Evolution of the Frontal Lobes

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There is a fossil record of the evolution of the brain, which can be used for insight into the evolution of human frontal neocortex. The evidence is from brainlike endocasts, molded by the cranial cavities of fossil animals. One can use this evidence to understand the evolution of the brain by comparing endocasts to brains in living species and relating the external morphology of the brain revealed in endocasts to its internal anatomy and functions.

In mammals and birds, endocasts are superficially like freshly prepared brains. They are in a real sense "fossil brains" (Edinger, 1929). The endocast of the Neandertal on the left in Figure 1 is a plaster cast prepared from a cleaned skull. On the right, the Taung australopithecine skull shows some of an endocast made by natural processes after death (see also Figure 5, below), when sand and other debris replaced soft tissue and became packed tightly in the cranial cavity, and the skull and its contents hardened and fossilized. Mammalian endocasts, whether natural or cast from a cleaned skull, can be treated as if they were brains with dura intact. Direct information from an endocast is on the size and shape of the brain, but by analogy to living brains, the fossils can also tell us about the capacity of brains to process information. In this chapter I review what we know about the evolution of the frontal lobes, emphasizing fossil endocasts and interpreting them as if they were living fresh brains of similar size and shape.

Figure 1. Left: Endocast of the 40,000 year old La Chapelle-aux-Saints *Homo neanderthalensis*: length=18 cm, volume=1620 ml. Right: skull and natural endocast of the 2.6 million year old Taung child, *Australopithecus africanus*. The hand holding the skull is that of Professor Phillip Tobias of the University of Witwatersrand, South Africa, to suggest scale; endocast volume about 410 ml.

The frontal lobes form an elaborate information-processing system anterior to the cerebral central sulcus. Within the frontal lobes there are localized projections for motor control of body, limbs, and eye movements; executive functions in the prefrontal cortex; autonomic and emotion-control in the orbital area; and a lateralized Broca's area for language functions, usually in the left hemisphere. An important limitation on the evolutionary analysis of neural structure and function is that localization in the frontal lobes and elsewhere in the brain is not purely genetic. Frontal lobes in human adults like much of the rest of the brain are "programmed" by epigenetic factors, that is, by the way a brain develops in its prenatal as well as postnatal environment. This may be most obvious in the human species for the neural control of language, which is determined to a significant extent by learning and socialization. A second language, for example, may be localized differently in the brain from the language learned in infancy. It should, therefore, be appreciated that although the evolution of the complex systems localized in the frontal lobes involved genetic control, it also involved the environments in which the growth and development of the brain takes place. The nature-nurture issue as it affects our knowledge of the brain is reviewed insightfully by Krubitzer and Kahn (2003).

The evolutionary picture presented here emphasizes the brain's nature as determined from fossil endocasts. Nurture is represented only by scenarios of selection pressures that may have made some neural adaptations more appropriate than others for changing environments. Important developments in evolutionary analyses, such as the reconstruction of phylogenies ("cladistics") and molecular approaches, are considered only in passing.

Evolutionary change in the frontal lobes may be recorded in endocasts such as those shown in Figure 1, and in the other endocasts described in this chapter. Their quantitative analysis depends on inferences from the comparative neuroanatomy of living brains. Although primate endocasts typically show a few cortical fissures such as the rhinal fissure that separates neocortex from paleocortex, they rarely show a central sulcus. It has been possible to prove that the neocortex as a whole evolved to relatively larger size in mammals in which the rhinal fissure is visible in the endocast (Jerison, 1990), but without an objective way to locate the central sulcus one cannot measure the size of the frontal lobes with sufficient precision for a quantitative analysis. With the help of evidence of comparative neuroanatomy, however, fossils can be used for inferences about the evolution of similarities and differences among living species and how these developed over time.

Quantitative Comparative Neuroanatomy

We have had quantitative data on the frontal lobes of living primates beginning with Brodmann's (1913) work, now significantly extended with modern methods (Falk & Gibson, 2001; Fuster, 1997; Semendeferi et al., 1997, 2002). On the basis of thalamic projections from the *nucleus medialis dorsalis*, Uylings and Van Eden (1990) have been able to measure the size of prefrontal cortex in rats as well as in primates, enabling one to think of the evolution of the frontal lobes as a feature of the evolution of the mammalian brain. On the fossils, Edinger (1975) has catalogued most of the specimens, and I (Jerison, 1973, 1990) have analyzed many of them quantitatively. Falk (1992), Holloway (2004), Martin (1990), Radinsky (1970, 1974), and Tobias (1971) have published more specialized reviews that feature primate fossil endocasts. Although dated in some ways, Gerhardt von Bonin's essay (Bonin, 1963) is very much worth examining for his insights into the problems of quantification and his conclusions about the evidence.

How should we treat the available quantitative evidence? Size matters. That is the first point. The gross size of the brain provides important information about the brain's function. The reason is that brain size estimates information processing capacity in mammals, which may be inferred from Figure 2.

