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M. I. Posner and M. K. Rothbart

Brain, Evolution of

When did the human brain evolve, and how did it happen? Obviously, to answer this question will require a time machine, and thousands of generations of observations to ascertain both the variability and direction of selection pressures in the past. We can, however, flesh out an initial understanding of how we got to be the animal *par excellence* that utilizes its brain for intelligent rationalizations based largely on the use of arbitrary symbol systems. The evidence consists of two components: (a) the 'direct' evidence from the fossil record; and (b) the 'indirect' evidence of the comparative neuroscientific record of extant living animals, particularly those most closely related to us, such as the chimpanzee. There is a third possibility: since the human genome project has sequenced almost all of the genetic code, the future study of evolutionary neurogenetics might provide more data about the actual genetic history of our Genus through time, as well as that of the great apes mentioned above. As this latter possibility is simply a mote in our eye at present, this article must concentrate on the evidence provided by the first two components.

1. Lines of Evidence

1.1 Direct Evidence

The term *paleoneurology* is used to describe evidence appraising the size and morphology of the casts made from the inside of actual fossil cranial remains. Occasionally, the casts are 'natural,' i.e., where fine sediments have filled the inside of the cranial cavity, and became compacted through time. These casts often retain whatever morphological details were imprinted on the internal table of bone of the cranium. The famous australopithecine Taung child's skull, described by Dart (1925), is one of the best-known examples. Curiously, these 'natural' endocasts are only found in the S. African australopithecines, of which several exist, and date from about 2.5 MY to about 1.5 MY. Most often, the paleoneurologist makes a cast of the inside of the fossil skull using rubber latex, or silicone rubber, and extracts this from the cranium. The partial cast is reconstructed by adding plasticine (modeling clay) to the missing regions. The whole is then measured by immersion into water, and the amount of water displaced is regarded as the volume

of the once-living brain. Other measurements and observations are made on the original cast.

During life the brain is surrounded by three dural sheaths (dura mater, arachnoid tissue and its cerebrospinal fluid, and pia mater) that interface between the actual brain tissue (cerebral cortex, mostly) and the internal table of bone of the skull. The gyri and sulci (convolutions) of the once-pulsating cerebral cortex are rarely imprinted on the interior of the skull, and the degree of replication often varies in different regions, i.e., sometimes the frontal lobe imprints more details than the parietal lobe. The degree of replication also varies in different animals. Two extremely important considerations emerge from this: (a) the resulting imprints are never complete and thus 'data poor,' and never include subcortical structures; and (b) controversial interpretations of what the underlying brain once looked like are guaranteed. Nevertheless, these endocranial brain casts do provide extremely important information regarding the size, shape, rough estimates of the lobar dimensions of the brain, and cortical asymmetries that have relationships to hemispheric specializations, including handedness. In addition, if the imprints of the underlying gyri and sulci are available, these can provide important information regarding the organization of the cerebral cortex, and whether the patterns of these are the same or different as in known extant primate brains. The infamous 'lunate sulcus' is a good example, as it is a demarcation boundary between purely sensory primary visual striate cortex (PVC) and multi-modal association cortex. When the lunate sulcus appears in an anterior position, it is most similar to the condition known in modern apes. When it is found in a posterior position, it is more in a human-like condition. Ascertaining its correct position is essential in deciding whether or not such a fossil hominid had a brain organized along human or ape lines. Finally, meningeal arteries and veins that nourished the dura mater also imprint on the internal table of bone and these sometimes show patterns that are useful for deciding taxonomic issues; these have no known relationship to behavioral functions of the brain.

1.2 Indirect Evidence

This line of evidence is 'data rich,' providing comparative neurological information on living species, such as brain size (both absolute and relative, i.e., related to body size), the actual makeup of the brain from the gross to microscopic levels, including neural nuclei, fiber systems and interconnections, and distribution of neurotransmitters and neuroreceptors. Additionally, the brain can be studied ontogenetically, and neuroscientists can actually study the relationships between how the brain varies neurologically and how these variations relate to the behavioral variation. This richness is simply lost to the paleoneurologist as it is not available as direct evidence. However, it is necessary to realize that the extant living species, e.g., chimpanzee, macaque, are end points of their own evolutionary lines of development and are not our ancestors, however closely related. It is the blending and complementation of these two approaches which provide the best set of evidence for when and how our brains evolved.

