4

Evolution of the human brain

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Abstract

Direct palaeoneurological evidence about the evolution of the hominid brain comes from study of the size and surface features of the endocasts of once-living brains. Because of intervening tissues, the detailed surface features of the brain are seldom clearly expressed on the inside surface of the skull. Therefore convolutional details of the brain's surface are the least reliably preserved features. Cerebral asymmetries are more reliably preserved. Overall size, despite its questionable significance, is the most reliable evidence of evolutionary change.

In the last 3–4 million years brain volume within the hominid lineage has increased from less than 400 ml to roughly 1400 ml. The first clear increase in hominid brain size is seen in early *Homo*, at *c.* 2 m.y.a. in East Africa (most reliably in cranial specimen KNM-ER 1470). This is an evolutionarily significant change that cannot be simply accounted for in terms of increased body size alone. From the appearance of *H. erectus* at *c.*1.7 m.y.a. to the present, the brain increases nearly twofold: from *c.*800 ml to 1500 ml in Late Pleistocene *H. sapiens*, without any apparent change in body size.

With regard to brain reorganization, left–right cerebral hemispheric asymmetries exist in extant pongids and the australopithecines, but neither the pattern nor direction is as strongly developed as in modern or fossil *Homo*. KNM-ER 1470 shows a strong pattern that may be related to handedness and tool-use/manufacture. The degree of asymmetry appears to increase in later hominids.

The appearance of a more human-like third inferior frontal convolution provides another line of evidence about evolutionary reorganization of the brain. None of the australopithecine endocasts show this region preserved satisfactorily. There is a consensus among palaeoneurologists that the endocast of the specimen KNM-ER 1470 does show, however, a somewhat more complex and modern-human-like third inferior frontal convolution compared with those of pongids. This region contains Broca's area, which in humans is related to the motor control of speech. Unfortunately, later hominid endocasts, including *H. habilis* and *H. erectus* through archaic *H. sapiens* to the present, seldom show the sulcal and gyral patterns faithfully. Thus nothing palaeoneurological can be said with confidence about possible changes with the emergence of anatomically modern *H. sapiens*. On the other hand, there is nothing striking about Neanderthal brain casts in comparison to more recent *H. sapiens*, except their slightly larger size, suggesting no significant evolutionary change thereon [eds].

4.1 Introduction

The evolution of the brain from some primitive *Australopithecus* stage to our present condition has taken some three million years to achieve. At the least, this has certainly involved an increase in brain size of roughly 3+ times. The expression 'at the least' is used here because how one views human brain evolution is often dependent on how one views the product of brain function, i.e., human behaviour. For most of us, this involves the concept of culture, and whether or not we perceive this phenomenon as unique to

humankind. Is culture species-specific? Do any other animals 'have it'? Is there a discontinuity between human and other animal behaviour? Are human beings simply more clever than their nearest relatives, the chimpanzees and gorillas, or do human beings possess brains that provide both continuity and emergent properties when behaviour is compared? Different accounts of human brain evolution will often reflect how these questions are answered (cf. Ingold, this volume; Chapter 7; Gibson and Ingold 1993). Conversely, views of the similarities and differences in human and other primates' behaviour can effect how the brain is viewed in structural, functional, and evolutionary terms. For those preferring an approach of total continuity between ourselves and other primates, the size of the brain is a sufficient neural variable. After some Rubicon is reached (for example, 750 ml) human behaviour suddenly cuts in. For others preferring to believe in some discontinuity, the size of the brain is important, but insufficient as an explanatory variable: it is also necessary to consider how the brains of different animals are organized.

Since many animal species overlap with regard to their brain weights, yet demonstrate species-specific behavioural repertoires, it is difficult to understand how brain size alone can account for the behavioural differences in sensorimotor function, sexual, and agonistic behaviour, special sensory adaptations (for example, vision, auditory, and olfactory modes), and the integration of these with both the general and specific cognitive orientations to ecological diversity and specialization. Even between and within genera as closely related as *Papio* and *Macaca* monkeys, there are only minor differences in brain size, yet clear behavioural differences do exist that cannot be explained at the neural level.

In my view, human beings are unique in their ability to maintain a behavioural system based on culture, using both extrinsic arbitrary and iconic symbol systems to depict reality and unreality (Holloway 1967, 1969*a*, 1976*a*; 1981*a*, cf. Mundinger 1980). However clever other primates may appear, whether in their natural settings or within human manipulated laboratories, only humans have the temerity to study themselves and other species, and share their findings and hypotheses.

There are many difficulties in the task of understanding how our brain evolved. Firstly, there are no brains to study except those of the living. Comparative neuroanatomy can study only the present terminal products of separate evolutionary developments. Thus, in a strict empirical sense, we have no evidence for human brain evolution beyond its size and other critical morphological features to allow us access to the forces of natural selection that worked on past behaviour patterns. These patterns are the important but missing interfaces between evolving brain structure and function (Holloway 1970, 1979), some of which (for example tool-making, hunting and/or scavenging, food-sharing) may exist in the archaeological record, but require interpretation, and are always difficult to interpret without evoking controversy.