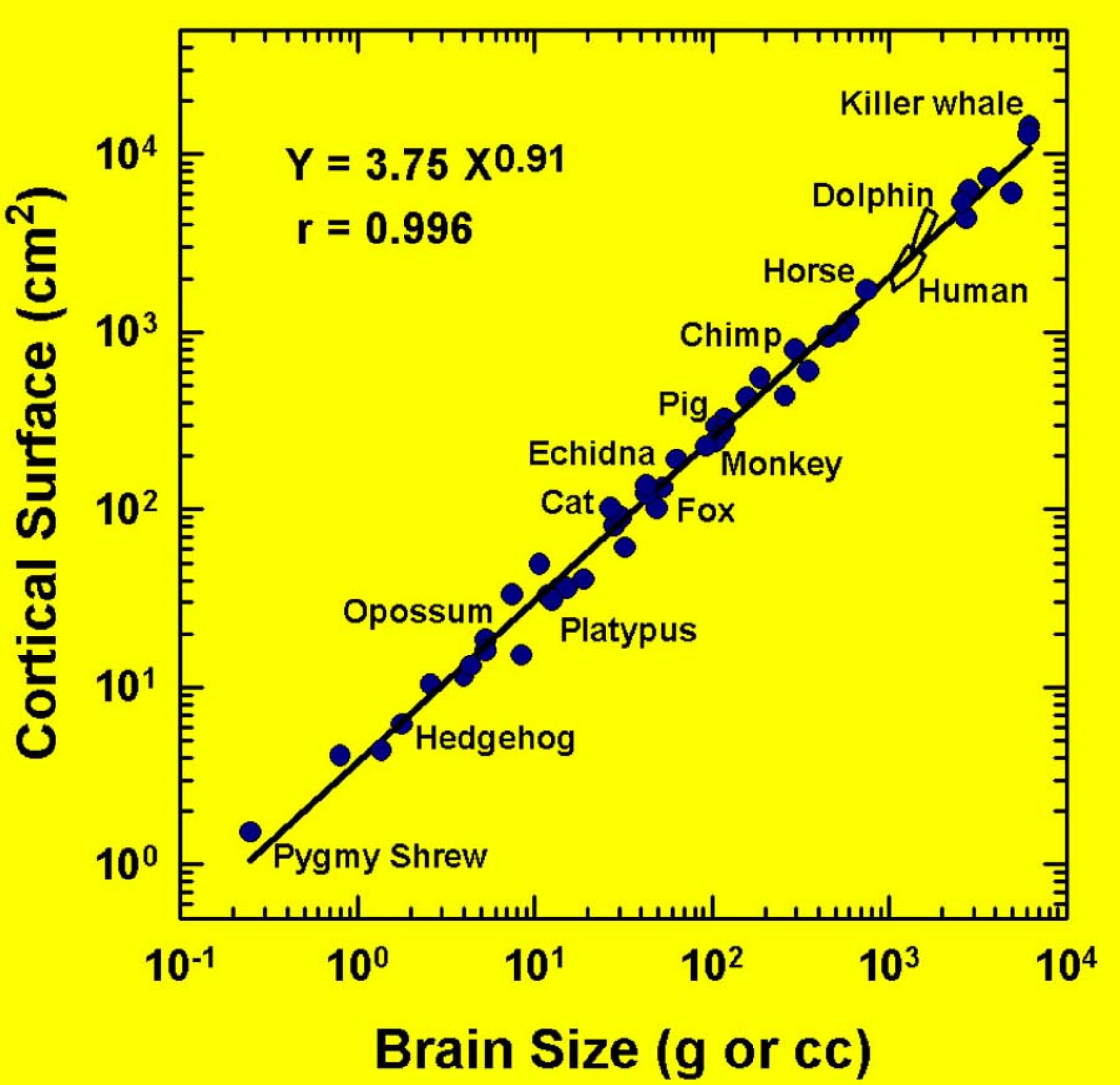

Figure 2. Cortical surface area as a function of brain size in fifty species of living mammals. Correlation: r=0.996; regression: $Y = 3.75 X^{0.91}$. A few of the species are labeled to suggest the diversity of the sample. Human and dolphin data are presented as minimum convex polygons based on 23 points for humans and 13 points for dolphins and suggest within-species diversity for this measure. (Data from Brodmann, 1913: Elias & Schwartz, 1971; Ridgway, 1981, and Ridgway & Brownson, 1984. From Jerison, 1991, by permission.)

The graph in Figure 2 shows how cortical surface area is related to brain size in living mammals. To two significant figures the correlation is perfect, suggesting an almost deterministic connection. The relationship to processing capacity reflects the efficient packing of neurons in the brain. For example, Powell's group at the University of Cambridge reported that the number of neurons under a given surface area of cortex is very similar in several diverse mammal species (Rockel, Hiorns & Powell, 1980; Cf.

Haug, 1987). The number of cortical neurons is thus estimated by the total area of the cortex. [The numbers are quite large, about 10 million neurons per square centimeter of neocortical surface. These lead to the order of 2 x 10^{10} for humans and about 10^{7} for a mouse (Packenberg & Gundersen, 1997; Braitenberg & Schüz, 1998).] Since neurons are basic information-processing units in the brain and brain size estimates their number, brain size also estimates overall information-processing capacity by the cerebral cortex.

Extending this inference to our view of the frontal lobes is straightforward. First, a multivariate analysis of the sizes of major brain structures such as basal ganglia, cerebellum, and neocortex in a large number of mammal species reveals that a general "size factor" accounts for much of the variance in the sizes of the parts of the brain (Jerison, 1997; Cf., Stephan et al., 1981). In a bivariate analysis, Semendeferi, et al, (1997) showed that this is specifically true for the volume of the frontal lobes in hominids (humans and apes, including gibbons). The relationship is of special interest for this chapter. It is graphed in Figure 3.

