.Q.'s) are "relative," as each species value depends on the allometric equation used.



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 convolitional 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 interpretative controversy among paleoneurologists.

appears that the relationship between brain and body size is constrained more strongly by metabolic factors than by surface-area/volume relationships, as 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 about 0.66.

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 under 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 hominid endocasts in showing *Homo*-like derived rather than pongidlike retained primitive characteristics.

The second figure shows a lateral view of pongid 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: *primary visual striate cortex*. Anterior to this cortex is what we commonly call *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 compensa-

tory 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 roughly 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 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 interesting 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 where an animal's brain weight is divided by an allometric equation derived from a particular taxon. For example, the equation

$$E.Q. = \frac{\text{brain weight}}{.0991 \times (\text{body weight})^{.76237}}$$

provides an *encephalization quotient* (E.Q.), where 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 E.Q. is 2.87. For chimpanzee and gorilla the E.Q.s are 1.14 and 0.75, respectively. If an allometric equation for insectivores were used, the human, chimpanzee, and gorilla E.Q.s would be 28.8, 11.3, and 6.67. The important points here are twofold: first, the human animal always has the highest E.Q. regardless of the denominator; second, the E.Q. values and their relative values among species can vary by as much as 20 percent. When these equations are applied to fossil hominids, their relative closeness to modern humans or to our pongid 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 E.Q. 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:

$$E.Q. = \frac{\text{brain weight}}{\text{body weight}^{.64906}}$$

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 E.Q.s are expressed as a direct percentage of the human value. For example, the chimpanzee E.Q. is 0.39 (39 percent) and the gorilla value 0.23 (23 percent). Unfortunately, it is a matter of taste as to which E.Q. equation one selects, or which groups or taxa one wishes to compare and discuss.

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 about 80 percent of most populations), and both the motor and 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, 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 cerebral dominance. *Asymmetries* are extensions of parts of the cerebral cortex extending beyond their counterparts on one 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 torquellike *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 hominids show overwhelmingly the human *petalial* pattern, and Toth has discovered that many of the early stone tools were apparently made by right-handers. Some of the australopithecine 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 hominid evolution before the great expansion of brain size, although it must be made clear that this is a controversial area.

Sexual dimorphism of the human brain can be found 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. 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 m.y. of human brain evolution is a speculative matter. The earliest australopithecines (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 posterior parietal "association cortex" had increased beyond the ape level. Cerebral asymmetries are also present, but these are more strongly represented in early *Homo*, a period of time that coincides with a major expansion of brain size (to ca. 750 ml. from 450 ml.) at ca. 2 m.y. ago. Coincident with these patterns are stone tools and evidence for hunting and scavaging. The remaining doubling of size, to ca. 1,400 ml., is perhaps best explained through allometric processes where natural selection favored increased body size, longer periods of childhood growth, and, one assumes, more sophisticated brains. 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 hominid discoveries.

[R.L.H.]

Further Readings

- Bryden, M.P. (1982) *Laterality: Functional Asymmetry in the Intact Brain*. New York: Academic.
- Connolly, C.J. (1950) *External Morphology of the Primate Brain*. Springfield, Ill.: Thomas.

- Damasio, A.R., and Geschwind, N. (1984) The neural basis for language. *Ann. Rev. Neurosci.* 7:127-147.
- de Lacoste-Utamsing, M.C., and Holloway, R.L. (1982) Sexual dimorphism in the corpus callosum. *Science* 216:1431-1432.
- Geschwind, N., and Galaburda, A.M., eds. (1984) *Cerebral Dominance: The Biological Foundations*. Cambridge, Mass.: Harvard University Press.
- Holloway, R.L. (1975) The Role of Human Social Behavior in the Evolution of the Human Brain. 43rd James Arthur Lecture. New York: American Museum of Natural History.
- Holloway, R.L. (1978) The relevance of endocasts for studying primate brain evolution. In C.R. Noback (ed.): *Sensory Systems in Primates*. New York: Plenum, pp. 181-200.
- Holloway, R.L., and de Lacoste-Lareymondie, M.C. (1982) Brain endocast asymmetry in pongids and hominids: some preliminary findings on the paleontology of cerebral dominance. *Am. J. Phys. Anthropol.* 58:101-110.
- Kinsbourne, M., ed. (1978) *Asymmetrical Function of the Brain*. Cambridge: Cambridge University Press.
- LeMay, M. (1976) Morphological asymmetries of modern man, fossil man, and nonhuman primates. *Annals N.Y. Acad. Sci.* 280:349-366.
- Martin, R.D. (1983) Human Evolution in an Ecological Context. 52nd James Arthur Lecture. New York: American Museum of Natural History.
- Passingham, R.E. (1982) *The Human Primate*. Oxford: Freeman.
- Radinsky, L.B. (1979) The Fossil Record of Primate Brain Evolution. 47th James Arthur Lecture. New York: American Museum of Natural History.
- Stephan, H., Frahm, H., and Baron, G. (1981) New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatol.* 35:1-29.