2. Characteristics of the Human Brain

2.1 Brain Size, Absolute and Relative

The human animal is obviously obsessed with size, and those who study the brain comparatively, perhaps more so. With an average brain weight of 1,330 grams (Tobias 1971), the human species has the largest absolute brain size within the primate order, but is actually dwarfed by elephants and some of the Cetacea, where brain weight can exceed 7,500 grams. Of course, the body weights are very much higher in elephants and whales. But even for its body weight, *Homo sapiens* does not have the largest relative brain weight, being outdone by several monkeys, some rodents, and even some fish. Normal modern human brain size varies between roughly 900 and 2,000 grams, although some very small number of exceptions does occur, with sizes ranging from about 750 to 900 and 2,000 to 2,200 grams. There exist both human population variation as well as differences between the sexes. In general, Arctic peoples have larger brains than those living in the tropics, and the smallest brains appear to be found among Ituri forest pygmies, also displaying small stature. Males in all populations for which good autopsy data have been gathered show brain sizes on the average of 100–150 grams greater than females, an amount roughly the same as the range of modern human racial variation. It should be pointed out that these differences, and their possible relationship to cognitive skills, are highly controversial and simple correlations are deceptive (Holloway 1996). Table 1 provides a listing of the major fossil hominid taxa and their respective brain sizes. Notice that the range of values from the earliest australopithecine to modern *Homo* is roughly 1,000 ml, or about the same amount as the normal range of variation within our species.

2.2 Encephalization (Encephalization Coefficient, E.Q.)

Nevertheless, the human animal does come out on top of the evolutionary heap when its absolute brain and body weights are considered together. When the log (base 10) of brain weight is plotted against the log 10 of body weight for a group of relevant taxa, the result is a linear line, where (log 10) brain weight = a + b (log 10) body weight. For a large array of primate data (Stephan et al. 1981), the slope of the line (b in the

Table 1
Some fossil hominid brain volumes

Group	Number	Location	Average Brain Volume	Range	Dating (MY)
A. afarensis	3	E. Africa	435	400–500	3–4
A. africanus	8	S. Africa	440	420–500+	2–3
A. aethiopicus	1	E. Africa	410	410	2.5
A. robustus	6	E. & S. Africa	512	500–530	1.6–2.0
H. rudolphensis	2	E. Africa	775	752–800	1.8
H. habilis	6	E. Africa	612	510–687	1.7–2.0
H. ergaster	2	E. Africa	826	804–848	1.6
H. erectus	2	E. Africa	980	900–1067	1.0–1.6
H. erectus	8	Indonesia	925	780–1059	1.0
H. erectus	8	China	1029	850–1225	0.6
Archaic *H. sapiens*	6	Indonesia	1148	1013–1250	0.13
Archaic *H. sapiens*	6	Africa	1190	880–1367	0.125
Archaic *H. sapiens*	7	Europe	1315	1200–1450	0.5–0.25
H. sapiens (Neand.)	25	Europe, M. East	1415	1125–1740	0.09–0.03
H. sapiens sapiens	11	World	1506	1250–1600	0.025–0.01

Source: Holloway 1997.