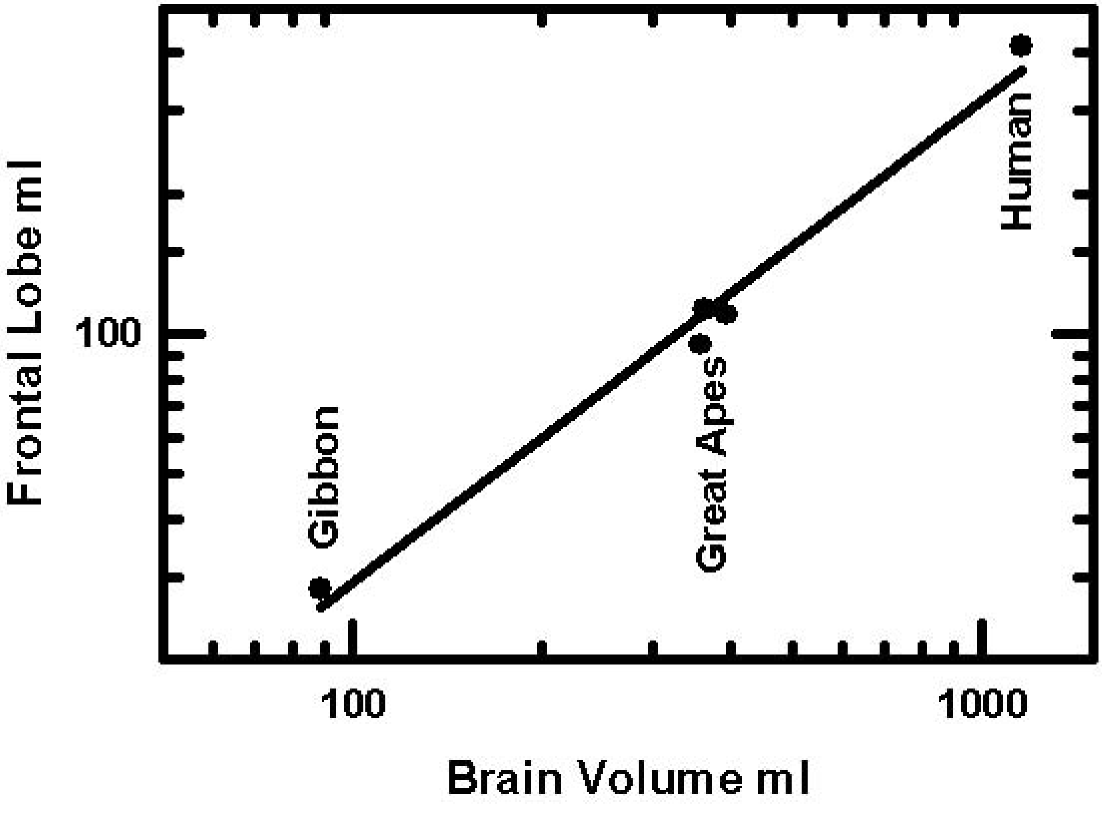

Figure 3. Frontal lobe volume as a function of the size of the brain size in selected hominids. Correlation: r = 0.986; Regression: $Y = 0.26X^{1.03}$. (Adapted from Semendeferi, Damasio, Frank & Van Hoesen, 1997, for brain volume.)

That the exponent in Figure 3 is slightly greater than 1.0 implies an interesting rule for the size of the frontal lobes in these primates. According to that rule, as hominid brains become larger the frontal lobes become disproportionately enlarged. One can determine that the gibbon's frontal lobes make up 32% of its brain whereas in humans it is 37%. Had the great apes not contributed data to Figure 3, which enabled one to calculate the regression equation, one might have guessed that the very large human frontal lobes represented a uniquely human advance. The orderliness of the regression in Figure 3 makes it easier to think of a genetic instruction based on brain size that is common at least to hominids. The rule is that a brain programmed to reach a particular size will have frontal lobes of the size required by the equation. The rule should be interpreted as showing that there is no uniquely human program for an enlarged frontal lobe. There is, incidentally, no special problem in imagining a genetic program to control an equation; it is conceptually equivalent to a computer program doing the same thing. Other genetic instructions presumably tell the developing nervous systems to “grow” a brain to a particular adult size, and these are probably unique, determining the encephalization of each species.