BRANISELLA see BRANISELLINAE; OLIGOCENE

BRANISELLINAE

Extinct subfamily of cebid platyrrhine monkeys including only *Branisella boliviana*. This form is the oldest and most archaic of the ceboid primates, known from a level of the late Oligocene Bolivian deposit at La Salla, which has been recently redated at ca. 27 m.y. *Branisella* upper molars are in part morphologically conservative, although they do resemble those of the cebid *Saimiri*. Its lower jaw is very shallow, as in the relatively primitive parapithecoid catarrhines.

See also ANTHROPOIDEA; CEBIDAE; PARAPITHECIDAE;
PLATYRRHINI. [A.L.R.]

Further Readings

- Rosenberger, A.L. (1981) A mandible of *Branisella boliviana* (Platyrrhini, Primates) from the Oligocene of South America. *Int. J. Primatol.* 2:1-7.

BRECCIA CAVE FORMATION

Breccia refers to a type of sedimentary rock that consists of angular to subangular, freshly broken frag-

ments that generally have not been transported far from their points of origin. Taking the five South African australopithecine-bearing deposits as an example, one sees that these fossiliferous breccias are composed principally of loose blocks in beds of sand, all cemented into a solid mass by the deposition of calcium carbonate within a subterranean solution cavity in limestone. The Transvaal sites of Kromdraai, Makapansgat, Sterkfontein, and Swartkrans represent the remains of breccia-filled solution chambers that formed in dolomitic limestone; the breccias at Taung, however, developed within a limestone tufa fan that extended outward from the dolomite of the Gaap (or Kaap) Escarpment along the southeastern margin of the Kalahari Desert.

Generally such breccia-filled caves begin with subterranean dissolution in limestone formations that are below the level of the water table. As the water table is lowered through time, these dissolution chambers remain as voids within the parent rock. Small openings from the chamber to the terrestrial surface form through progressive enlargement by rainwater of fissures and cracks in the parent rock. These small openings admit circulating air in the chamber, leading to the formation of stalactitic and/or stalagmitic travertines (dripstones) by the evaporation of calcareous waters that have percolated through the parent limestone. Through time, and the enlargement of these openings, the chamber may fill with sands and other surface debris, mixed with infalling blocks from walls and roof. The sand and debris, including bones and teeth, become cemented to form breccia by the deposition of waterborne carbonates that have continued to percolate through the parent limestone.

Eventually the talus cone of sediment that has formed in the chamber may become so extensive as to choke the opening through which it entered. With time a new solution channel may form a shaft through the sediment, resulting in the erosion of some of the original breccia together with the deposition and calcification of more recently derived sediments. By the same token other vertical avenues may open to the surface, and these may result in the deposition of "younger" material upon the original breccia mass. Erosion of the parent rock may eventually expose these breccia-filled chambers to the surface. A complex series of processes of dissolution, filling, cementation, secondary decalcification and erosion, and subsequent deposition and cementation are involved in the formation of cave breccias, making accurate stratigraphic interpretation of such sites extremely difficult.

See also KROMDRAAI; MAKAPANSGAT; STERKFontein;
SWARTKRANS; TAUNG. [F.E.G.]