Table 2
Some examples of encephalization quotients

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

Source: Holloway 1997.
Formulae:
a EQ Homo = Brain wt/1.0 Body $wt^{0.64906}$, b EQ Jerison = Brain wt/0.12 Body $wt^{0.66}$, c EQ Primates = Brain wt/0.0991 Body $wt^{0.76237}$, d EQ Stephan = Brain wt/0.0429 Body $wt^{0.63}$
Note: Each formula is based on a different set of data. The EQ Homo equation simply uses the average brain and body weight for *Homo sapiens*, and assumes an intercept where both brain and body weights are zero. The value of whichever animal is calculated is then given as a direct % of modern *Homo sapiens*. EQ Jerison is based on data for almost 200 mammals, while the EQ Primates is based on Martin's (1983) data set for primates only. The EQ Stephan equation is based on insectivores only. The numbers in the parentheses are the % of the *Homo sapiens* value.

equation above) is about 0.76, and the correlation coefficient is 0.98, indicating that the relationship is almost perfect. This relationship will naturally vary depending on the databases and the transformations used. This is known as an allometric equation, and these are used frequently in biology to assess the underlying relationships between the size of parts of the body and the whole. The slope sometimes has an interpretation suggesting functional relationships between the brain and other variables. For example, in the above example, the slope is 0.76, extremely close to 0.75 or 3/4, which often describes a metabolic relationship (Martin 1983). The slope of 0.666, or 2/3, has been championed by some (e.g., Jerison 1973) as indicating an important geometric relationship between volume and surface area. It is important to realize that these slopes vary depending on the taxa examined. In general, as the taxa become more similar, the slope decreases. Species within a genus generally have a slope around 0.3; within a species the slope is smaller yet, being about 0.2, and the correlation coefficient is also reduced.

Just as the human animal is curious, it is also vainglorious, always trying to find a measure that places it at the top. Thus we can fabricate a device, the *Encephalization Coefficient*, or E.Q., which shows that relative to any database, the human animal is the most encephalized animal living. The point for *Homo sapiens* shows a clear positive residual above the expected regression line, and in fact the human value is about three times that expected for a primate with its body weight. Table 2 provides a number of different equations based on differing databases, which happily give *Homo sapiens* the highest value. (Actually, young

immature dolphins will provide a higher number, but when compared to an immature human, the value is higher in the latter.) Two additional points should be made: (a) E.Q.s are relative to the databases used, and thus there is an inherent 'relativity' to relative brain sizes; and (b) E.Q.s do not evolve, only brain weight/body weight relationships do, and E.Q.s are simply a heuristic device enabling comparisons between taxa; they have no reality outside of the database chosen, or species within a taxa, and are not designed to discuss within-species variation. For example, female humans are 'more' encephalised than males, given their smaller body sizes and smaller brains but the relationship is simply a statistical artifact with no known behavioral manifestation given their equal overall intelligence.

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

2.3 Brain Organization and Reorganization

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

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

When used in a comparative or evolutionary context reorganization means changes in the sizes and proportions thereof of neural nuclei and their fiber tracts. Given that chimpanzees and hominids last had a common ancestor some 5–7 MY, and that chimpanzees appear to have large PVC cortices, we infer that one aspect of human brain evolution has been some reorganization of the cerebral cortex, namely an increase in posterior association cortex (or, equally, a reduction in PVC) involved in polymodal cognitive tasks, where visual, auditory, and motor information are brought together in a synthetic whole. The trick, of course, is to demonstrate objectively when, where, and why these changes took place. This example of PVC has been purposefully chosen because one of the sulcal landmarks of the cortex that defines the anterior border of PVC is the 'lunate' sulcus, named for its crescentic shape, and there is some hope of identifying its position on some of the early hominid brain endocasts.

Neuroanatomists have been trying for many decades to demonstrate the major differences between us and other primates, and aside from gross brain size, very little has been shown. The frontal lobe, and particularly its prefrontal portion, has been a favorite target and indeed, Brodmann (1909) claimed it was proportionally larger in humans, a view most recently championed by Deacon (1997). Unfortunately, other works have shown that the human brain has just as much frontal lobe as would be expected for a primate of its brain weight (Semendeferi et al. 1997, Uylings and van Eden 1990), although the picture regarding prefrontal cortex has yet to be determined objectively using cytoarchitectonic criteria, which is how prefrontal cortex is differentiated from the pure motor cortex behind it. Hominid brain endocasts do not, alas, provide any sulcal landmarks with enough

reliability to determine the boundaries of prefrontal cortex, which is so important to impulse control, and higher cognitive functions such as planning and abstraction. Thus these regions cannot be measured in a phylogenetic sequence. The Neandertals, living from about 200,000 to about 28,000 years ago have frequently been described as having smaller frontal lobes; this is not based on objective measurements, but rather a perception that the large brow ridges on these humans were constraining frontal lobe development. Studying the Neandertal brain endocasts and comparing them to modern humans, I have failed to see any significant difference between these two groups.