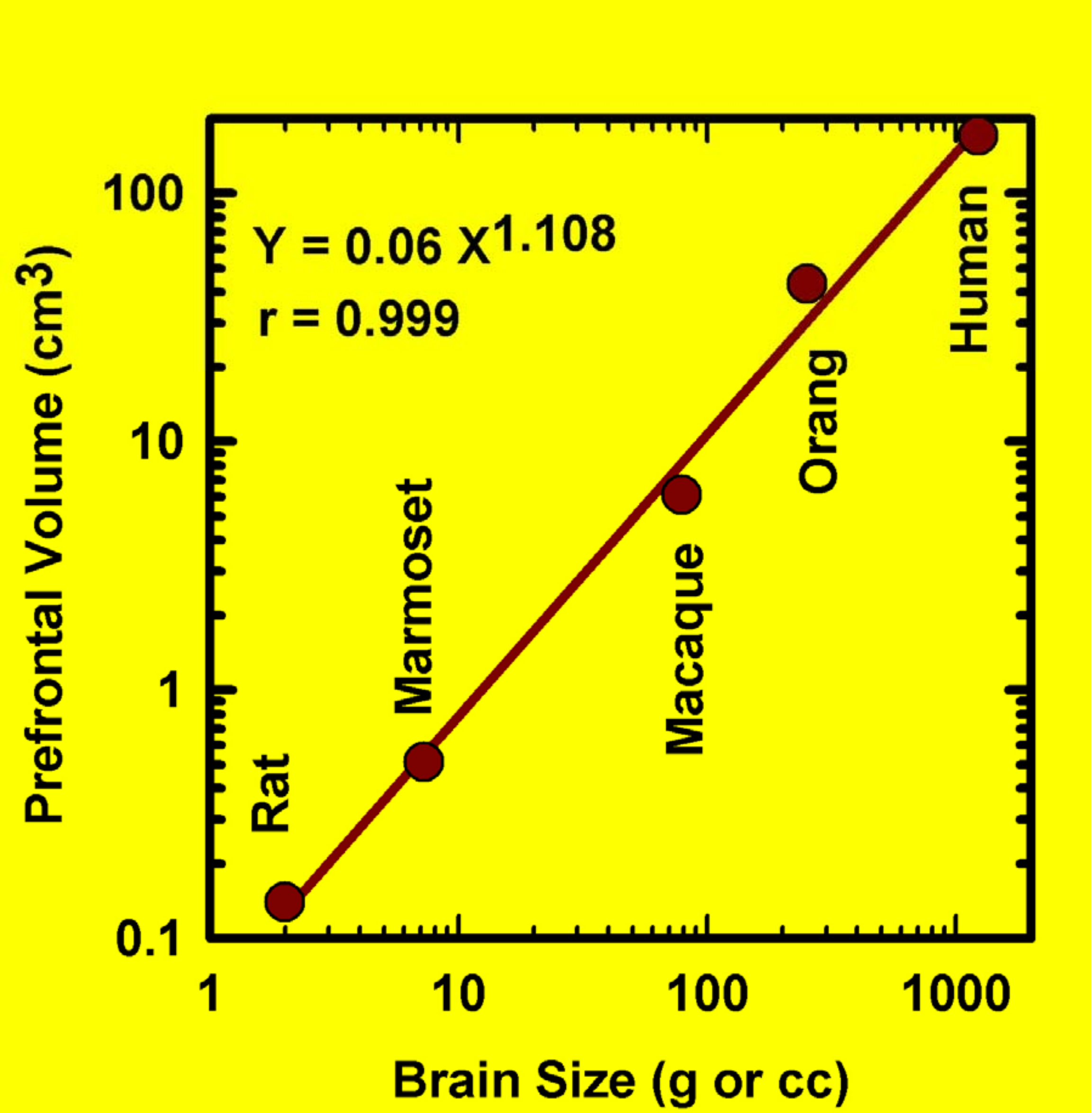

Figure 4. Prefrontal cortex volume as a function of brain size. Correlation: r = 0.999; Regression: $Y = 0.06 X^{1.08}$ (adapted from Uylings & Van Eden, 1990, in Jerison, 1997, by permission.

An independent set of data by Uylings and Van Eden (1990) indicated that a similar rule works for prefrontal cortex as a mammalian feature (Figure 4). As mentioned earlier they defined prefrontal cortex conventionally as cortex receiving projections from the dorsomedial nucleus of the thalamus and measured its volume in a rat as well as in primates (see Preuss, 1995, and Jerison, 1997, for more on this identification). In other reports on the size of the prefrontal area, Semendeferi and her colleagues verified the Uylings and Van Eden results for primates, basing their identification on cytoarchitectonic criteria (Semendeferi et al., 2002).

As evolutionary evidence, the functional relationships in Figures 3 and 4 can be treated as representing a trait shared by the species on the graphs. For a cladistic phylogenetic analysis, this implies that the trait was present in their common ancestor. According to present evidence, which will be reviewed again in a later section of this chapter, the common ancestor for the hominid species in Figure 3 lived at least 30 million years ago, during the Oligocene epoch. If the analysis in Figure 4 is correct, showing that a similar rule works for rats, this would associate prefrontal specialization with the evolution of neocortex. Neocortical localization of motor functions comparable to those localized in the primate frontal lobes, is of course a trait in all living mammals (Johnson, 1990; Cf. Benjamin & Golden, 1985; Kolb & Tees, 1990). At least some of the functions of the frontal lobes, therefore, must have arisen in the common ancestor of all living mammals.

Neocortex was definitely present in mammals 70 million years ago, in late Cretaceous times. A rhinal fissure is visible in endocasts of mammals living then, and from data on living brains we know that brain dorsal to this fissure is neocortex. The traits that generate the functions of Figures 3 and 4 were therefore present at least 70 million years ago.

To complete this review of the "age" of the brain, let us recognize that neocortex as a brain structure is present only in mammals and in no other living vertebrates. It may, therefore, have appeared in the earliest mammals during the Triassic period, over 200 million years ago (Jerison, 1990). Regardless of how we date neocortex and the frontal lobes, the brain trait governing the functions in Figures 3 and 4 is an ancient adaptation. According to this evolutionary evidence, any living mammal can serve as an animal model for studying frontal lobes structure and function.

In a discussion of the evolution of prefrontal neocortex a few years ago, I pointed out that its acknowledged executive functions have to involve connections with much of the rest of the brain (Jerison, 1997). We should, therefore, expect the size of prefrontal neocortex to be related to the size of the parts of the brain that it controls, which add up to pretty much the whole brain. The results graphed in Figure 4 should not surprise us. The results in Figure 3 are also expected, given the way the brain hangs together. Major structures within the brain tend to be correlated with one another in size as reflected in multivariate analyses that identify a "general size" factor. With respect to the utility of animal models, one may also remember that cognitive control in the prefrontal lobes was first discovered and clearly established by research on baboons (Jacobsen, 1931).