Secondly, the relationships between neural variables (for example, brain size, neocortical size, types of nuclei) and behaviour are not thoroughly understood, and only recently are relatively non-invasive techniques such as MRI (magnetic resonance imaging) or PET (positron emission tomography) scanning beginning to suggest how different parts of the brain interact and relate to complex cognitive behaviours. Thirdly, the actual evidence from brain evolution in any animal lineage can only be related to surface features of the brain, which in turn relate only to a limited subset of all behavioural repertoires. This problem is particularly severe in hominid brain endocasts.

Finally, there is a vast hiatus in our knowledge regarding variation in species-specific behaviour and its relationship to neuroanatomical variation of the neural substrate. This problem is compounded by the lack of such knowledge for within-species variability, which in the human case is almost always attributed to cultural factors alone. The appendix to this chapter, p. 98, on sexual dimorphism of the corpus callosum, is one such example.

What follows in this chapter is a preliminary examination of our knowledge of how the human brain evolved based on several lines of evidence, written explicitly from the viewpoint that while size is important, other phenotypic characters must be given consideration, as size, taken alone as a neural variable or parameter, cannot explain species-specific behaviour beyond general formulations relating to intelligence, however defined.

For accounts written from other perspectives, see Jerison (1973), for example, who focuses on the relationships between overall brain size and information-processing, i.e., intelligence—a term that it is very difficult to define without controversy and to compare across different taxonomic units. Tobias's (1971) book on hominid brain evolution is similarly oriented, and in particular adopts Jerison's (op. cit.) 'extra neuron numbers' approach, and is directed toward a positive-feedback interaction between behavioural complexity (culture) and brain size. In earlier versions of my own work (Holloway 1964, 1966, 1967, 1968, 1969*b*, 1970, 1979, 1981*a*) I tried to explain the evolution of brain size as an outcome of positive feedback between behavioural complexity and the neural components (nerve cells) that make up the brain, as well as of

interactions between its components. Many anatomists concerned with human evolution, aside from Dart and his mentor G. E. Smith, have thought and do think of brain size as *the* most important ingredient of hominid evolution, and most appear to have great faith in 'cerebral Rubicon' models that have been around since Darwin's time. The value of 750 cc stated by Keith (1948) is the more or less implicitly assumed value at which 'true' hominid behaviour (culture) emerges. Indeed, by focusing only on brain size, hominid evolution is most often viewed as a process in which the brain was the last organ to undergo any evolutionary change (see for example, Washburn 1960). My own perspective is that the brain was always undergoing evolutionary change, from pre-*Australopithecus* to the Upper Pleistocene. I find Rubicon models too confining, as they rely only on brain size and do not consider the interaction of neural variables or the organization of the brain as important substrates for biobehavioural evolution. Additionally, there is something suspect about a parameter that is continuous but will evince qualitative functional changes with a simple increase in quantity alone (Holloway 1964, 1967). Finally, brain size is a variable over which one can all too easily find oneself hoisted by one's own petard. Too literal a reliance on a close causal relationship between size and function leads to all kinds of interpretative problems within species, i.e., as between subspecies, sexes, etc.

Other workers have focused on energy models, particularly metabolism, in attempts to understand the unique size of the human brain, both in relative and absolute terms (see for example Martin 1981, 1982, 1983; Little 1989; Parker 1990). Longevity and prenatal and postnatal developmental durations have been studied in depth by Sacher (for example Sacher 1982; Sacher and Staffeldt 1974) the better to understand the comparative situation among living animals. Others, such as Blumenberg (1983), have proposed complex feedback schemes between hunting behaviour, diet, neuropeptides, and the enlarged hominid brain. Passingham (1982) (see also Sawaguchi and Kudo 1990) has focused on the role of the cerebral cortex in human evolution, relying heavily on quantitative data on the brain structures of living primates obtained through the study of allometry. This region of the brain has most recently been hypothetically associated with language as a form of social grooming, with primate brain evolution viewed as simply an ever-increasing capacity for social grooming (Dunbar 1992; Aiello and Dunbar 1993). For a critique, see Halloway (1993). In the human animal, as group sizes became too large for physical social grooming, language evolved as a cheap substitute for manual grooming. Others, such as Milton (1981, 1993), believe brain size is essentially related to the food quest. Parker and Gibson (1979, 1990; cf. Gibson 1990, and this volume, Chapter 14) appear to believe that the cognitive stages elaborated by Piaget can be correlated with evolutionary developments in primate cognition, and directly related to both brain size and ontogeny.