Similarly, regions such as 'Broca's and Wernicke's areas,' anterior and posterior association cortical regions involved in motor (Broca's) and receptive (Wernicke's) aspects of speech, are not determinable on most fossil brain endocasts, although we can determine, for example, that Broca's region is more human-like on the brain cast of early *Homo*, some 1.8MY. This is the famous KNM-ER 1470 endocast of *Homo rudolphensis* from Kenya, which had a brain volume of 752ml, but which may not be a direct ancestor to our own line of *Homo*.

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

2.4 Human Brain Asymmetry

The cerebral cortices of the human brain are usually asymmetrical, and tend to grow in a torque manner, reflecting minor differences in maturation rates. The hemispheres are seldom, if ever, equipotential in terms of functioning. Our left hemisphere is often characterized as 'analytic' and involved with language tasks, while our right hemisphere appears most competent in visuospatial integration, and is often thought of as the 'intuitive' or 'gestalt' hemisphere. These characterizations, while crude, hold up fairly accurately for right-handers and many ambidextrals. From radiographic studies, it was possible for LeMay (1976) to ascertain different petalia patterns for right- and left-handed humans with a high degree of precision. These petalias are small extensions of cerebral cortex that extend farther in one part of a hemisphere than on the other side. For example, we speak of a left-occipital right-frontal torque pattern of petalias as occurring with high frequency in right-handed individuals. This means that the left occipital lobe bulges somewhat more posteriorly on the left hemisphere while the right hemisphere is somewhat broader in width in the frontal lobe. In true left-handers, who are represented in human populations by about 8–10%, the pattern is reversed, meaning they exhibit a right-occipital left-frontal pattern. Petalia patterns for a large collection of apes indicated that while chimpanzees, gorillas, and orangutans sometimes demonstrated asymmetries, they did not show the particular torque pattern described above for humans. The gorilla, incidentally, was the most asymmetrical of the apes (Holloway and de LaCoste-Lareymondie 1982). On the other hand, brain asymmetries, particularly in the *planum temporale* (temporal cortex) of the chimpanzee, show a strong left-hemispheric size difference compared to the right (Gannon et al. 1998). This is simply puzzling as we do not have any evidence that chimpanzees use this structure in communication as do humans, and the fact that we share this difference with chimpanzees suggests that brain organizational features relating to complex cognitive functioning has been around for at least 5–7MY. As our non-invasive scanning techniques become more sophisticated, we can expect to learn how these asymmetries function is animals other than ourselves.

Hominid brain endocasts, when complete for both sides (unfortunately, this is very rare) allow the paleoneurologist to assess the cerebral asymmetries, and indeed, even australopithecines appear to show beginnings of the right-handed torque pattern found in humans, and, as one progresses through time, the petalia patterns become more accentuated in the modern human direction. If we add to these observations those of Toth's (1985) studies on the early stone tools of about 2MY, which strongly suggest right-handedness, this underlines the fact that our early ancestors, brains, despite their small size (sometimes

within the extant apes' range), were reorganized, and that they probably had some modes of cognition very similar to our own.