The quantitative neuroanatomical functions presented in Figures 2-4 are those most useful for interpreting fossil endocasts. Because endocasts do not record the precise position of the central sulcus, it is impossible to analyze of the evolution of the frontal lobes quantitatively with the evidence of fossil endocasts alone. Instead, the fossil evidence reviewed here in Figure 1 and Figures 5 - 7 provide a gallery of specimens that document all of the past 55 million year of brain evolution in primates, in effect, a qualitative analysis of the available information. All of these primate endocasts display temporal lobes as in living primates and suggest the position of a Sylvian fissure. Frontal lobe was almost certainly differentiated in all primates.

In passing, a morphological observation well known to those who have dissected a variety of primate brains: the "orbital" surface of the frontal lobe in primates is the ventral anterior projection of the frontal lobes that covers the orbits of the eyes. It is surprising that some illustrations that present human and other primate brain-skull relations miss this relationship and typically place the whole brain, even including the olfactory bulbs, posterior to the orbits. The shape of the primate brain in the region of the frontal lobes is related to the way the brain grows to its adult shape, molded by pressures related to its fitting into the space available for it. Primate brains are more globular than brains of other mammals because of the space into which they grow. They squeeze into this space, and the anterior portion of the brain squeezes in above the eyeballs.

The Fossils

In approaching fossil evidence, including that on the evolution of the frontal lobes as a part of the brain, we rely on the time-honored uniformitarian "hypothesis" developed by geologists in Darwin's time. This is a parsimony principle, which asserts that present structure-function relationships have been true in the past. It continues to be universally accepted.

The first question we ask of fossils is their dating. Since frontal lobes are a feature of the brain of all living primates, and we assume that the relationships in Figures 3 and 4 are present for all anthropoid primates, the history of anthropoid frontal lobes as brain structures begins no later than the late Eocene, about 40 million years ago, when a common ancestor was alive. The history is at least 15 million years older, dating to the early Eocene, about 55 million years ago, the dating of the oldest known primate endocast sketched below in Figure 6. A still older history should be assumed, because the earliest mammals in which there is presently firm evidence of neocortex lived during the Cretaceous period, and neocortex in all living mammals includes localized motor cortex homologous to primate motor cortex in the frontal lobes. The history of frontal lobes should thus be dated to at least 70 million years ago according to present evidence. An earlier Cretaceous mammal, *Repenomamus robustus*, which lived about 130 million years old, has just been discovered (Hu et al., 2005), and an unpublished CT scan of this animal has been prepared to show the dorsal surface. It appears to show a rhinal fissure, and if this is verified it would push back the known history of neocortex to that time. As more fossils are analyzed there is no reason to reject the idea that neocortex appeared with the earliest mammals, more than 200 million years ago.

Hominin Fossils

There is only speculation that can be added to the obvious information in Figures 1 and 5 about the appearance of the frontal lobes in the more direct human (hominin) lineage. The Neandertal endocast shown in Figure 1, with a volume of 1.6 liters signifies a 1.5 kg brain. (Living human brains fill about 95 percent of the cranial cavity.) The Neandertal brain was large but well within the range of living brains (Pakkenberg & Voigt, 1960; Cf. Allen et al., 2002). In any event, it is unlikely that this large brain did not have frontal lobes as large as living humans. Perhaps we need a reminder that although brain size gives us useful information it is not the same as intelligence, and the fossil evidence tells us little about the intelligence of our cousins among the hominins. To the extent that brain size is relevant, however, it tells us that this brain was comparable in size to ours. It is enough to note that frontal lobes are almost certainly not larger on the average in living humans than they were in our cousins, the Neandertals.

The 40,000 year old La Chapelle-aux-Saints Neandertal in Figure 1 is unusual among hominid endocasts in a more interesting way, because lateral frontal gyri are visible. There is a fairly clear impression of part of the third frontal convolution of the left hemisphere, which would be in Broca's speech area in a living brain. Figure 3 shows that these convolutions had appeared at least 40,000 years ago. One does not know whether the area functioned as a speech area as in living humans, of course, nor do we know that it did not. From other remains, such as the appearance of the base of the skull, phoneticians have been able to argue about the kinds of sounds that Chapelle-aux-Saints could generate and the vowel structure of those sounds. These may have been more limited than those of living humans, but we know that linguistic communication is possible for us, even with limited capacities for vocalization. From the size of their brains, one would assume that Neandertals could handle the same amount of information as living humans, though we have no way of specifying the information. The evidence is enough not to rule out the evolution of the capacity for language at least 40,000 years ago, and it would presumably have been present in the earliest Neandertals, perhaps 200,000 years ago.

The issue has been discussed in more detail by Tattersall (1995). A similar argument has been presented for the evidence from convolutions in the Taung australopithecine (Falk, 1992; Holloway et al., 2004), which would push the neural history of the speech and language areas back more than two million years. Figure 5, below, presents some of the bones of contention, additional views of australopithecine endocasts.

An interesting argument might be developed from the possibility of structural lateralization in the brain. It has been possible to show that in living brains there is some morphological lateralization, a measurable difference between the left and right hemisphere, mainly in details in the pattern of convolutions. The clearest lateralized difference of superficial features is in the appearance of the Sylvian fissure in living humans (Sowell, Thompson & Toga, 2004). This difference is related to the only well-established functional morphological difference between the right and left hemisphere in the living human brain, that is, in the size and shape of the planum temporale hidden on the temporal lobes within the Sylvian fissure and not visible on endocasts. The extent of the planum in the left hemisphere has been related to the adaptation for speech and language. It is usually somewhat expanded in the left hemisphere, and it affects the length and shape of the Sylvian fissure, but the Sylvian fissure does not leave clear enough impressions on human endocasts to enable one to measure the possible lateralization in fossils. One would wish it were otherwise, that endocasts might provide clearer clues about the history of this uniquely human trait. Despite the recognized asymmetries in living brains, their utility for functional analysis remains unclear (Walker, 2003). Fossil skulls are not well enough preserved to be able to argue from asymmetries.