All these writers and many others not mentioned here ignore to one degree or another the organization of the brain as an integral part of primate neurological evolution that must also be integrated with size variables. Indeed, most of the writings of the 1970s and 1980s have tended to focus on brain–body size relationships, in which the brain, treated as a dependent variable, enlarges mainly through selection pressures operating on body size. Radinsky's many articles (for example, 1972, 1975, 1977, 1979) have stressed the allometric approach within the palaeoneurological context. Still others, for example Armstrong (1983, 1985, 1990), have looked more carefully at certain neural structures other than the cortex (for example, the thalamus), and have proposed models that emphasize the *quantitative organization* of primate brains in relationship to social behaviour. For recent reviews of these models and their histories, see Blumenberg (1983, 1986), Falk (1980*a*, 1982, 1987), and Armstrong (1990).

This chapter will focus mainly on integrative work that attempts to synthesize comparative and palaeoneurological approaches. The 1970s and 1980s have witnessed a virtual explosion in the neurosciences generally (with the early 1990s particularly spectacular), and the evolution of the brain taken as an integrated topic has shifted enormously from explanations of a single neural variable (for example, brain size) and a single selection pressure (for example, for 'intelligence'), to a complex interweaving of many neural variables and a multifaceted view of probable selection pressures involving multiple behavioural levels. Steklis and Erwin's (1988) volume, *Neurosciences* (Comparative Primate Biology, Vol. 4) is an invaluable compendium of recent advances in our knowledge of the Primate Brain, particularly as regards newer knowledge about cortical cytoarchitectonics in a growing list of primate species. (In particular, see the papers there by Allman and McGuinness, Yin and Medjbeur, Pandya *et al.*, Kaas and Pons, and Kaas and Huerta. Elsewhere, see Allman 1990 and Pandya and Yeterian 1990.)

4.2 The human brain

In overview, the human brain is the largest among the primates, but certainly not the largest in either absolute or relative terms among the mammals.

Whales, dolphins, and elephants have larger absolute brain sizes, while some small mammals, including some primates, have relatively larger brains. The human brain, averaging approximately 1330 grams[1] (Tobias 1971), represents some 2 per cent of our body weight, yet continuously uses 15 per cent of our cardiac output, and consumes about 20 per cent of our metabolic resources (see Chien (1981) and Martin (1983) for examples and further references). There are no 'new' evolutionarily-derived structures in the human brain as compared to that of other mammals and, in particular, to that of other primates. Nuclear masses and the fibre systems interconnecting them appear to be the same, that is they exist and are homologous structures; they need not be structurally 'identical'. Deacon's (1988*a*, *b*, and 1990*a*, *b*) writings are an important reminder of the close homologies of human and macaque cortical fibre systems in those regions classically regarded as language 'centres'. What seem to vary are the quantitative relationships between and among these nuclei and fibre tracts, and the different ways in which the cerebral cortex becomes structurally and functionally subdivided and ultimately integrated. I am referring here to cytoarchitectonic differences in the cerebral mantle, as commonly illustrated by the famous 'maps' of Brodmann (1909) (see Fig. 4.1 [eds]). (Recent discussions of some of these differences may be found in Kaas and Pons 1988, Kaas and Huerta 1988, and Armstrong and Falk 1982.)