- Damasio, A.R., and Geschwind, N. (1984) The neural basis for language. *Ann. Rev. Neurosci.* 7:127-147.
- de Lacoste-Utamsing, M.C., and Holloway, R.L. (1982) Sexual dimorphism in the corpus callosum. *Science* 216:1431-1432.
- Geschwind, N., and Galaburda, A.M., eds. (1984) *Cerebral Dominance: The Biological Foundations*. Cambridge, Mass.: Harvard University Press.
- Holloway, R.L. (1975) The Role of Human Social Behavior in the Evolution of the Human Brain. 43rd James Arthur Lecture. New York: American Museum of Natural History.
- Holloway, R.L. (1978) The relevance of endocasts for studying primate brain evolution. In C.R. Noback (ed.): *Sensory Systems in Primates*. New York: Plenum, pp. 181-200.
- Holloway, R.L., and de Lacoste-Lareymondie, M.C. (1982) Brain endocast asymmetry in pongids and hominids: some preliminary findings on the paleontology of cerebral dominance. *Am. J. Phys. Anthropol.* 58:101-110.
- Kinsbourne, M., ed. (1978) *Asymmetrical Function of the Brain*. Cambridge: Cambridge University Press.
- LeMay, M. (1976) Morphological asymmetries of modern man, fossil man, and nonhuman primates. *Annals N.Y. Acad. Sci.* 280:349-366.
- Martin, R.D. (1983) Human Evolution in an Ecological Context. 52nd James Arthur Lecture. New York: American Museum of Natural History.
- Passingham, R.E. (1982) *The Human Primate*. Oxford: Freeman.
- Radinsky, L.B. (1979) The Fossil Record of Primate Brain Evolution. 47th James Arthur Lecture. New York: American Museum of Natural History.
- Stephan, H., Frahm, H., and Baron, G. (1981) New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatol.* 35:1-29.

BRANISELLA see BRANISELLINAE; OLIGOCENE

BRANISELLINAE

Extinct subfamily of cebid platyrrhine monkeys including only *Branisella boliviana*. This form is the oldest and most archaic of the ceboid primates, known from a level of the late Oligocene Bolivian deposit at La Salla, which has been recently redated at ca. 27 m.y. *Branisella* upper molars are in part morphologically conservative, although they do resemble those of the cebid *Saimiri*. Its lower jaw is very shallow, as in the relatively primitive parapithecoid catarrhines.

See also ANTHROPOIDEA; CEBIDAE; PARAPITHECIDAE;
PLATYRRHINI. [A.L.R.]

Further Readings

- Rosenberger, A.L. (1981) A mandible of *Branisella boliviana* (Platyrrhini, Primates) from the Oligocene of South America. *Int. J. Primatol.* 2:1-7.

BRECCIA CAVE FORMATION

Breccia refers to a type of sedimentary rock that consists of angular to subangular, freshly broken frag-

ments that generally have not been transported far from their points of origin. Taking the five South African australopithecine-bearing deposits as an example, one sees that these fossiliferous breccias are composed principally of loose blocks in beds of sand, all cemented into a solid mass by the deposition of calcium carbonate within a subterranean solution cavity in limestone. The Transvaal sites of Kromdraai, Makapansgat, Sterkfontein, and Swartkrans represent the remains of breccia-filled solution chambers that formed in dolomitic limestone; the breccias at Taung, however, developed within a limestone tufa fan that extended outward from the dolomite of the Gaap (or Kaap) Escarpment along the southeastern margin of the Kalahari Desert.

Generally such breccia-filled caves begin with subterranean dissolution in limestone formations that are below the level of the water table. As the water table is lowered through time, these dissolution chambers remain as voids within the parent rock. Small openings from the chamber to the terrestrial surface form through progressive enlargement by rainwater of fissures and cracks in the parent rock. These small openings admit circulating air in the chamber, leading to the formation of stalactitic and/or stalagmitic travertines (dripstones) by the evaporation of calcareous waters that have percolated through the parent limestone. Through time, and the enlargement of these openings, the chamber may fill with sands and other surface debris, mixed with infalling blocks from walls and roof. The sand and debris, including bones and teeth, become cemented to form breccia by the deposition of waterborne carbonates that have continued to percolate through the parent limestone.

Eventually the talus cone of sediment that has formed in the chamber may become so extensive as to choke the opening through which it entered. With time a new solution channel may form a shaft through the sediment, resulting in the erosion of some of the original breccia together with the deposition and calcification of more recently derived sediments. By the same token other vertical avenues may open to the surface, and these may result in the deposition of "younger" material upon the original breccia mass. Erosion of the parent rock may eventually expose these breccia-filled chambers to the surface. A complex series of processes of dissolution, filling, cementation, secondary decalcification and erosion, and subsequent deposition and cementation are involved in the formation of cave breccias, making accurate stratigraphic interpretation of such sites extremely difficult. --

See also KROMDRAAI; MAKAPANSGAT; STERKFontein;
SWARTKRANS; TAUNG. [F.E.G.]