Figure 5. Endocasts of two australopithecines, the Taung child found in 1923 (right hemisphere) is on the left, and Sts60 (left hemisphere) is on the right. These fossils are presently dated at between 2 and 3 million years ago. Endocast volumes about 410 ml.

At this time, on the basis of molecular dating of the evidence of mitochondrial DNA and verified by newly discovered fossils, the human lineage appears to have become differentiated from that of apes about six million years ago. We nevertheless share about 99 percent of our genes with our cousins, the apes (Deacon, 1997), although the remaining one per cent is undoubtedly the significant fraction for us, because it presumably includes regulator genes governing the growth of the brain to human size and perhaps the evolution of specialized circuitry related to the language sense (Pinker,1994).

In the endocasts of *Australopithecus africanus* shown in Figure 5 there is no clear demarcation of the Sylvian fissure, but in both there appears to be the impression of the middle cerebral artery. This is typical of the impression of the hominin brain as revealed in an endocast (Bonin, 1963) and appears on the endocasts of most of them. Other features have been discussed, most curiously the impression of the *Affenspalte* (the human lunate sulcus), which is the anterior border of primary visual cortex . It has been debated for evidence of the first appearance of a language area homologous to Wernicke's area (Falk, 1992). At this time the issues in that debate remain unresolved, although if a language system can be identified, the origins of language would be pushed back in time even further, to the earliest evidence of australopithecines about 5 million years ago.

A Gallery of Fossil Primate Endocasts

Qualitative evidence on the evolution of the frontal lobe can be viewed in fossil endocasts. We have already seen some of it, beginning with Figure 1, in which we saw a Neandertal endocast and a partially hidden australopithecine endocast not completely removed from the fossil skull. The latter is of the first australopithecine discovery in 1923 at Taung in South Africa. It is important for our knowledge of brain evolution, because it proved that the brain became enlarged later in human evolution than did other traits defining hominins (Tobias, 1971). The famous and infamous Piltdown fraud of 1913, which married a human cranium to an orangutan jaw, was designed to support evolutionary speculations of a century ago that the “missing link” in human evolution implied a coupling human intelligence as mirrored in the large brain with an ape’s body. The discovery at Taung destroyed that simple-minded paradigm by uncovering a skull with features closer to those of humans than to apes but with an ape-size brain. It was also obviously much older than the Neandertal or the pithecanthropine (*Homo erectus*) fossils known at the time, and it demonstrated that brain enlargement followed the evolution of other traits within the human lineage. A more complete picture of the Taung endocast and a second australopithecine endocasts were added to the gallery as Figure 5.

The fossil record of the primate brain begins much earlier. Fifty-five million years ago, early in the Eocene epoch, the remains of *Tetonius homunculus*, a prosimian related to living tarsiers, were left to fossilize in what is now the Bighorn Basin in Wyoming. From a sketch of its endocast in Figure 6 it is evident that *Tetonius* had visibly identifiable cortical structures that were almost certainly frontal lobes. Figure 6 sketches the endocasts of a number living and fossil prosimian primates, which are discussed more fully in Jerison (1973). Like their living relatives, all of these prosimians had similarly shaped brains, with enough of a suggestion of temporal lobes and a Sylvian fissure to identify frontal lobes fairly as having evolved by that time. Two later tarsier-related specimens, *Notharctus* and *Rooneyia*, are also illustrated. The adapids, another lineage of prosimian primates related to living lemurs, are known from middle and late Eocene strata, about 40 or 50 million years ago. The endocasts of two of them, *Smilodectes* from North America and *Adapis* from France are also sketched in Figure 6, below, and also indicate the presence of frontal lobes.

Figure 7 follows and completes the gallery with additional lemuroid evidence, the endocast of the fossil *Adapis parisiensis* compared to the brain of the living bushbaby, *Galago senegalensis*. Figure 7 shows how good an endocast can be as a representation of the brain. It is, incidentally, also evidence of the evolutionary trend in some mammalian groups in which brains became more encephalized. The bushbaby is a fairly small primate, weighing about 250 g. Its Eocene relative, the lemuroid, *Adapis parisiensis*, probably weighed about 1600 g, yet its brain was about the same size as the bushbaby’s. This is an example of encephalization within the primate lineage, which was analyzed graphically in Jerison (1973, Fig. 16.6). According to that analysis, galagos are somewhat more encephalized than average living mammals and Eocene lemuroids were less encephalized. As a group, the living prosimians are average among the mammals in encephalization. Living monkeys and apes are about twice as encephalized as the average, and living humans are about five times as encephalized. The specimens in Figure 6 are representative of a prosimian assemblage, the adapids on the low end, about half as encephalized as average living mammals, and the tarsier-like fossils very near average for living mammals. On the frontal lobes, lacking data comparable to Figure 3 for these animals, one is limited to the qualitative judgment that can be made from the sketches. The basic judgment should be that the frontal lobes expand as the brain as a whole expands. During the 50 million years of evolution represented by the species in Figure 6, we expect the frontal lobes to follow the same trend as the brain as a whole. The particular species, the adapids of the Eocene and the living galagos, have very different environmental niches, of course, and brains tend to be appropriate to the niches. Other data, however, support the view that across a wide range of niches there was increased encephalization across the 50 million year interval. It is likely that the frontal lobes were part of this trend.