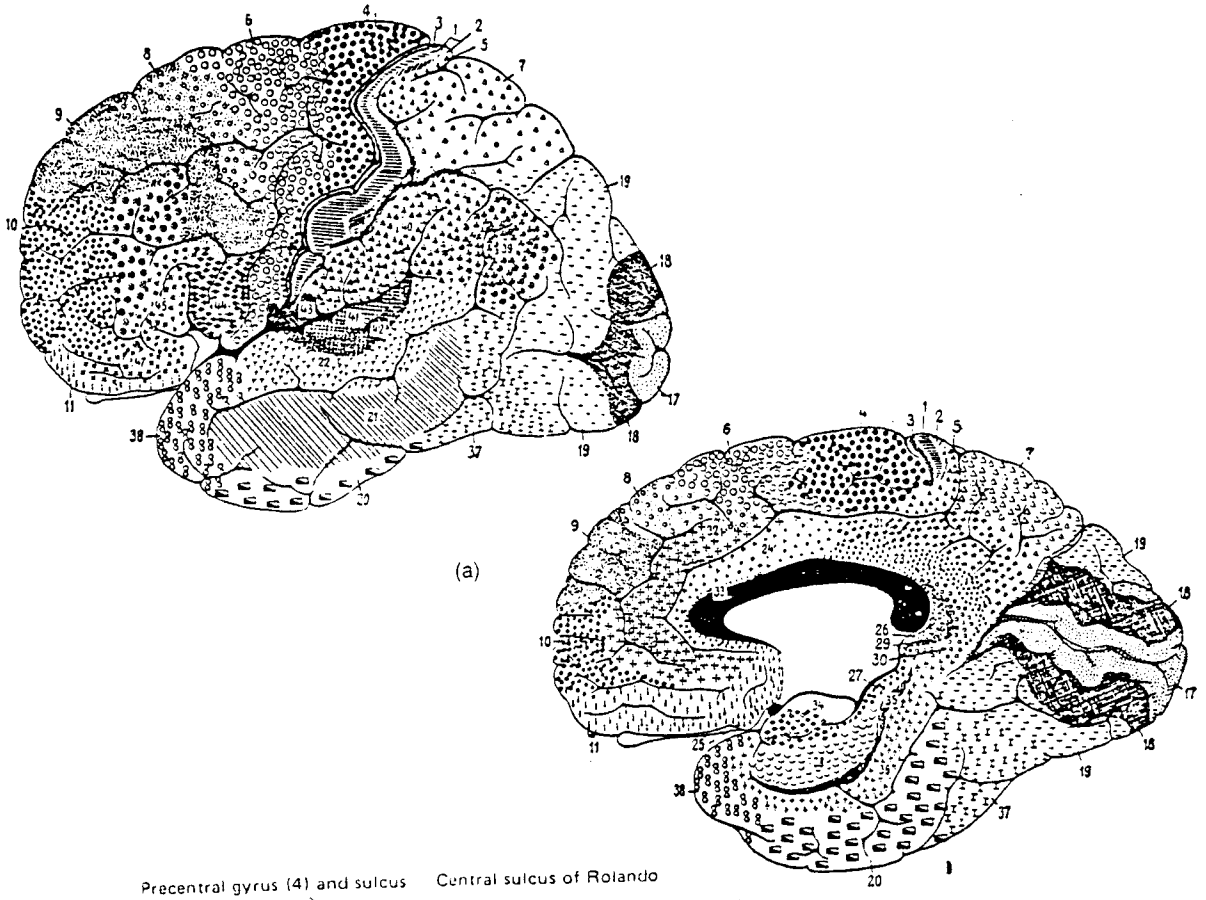
We must assume that species-specific behaviour depends on the size and underlying organization of each species's brain, its ontogenetic development, and how that occurs within varying environments, both material and social. When this chapter refers to *reorganization* of the brain during evolution, it means that natural selection has worked upon *quantitative shifts* in the relative sizes of brain *components*, and that such changes have had important consequences for behaviour (see, for example, Holloway 1964, 1968, 1970, 1979, in press, *a*). Such reorganizational changes have come about largely through heterochrony (Gould 1977; Shea 1983; Deacon 1990a, *b*), that is, changes in the timing (initiation, duration, and termination) of mitotic divisions and selective death of cell populations, leading to species-specific differences in both hyperplasia and hypertrophy of nerve-cells. (Hyperplasia refers to the number of cells produced, while hypertrophy refers to the size of the cells, both of which determine, at least quantitatively, synaptic connectivity.) Thus far, no significant differences among primates have been discovered at the neurochemical or molecular neurobiological levels.

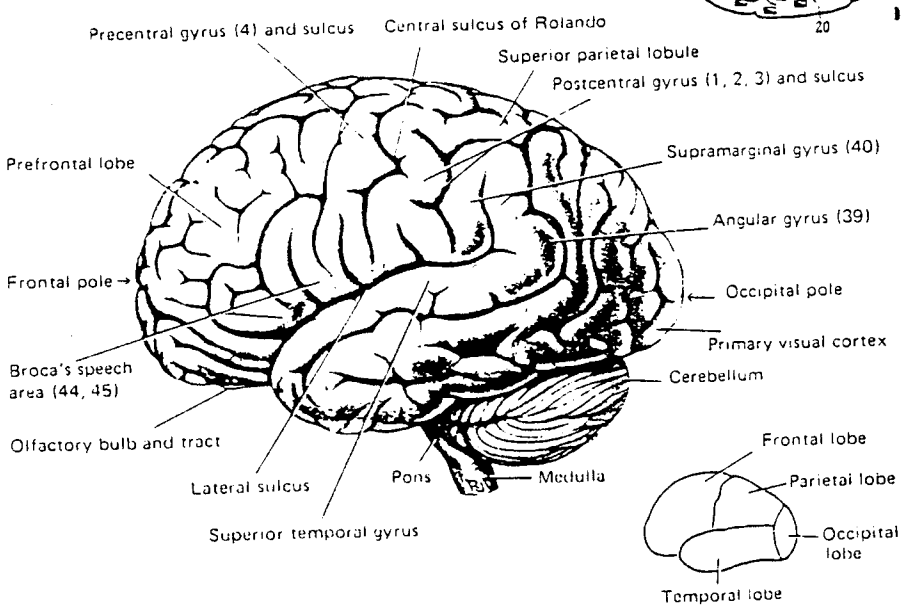
The brain is an extremely complex set of organs, containing billions of parts if one is referring to nerve-cells alone. These cells are in one of two states: firing, or not. The effects of their firing can be either excitatory or inhibitory, thus leading to a dual set of 'digital' states. However, whether or not a nerve-cell fires will depend on a process of summation of many thousands of inhibitory or excitatory connections with other nerve-cells. Estimates of one nerve-cell in the visual cortex's having as many as 10 000 connections are common. This might be considered the 'analogue' condition of the nerve-cells. The complexity increases vastly when one adds to this picture the fact the brain has both 'serial' and 'parallel' organization among its many components, such that information about the environment can be evaluated both directly and indirectly, in present and in future perspectives depending on how experience becomes organized in both short- and long-term memory, how it is stored, how it is retrieved, and how it is transformed. These functions involve other brain structures as well as the cerebral cortex (for example, the thalamic nuclei, the hippocampus, the septum, the reticular formation, etc.).