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

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

Table 4 outlines the major size changes in the human brain during its evolutionary odyssey. Paleoneurological data simply are not detailed enough to integrate the two tables of size and reorganizational changes into one holistic sequence of events. Basically, the paleontological record supports an early reorganizational change resulting in an increase in posterior cortex associated with visuospatial processing, perhaps accompanied by a relative small allometric increase in brain size from *A. afarensis* to *A. africanus*. This would correlate well with geological and paleontological evidence that shows that early hominids were expanding their ecological niches and becoming more diverse in their subsistence patterns in mixed habitats. We know this based on the fact that stone tool types are becoming standardized in form, tool inventories grow larger, and right-handedness is highly probable. With the advent of *Homo*, we find strong evidence for a major increase in brain size, both allometric (related to body size) and non-allometric, and a reorganized frontal lobe, broader, and showing a more modern human-like Broca's area. This suggests that indeed there had been some strong and dramatic selection pressures for a somewhat different style of sociality, one most probably based on a primitive proto-language that had some arbitrary symboling elements as the standardization of stone tools (e.g., Acheulean handaxes) increases, suggesting social cohesion and control mediated through symbolically-based communication. Needless to say, this is but one speculative account of the evidence. But from about 1.8 to roughly 0.5 MY, we think there were minor allometric brain size increases to the earliest *Homo erectus* hominids of Indonesia and China, where brain sizes ranged from 750 to 1250 ml in volume. We have very little evidence for body sizes, but we believe, on the basis of the KNM-WT 17,000 Nariokotome youth from Kenya at ca. 1.6 MY, that these did not differ significantly from our own.

This is also a time during which cerebral asymmetries are becoming more strongly pronounced. With the advent of Archaic *Homo sapiens*, about 0.15–0.2 MY, we find brain sizes well within modern human values, and no evidence for further allometric increases, except possibly for the Neanderthal humans in which it can be argued that their larger brain and body sizes (lean body mass: bone and muscle) were adaptations to colder conditions. If further changes took place in cerebral and/or subcortical organization, they are simply not apparent from a paleoneurological perspective. Yet, the Upper Paleolithic is the time when cave art makes its appearance, and one cannot help but wonder whether the explicit use of art involving symbolization might not also have been the time for the emergence of language. In fact, however, there is nothing in the direct fossil evidence, and in particular paleoneurology, which provides any evidence for such views. Claims for a single mutation are ridiculously speculative. Finally, it would appear that there has actually been a small reduction in brain size, probably allometric in nature, from about 0.015 MY to the present.

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

> In sum, the major underlying selectional pressures for the evolution of the human brain were mostly social. It was an extraordinary evolutionary 'decision' to go with an animal that would take longer to mature, reach sexual maturity later, and be dependent for its food and safety upon its caretakers (parents?) for a longer period of time. The benefits for the animal were many, including a longer learning period, a more advanced, larger, and longer-growing brain, and an increasing dependence on social cohesion and tool making and tool

Table 3
Summary of reorganizational changes in the evolution of the human brain

Brain Changes	Taxon
(1) Reduction of primary visual striate cortex, area 17, and a relative increase in posterior parietal cortex	*Australopithecus africanus* *Australopithecus afarensis*
(2) Reorganization of frontal lobe (3rd inferior frontal convolution, Broca's area)	*Homo rudolphensis*
(3) Cerebral asymmetries, left-occipital right frontal petalias	Australopithecines and early *Homo*
(4) Refinements in cortical organization to a modern *Homo sapiens* pattern	*Homo erectus* to present

Source: Holloway 1997.
Note: (4) is inferred, as brain endocasts cannot provide that level of detail necessary to demonstrate the refinements in cortical organization from surface features alone.