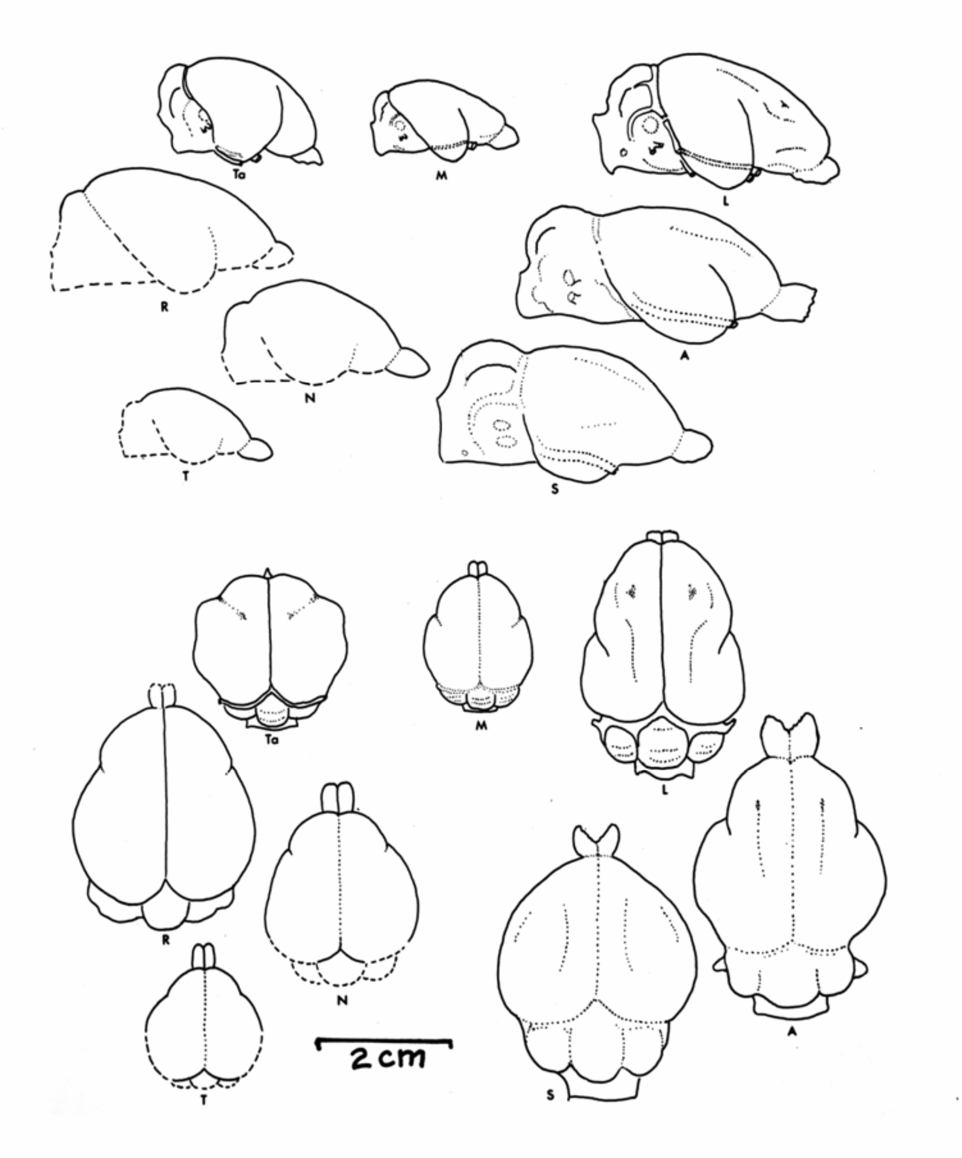

Figure 6. Three living and five fossil prosimian endocasts in lateral and dorsal view. Ta: *Tarsier spectrum* (living); M: *Microcebus murinus* (mouse lemur, the smallest living primate); L: *Lepilemur ruficaudatus* (living); R: *Rooneyia viejaensis* (Oligocene); A: *Adapis parisiensis* (late Eocene); T: *Tetonius homunculus* (early Eocene); N: *Necrolemur antiquus* (Middle Eocene); S: *Smilodectes gracilis* (Middle Eocene). (From Jerison, 1973, Fig. 16.3 and Table 16.1, by permission.)

The evidence in Figures 6 and 7 is on prosimian brain evolution. The fossil evidence on anthropoid (monkey, ape, and human) origins available at this writing goes back to the late Eocene, about 40 million years ago, but it begins mainly with postcranial skeleton and teeth and not the brain. At least one late Eocene or early Oligocene species, however, *Aegyptopithecus xeusis*, is now classified with the anthropoid primates, and its endocast has been described by Radinsky (1974). Although the animal was probably about the same size as living gibbons, its brain was evidently only half as large. It is not sketched here, because it is little different from the prosimian endocasts sketched in Figure 6. Further encephalization in the anthropoid lineage occurred later, probably during the Miocene epoch, about 15 or 20 million years ago.