The brain is also organized hierarchically (see Fig. 4.2 [eds]). This refers to the relationships between the cerebral cortex, the underlying basal ganglia, the limbic system, and the olfactory bulbs (the *telencephalon* or forebrain), which surround the *diencephalon*, including the thalamus, epithalamus, hypothalamus, and pineal gland. Next, moving 'downward', there is the brainstem, which contains the superior and inferior colliculi, which are visual and auditory in function (the *mesencephalon* or midbrain). Lastly, there are the more 'primitive' structures, which consist of the cerebellum, the pons, the medulla, and the third and fourth ventricles, which are integrated with the spinal chord (the *metencephalon* and *myelencephalon*).

This kind of structural similarity is found in almost all vertebrate brains, suggesting an extraordinary degree of genetic conservatism underlying the ontogenetic development of the brain. Additionally, the cerebral cortex is organized into vertical columnar units (Mountcastle 1978; Szentagothai 1978) containing very similar numbers of neuronal cells (both neurons and their metabolically-supporting neuroglial cells) in very similar ways in almost all mammals, indicating another structural and possibly functional level of great genetic conservatism. This suggests that it is the interconnections between neurons, and their growth and development, that are partly responsible for species-specific differences in behaviour.

Obviously, given the enormous differences between humans and other animals in the size of our brain, and in particular our cerebral cortex (this accounts for 76 per cent of our brain volume, as calculated





(b)

Fig. 4.1 (a) Maps from Brodmann (1909) of areas of the human cortex, each of which possesses a distinctive cytoarchitectonic structure. Top figure: lateral view; bottom figure: medial view. [eds].
(b) Lateral surface anatomy of human brain [eds].

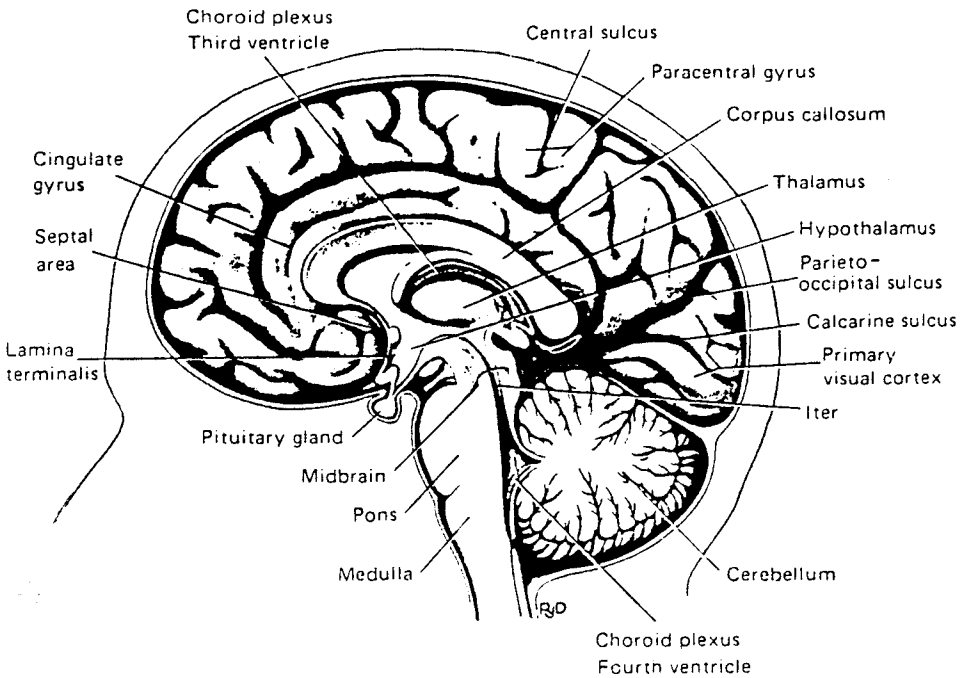


Fig. 4.2 Gross structure of the human brain [eds].

from the data of Stephan *et al.* 1981), genetic changes controlling both the rates and duration of mitotic division of certain neural masses have occurred during evolution. Both hyperplasia (the number of cells), hypertrophy (the size of neural units), and cortical columnar interconnections have been key evolutionary events in reorganizing brains and species-specific behaviour patterns.