Table 4
Brain size changes in hominid evolution

Brain changes	Taxon	Time (MY)	Evidence
1. Small increase, allometric[a]	*A. afarensis* to *A. africanus*	3.5–2.5	Brain endocast increase from 400 to 450 ml.
2. Major increase, rapid, both allometric and non-allometric	*A. africanus* to *H. habilis*	2.5–1.8	KNM–1470, 752 ml (300 ml increase)
3. Modest allometric increase in brain size to 800–1000 ml	*H. habilis* to *H. erectus*	1.8–0.5	*H. erectus* brain endocasts and postcranial bones
4. Gradual and modest size increase to archaic non-allometric	*H. erectus* to *H. sapiens neanderthalensis*	0.5–0.075	Archaic *Homo H. sapiens*, Neandertal endocasts 1200–1700 + ml.
5. Small reduction in brain size among modern allometric	*H. sapiens H. sapiens sapiens*	0.015–present	Modern endocranial volumes

Source: Holloway 1997.
a Related to increase in body size only.

using to cope with the environments that they encountered. Needless to say, language abilities using arbitrary symbol systems were an important ingredient in this evolution.
The fossil record shows us that there was a feedback between the complexity of stone tools (which must be seen as a part of social behavior) and increasing brain size and the expansion of ecological niches. The 'initial kick,' however, the process that got the ball rolling, was a neuroendocrinological change affecting regulatory genes and target tissue-hormonal interactions that caused delayed maturation of the brain and a longer growing period, during which learning became one of our most important adaptations.

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

4. *And to the Future?*

There appear to be two common presumptions about our future brain evolution. One is that our biological evolution has stopped. The second is that our brains will continue to grow in size, with bulging frontal lobes (sort of a cross between E.T. and X-Files ...), to handle our growing dependence on technology. What we have witnessed from the past fossil record is that our brains and bodies work largely in allometric fashion, and given the high metabolic cost of operating bigger brains (about 20–25% of our metabolic resources go to supporting our brains, which constitute only 2% of our total body weight), the second scenario seems highly unlikely. The first scenario is simply untrue, but it would require vast amounts of information from each generation of many living populations, something feasible perhaps, but not currently being collected. Furthermore, it is quite controversial whether brain size has any close relationship to intelligence, however intelligence is actually measured. Recent research based on MRI determinations of brain volume and selected batteries of cognitive tests have shown correlations between test scores and brain volume ranging from 0.4 to 0.6. (Andreasen et al. 1993). This is a figure significantly larger that previously reported (e.g., Van Valen 1974), and will need more replication studies. But if protein resources were to nosedive throughout the world for a significant period of time, selection would probably favor smaller body sizes in our species, and that would result in smaller brains, given an allometric relationship of

roughly 0.3 between stature and brain size. While genetic engineering may well provide some respite between the ever-increasing mass of humanity, ecological and nutritive degradement, this too is likely to be nothing more than short-term fending off of the unstoppable future. These degradations are part and parcel of the human brain's capacity to ignore warnings that should curtail greed and stupidity. The paleontological record for most mammals suggests that at the taxonomic level of the genus (such as *Pan*, *Homo*, *Canis*, *Notocherus*, etc.), one finds a recognizable record of that genus spanning approximately 5 to 10 million years. Our genus has a duration of about 2 MY. We, as a genus, despite our largish highly encephalized brains, have another 3 MY to go if we wish to be as successful in the paleontological longevity game.

See also: Body, Evolution of; Evolution of Cognition: An Adaptationist Perspective; Human Cognition, Evolution of; Intelligence, Evolution of

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R. Holloway

Brain Implants and Transplants

The concept of brain repair with cells or tissue transplants is immensely attractive. After all, tissue and organ transplantation has progressed significantly over the past 30 years, and allowed extended life to patients with deadly, and previously incurable, diseases of the heart, lungs, liver, kidneys, and other organs. Transplantation to the brain, however, presents an altogether different, complex series of problems. Even with our rapidly evolving knowledge about the brain, its intricate neural networks, sensitivity to injury, and delicate chemical balance, make this most complex organ so much more difficult to treat.

These problems notwithstanding, our understanding of the brain is advancing. It is no longer considered a stable, unchanging organ in the adult and the long-held dogma that repair and regeneration of the brain cannot take place is wrong. Trophic factors, neural transplants, and stem cell grafts are just a few of the many ways by which the central nervous system can be modified.

1. How do Transplants Work?

There are several ways in which implants or transplants can work in the central nervous system: (a) provide replacements for lost cells, with integration

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