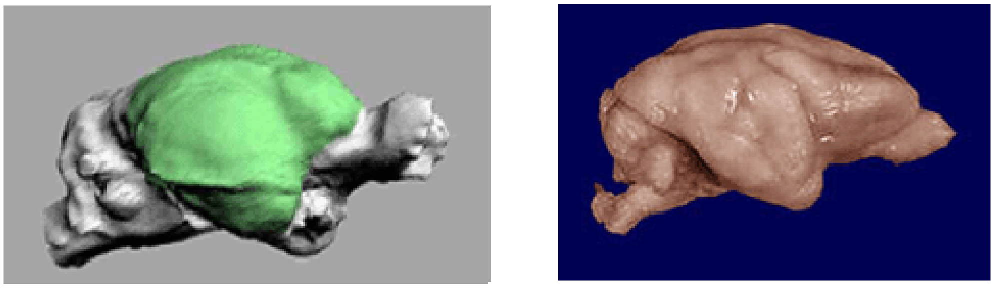

Figure 7. Endocast of the late Eocene prosimian *Adapis parisiensis* and the brain of the living bushbaby, *Galago crassidens*. Endocast from the Field Museum of Natural History in Chicago (FM 59259); brain from the University of Wisconsin (62-172): *http://brainmuseum.org/*

The olfactory bulbs and tract in living anthropoid primates, including humans, are reduced in size compared to all other living land mammals. This feature has misled biologists into thinking of reduced olfactory bulbs as evidence of an evolutionary advance. It is a primate trait, shared with cetaceans. Prosimians are intermediate between most mammals and the anthropoids in the reduction of olfactory bulbs, and in this respect Aegyptopithecus was more like prosimians than anthropoids. The reduction evidently occurred within the anthropoid lineage, and appeared later in their evolution. It was probably completed during the Miocene epoch, perhaps 15 million years ago. Fossils of that time are similar to living monkeys and apes in the reduction in the olfactory system.

I have speculated on this as related to the evolution of language in primates, specifically in humans, a fairly convoluted just-so story, which may even be correct. I will not repeat the speculations here (see Jerison, 1991, 2001), but one conclusion was that chimpanzee "language" is fundamentally different neurologically from human language. Specifically, I guessed that appropriate brain scans such as PET would reveal different patterns of activation in humans and language-trained chimpanzees. That guess appears to be correct, although the appropriate experiments are, of course, difficult to perform. The results of PET scans on a chimpazee while it worked on a language-like task (pressing one of an array of response keys representing various linguistic cues) have been reported in a preliminary way (Rilling, et al., 1999). Activation in the chimpanzee brain during such work was not lateralized and did not involve regions of the brain homologous to language areas in humans. Pet scans in people working on the same task showed unilateral activation in Wernicke's area as expected, whereas both human and chimpanzee scans showed activation in motor cortex and frontal eye fields, as expected for performance that involved in gazing at and operating the response keys on the response boxes.

Conclusions

The greatest disappointment in preparing this chapter is that at this writing there is not enough evidence to permit a quantitative analysis of the evolution of the frontal lobes based on the fossil record. However, from a qualitative perspective there is no question that frontal lobes as primate brain structures were present in the earliest records of primate brains. Furthermore, from the evidence on living anthropoid brains, in particular the evidence in Figure 3 and Figure 4, substantial frontal and prefrontal neocortex was present. The uniformitarian hypothesis leads to the view that frontal lobes were functioning as they do in living primates. Most human functions that have also been studied with appropriate animal models (Fuster, 1997) would be present in our ancestors within our lineage. Whether there was specialization for a language sense is impossible to determine.

What are the lessons for neurology from the evolutionary perspective? First, size matters. Brain size is an important variable for evolutionary analysis, and it is worth a closer look in other contexts. The importance of body size in different species has been recognized for some time as a determinant of the success of species in different ecological niches. Brain size, on the other hand, has had a sorrier fate. Its use a century ago in racist and sexist arguments was followed by critical analysis of the errors and bias (Gould, 1981). The evidence, nevertheless, is that size matters in biological systems (Schmidt Nielsen, 1984), including the brain and the frontal lobes. In this chapter, some of the story was told in the graphs. They showed the interdependence of measures, and how brain size as an independent variable estimates total information processing capacity. One should be encouraged to take and report these simple measurements routinely, even when they are not required for a particular research protocol. When any animal model is used, it is appropriate routinely to include gross measures on the specimen such as brain and body weight and age, and if the study uses modern imaging techniques such as CT or MRI there are usually computer programs available that can provide measurements from the scans, such as surface area and volumes. (Cf. Semendeferi et al., 2002)

Second, and perhaps most important for research in neurology, is the suggestion about constraints on the use of animal models. Some human frontal lobe motor functions can be studied in other mammal species whereas other functions, such as language, may be uniquely human. The organization of motor systems is likely to be similar in many different species, whereas an animal model for language is chancy, even in our nearest relatives, such as chimpanzee or bonobo.

A nuts and bolts conclusion: Given the imprint of cerebral circulation in some endocasts it would be helpful to be able to correlate that vasculature with localized regions of the brain. Gerhardt von Bonin (1963) discussed such relationships four decades ago, and although the methods of gross anatomy may seem old fashioned, here is a case in which discoveries remain to be made. It might enable one to do a quantitative analysis on the evolution of the frontal lobes by correlating the location of the central sulcus in living brains with the position of the vasculature, such as the middle cerebral artery in living and fossil species.

A final lesson is recognition of the limits of genetic relationships and the importance of development in a normal environment as determining the structure and function of the adult nervous system. That constraint was not emphasized in this chapter, except by citation of the important review by Krubitzer and Kahn (2003).

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Note on orthography

It is conventional in taxonomy to have genus capitalized and species lower case, both in italics. The spelling of Neandertal adopted here follows modernized German as adopted in 1908, but capitalized as are German nouns. Taxonomic convention dictates maintaining original spellings, and the spelling of the species *neanderthalensis* is retained, because it was named prior to 1908 with the old spelling.

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