While no one is certain how many 'genes' control the formation of the brain ontogenetically, it is estimated that perhaps as many as 40 000 genes may be involved. Obviously, an enormous amount of potential genetic variability exists for natural selection to work upon now, as it has in the past. Thus, one of the most formidable challenges facing any attempt to understand brain evolution is how to account for the complex mixture of both conservative and new genetic expression relating to all parts of the brain, and how these relate to behaviour, adaptation, and evolution within the primates, or, for that matter, any animal group. Deacon's (1990*a*, *b*) articles are unique in his appreciation of and attempts to clarify this complexity.

We know next to nothing about within-species neural variability and behaviour (see for example Holloway 1968, 1969*a*, 1976*a*, *b*, 1979, 1980, 1983*a*; Holloway *et al.*, in press, *b*). Even between-species neural differences cannot be directly related to different species' behaviour. We do not know which genes exist or control the ontogenetic unfolding of particular brain regions or nuclei or fibre tracts. Neurochemistry does not at present provide any convincing relationships between brains and behaviour except, say, between neurotransmitters and psychopathological states. The data for a neuroscientific explanation of readily observable behavioural differences between different breeds of mice, rats, cats, or dogs do not exist. Simply ask anyone what are the neural differences that might explain the behavicural differences between orang-utans, chimpanzees, and gorillas, or various species of *Macaca* and *Papio*. As for between species behaviour and quantitative variations in the brain, the best known mammalian examples are the *Chiroptera* (bats) as published by Pirlot and his colleagues (see Jolicoeur *et al.* (1984) for a similar perspective on these hiatuses and references to his own and his colleagues' works on bats and other animals).

Considering how much is known about animal behaviour under naturalistic field conditions, it is disappointing that so little synthesis can be made directly with neuroanatomical data. The Jolicoeur *et al.* 1984 studies on quantitative structures of the bat brain and their relation to feeding behaviours (herbivory, fructivory, predation) stand almost alone as one promising direction. If we consider for a moment the very wide range of behavioural differences among the living primates—i.e. lemurs, tarsiers, New and Old

World monkeys, chimpanzees, gorillas, orang-utans, and gibbons—we find an embarrassing lack of reliable neurological synthesis. None of the behavioural differences can as yet be linked with the animals' respective brain sizes or organizations. Brain size is simply insufficient for such a task of synthesis, although it is an essential starting-point, given that it comprises most of our reliable data-bases.

Considerable knowledge regarding brain size as a correlate with behavioural and other anatomical variables has been gained through allometric studies. In these, brain size is usually considered a dependent variable, and relationships are made to body weight, gestational duration, growth stages, longevity, metabolism, precocial or altricial development, and broad ecological areas relating to subsistence (for example folivory, frugivory, omnivory, and predation) (see Passingham 1982; Martin 1981, 1982, 1983; Milton 1981, 1993; Clutton-Brock and Harvey 1980; Harvey and Clutton-Brock 1985; Dunbar 1992; Aiello and Dunbar 1992; Armstrong 1983, 1990; Hofman 1982, 1983; Leutenegger 1982, 1987; Sawaguchi 1988, 1990; Sawaguchi and Kudo 1990; Sacher 1982; Shea 1983). All these analyses treat brain size as if the brain were an organ in its own right, seldom with any realization that many aspects of the behaviour being examined cannot be related to brain size in any causal manner. Brain size is good as a starting-point; but it seems to become a reified end in itself.

Most allometric studies plot the size of an organ (in this case the brain, or a part of the brain) against a large variable, such as body weight or total brain weight. There is inherent in such studies the 'mouse–whale' phenomenon, in which the values, once transformed into log (base 10) values, cannot do other than appear as a straight line, as the transformation is an often-used technique in reducing statistical variances in raw variables. (We can substitute *Microcebus*—the dwarf lemur—and *Gorilla* as examples of 'mouse' and 'whale' for the primates: see R. J. Smith 1980.) When such log–log plots are done, it is generally the slope of the regression line that is of most interest, as it specifies how one organ is scaling against another, or a total weight. Figure 4.3 shows a log–log plot of brain weight against body weight for some 85 species of primates, based on data kindly given to the author by Dr Heinz Stephan. The value for our own species is in the extreme upper right-hand corner of the figure. The closest three squares are the pongids, the gorilla, chimpanzee, and orang-utan. The correlation coefficient is about 0.97, without the *Homo sapiens* value, which is about three times higher than its predicted value based on body weight. The slope of the regression line without the *Homo sapiens* value is about 0.78 (and not 0.66, as was earlier declared by Jerison (1973) and many others; see Martin 1983, for references and further discussion). This number of about 0.78 (approximately 3/4) for the

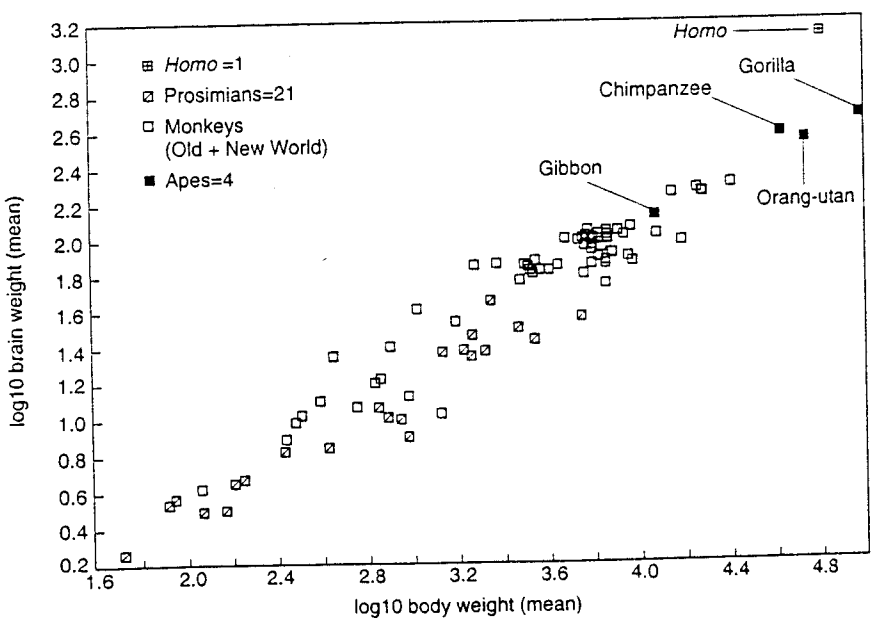


Fig. 4.3 A log–log (base 10) plot of the mean brain and body weights for 85 species of primates, including *Homo sapiens sapiens* (top right).

order as a whole is suggestive of a metabolic constraint between body weight and the weight of the brain, although no precise formulation has proved adequate as yet. 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. Within families, the slope is close to roughly 0.66. This latter exponent is suggestive of a geometric relationship between surface area and volume, i.e., the ratio 2:3. Lower-level taxa scale at lower exponents, such as roughly 0.3 between species of the same genus, or around 0.1 to 0.2 within a species (see Holloway and Post 1982; Holloway 1980 for further discussion). It is for this reason that encephalization quotients (see Section 4.4.1.2. below) are 'relative', as each species value depends on the allometric equation used.

An important point is that the slopes, whether 0.76 or 0.66 (or whatever value), reflect not a *law*, but *constraints* around which different species *vary*. While it is possible that some of the discrepancies between predicted and observed values may be purely statistical in nature—i.e., may arise from sampling phenomena—it is also possible that some of these departures may contain interesting and provocative insights into the neural biologies of particular primate species. The human case is simply the most obvious among primates.

The picture becomes very much more complex when components of the brain are log–log regressed against each other, or against brain weight. For example, the human animal shows enormous departures (in terms of percentages) of actual from predicted volumes in a number of brain structures. I have, elsewhere, mentioned the primary visual striate cortex, which, in a sample of 45 primate species, falls 121 per cent below expected volume (calculated from the data of Stephan *et al.* 1981, and discussed earlier in Holloway 1976*a*, 1979, and again in 1988*a*, 1992, yet ignored in Passingham *et al.* 1986 and Armstrong *et al.* 1991). The lateral geniculate body of the thalamus is similarly 'off target' (i.e., about 146 per cent below the value expected for *Homo sapiens*), as would be expected from its close relationship to the visual cortex. Indeed, I have found differences of up to 7000 per cent for some of the smaller structures in the human brain. It is interesting that the volume of the ventricles, which in the fetal brain provide the neuroblasts that eventually become the ten billion or so neurons in the adult cerebral cortex, is roughly 52 per cent greater than expected, which correlates with the fact that the human brain has the highest percentage of cerebral cortex among the primates.

Herein lies a rich treasure-trove barely explored (see also Deacon 1988*a*, *b*), which could have interesting potential for understanding, at least quantitatively, the differences in organization between our brains and those of other animals. I explicitly wish to suggest that it might at least be an interesting place to begin. As is always the case, it is tempting to interpret such differences in size of the neural components as direct evolutionary statements, assuming reasonably (at first glance) that what is big is important, and what is smaller has become that way through natural selection operating directly on behaviour, and thus on the genes controlling the ontogenetic development of particular neural masses. We really need many more quantitative data before such explanatory leaps can even legitimately be made, let alone reliably evaluated.

The cerebral cortex is an interesting and provocative example in this discussion. After all, we do pride ourselves as being that species that has so much of it . . . Yet, as Passingham and Ettlinger (1973) showed, and as has been discussed more recently by Passingham (1982), log–log regressions of cortical volume against brain weight show that the human animal has about as much cerebral cortex as would be expected for a primate of its brain weight. The human brain is 76 per cent neocortex. This is the highest primate ratio, followed next by the chimpanzee, with about 72 per cent; average values for most primates are about 50–60 per cent. (These figures are based on my analyses of the data of Stephan *et al.* 1981.) The actual value for human cerebral cortex volume is less than 1 per cent different from its allometrically expected value. The cerebellum for the human species is about 6 per cent greater than expected. Given statistical variation, and small sample sizes of such neural data within species, differences of 10 to 25 per cent are probably not significant. However, in the visual system, i.e., the primary visual striate cortex and the lateral geniculate nuclei, differences (−121 per cent and −146 per cent respectively) *are* significant, *and* these reductions signal a *relative increase* in the volume of parietal 'association' cortex, which is usually related to complex cognitive activities such as visuo-spatial integration, etc. Here is a prime example of reorganization.

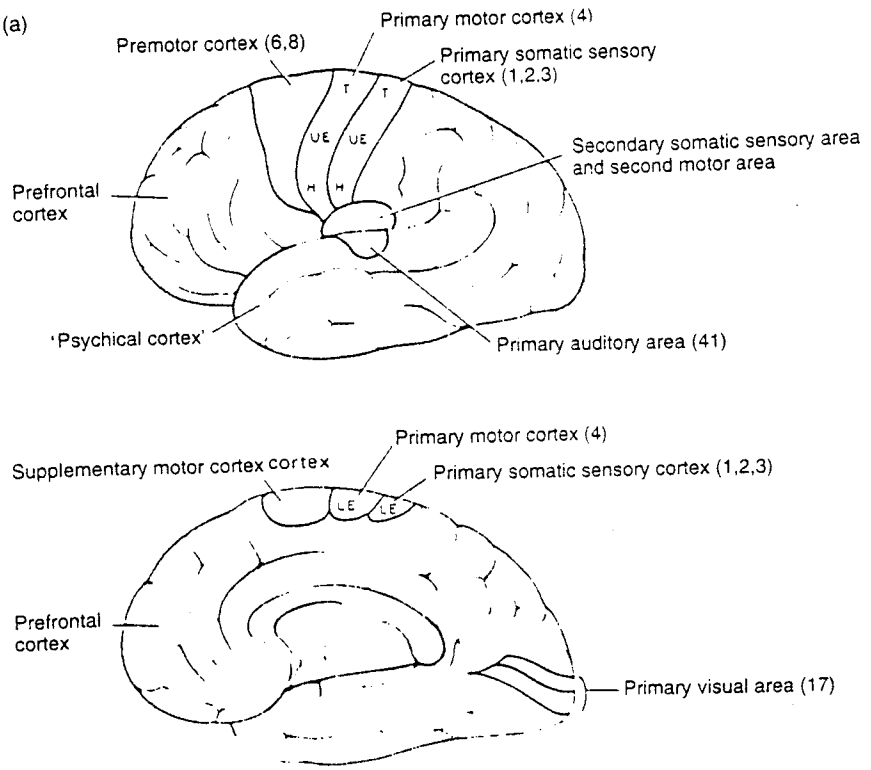
However, one must consider carefully these regression operations. In the case of the cerebral cortex, one is regressing the cortex against brain volume, *of which over 50 per cent is represented by the cerebral cortex alone* in primates generally, and 76 per cent in *Homo* specifically. It is thus hardly unexpected that the correlations are so tight, and the differences between observed and expected values so close. Perhaps some other measurement or set of ratio data would be more useful in underlining the unique relative volume of the human cerebral cortex (see Passingham 1982,

Passingham *et al.* 1986, Deacon 1990*a*, *b*, and Dunbar 1992 for other examples, and different emphases).

Quantitative studies on primate brains that go beyond brain weight or volume are still in their infancy (see for example Deacon 1988*a*, *b*; Frahm *et al.* 1982, 1984; Stephen *et al.* 1981; Matano *et al.* 1985*a*, *b*; Armstrong and Falk 1982; Passingham 1982; Passingham *et al.* 1986). Much of the quantitative evidence is based on a sample size of one for most species. Not all neural structures have been measured, including functionally meaningful divisions of the cerebral cortex according to cytoarchitectonic patterns (i.e., whether sensorimotor or 'associative', cf. Brodmann's areas; (see Fig. 4.4 [eds]). These examples hardly diminish the possible list of true gaps which exist in our knowledge at present.

Another example concerns that most favoured part of the cerebral cortex, the frontal lobe, which is regarded by so many as the chief expanding unit during human evolution. In 1964 (see also also Holloway 1968) I tried to show that the quantitative evidence for a *unique* increase in this part of the human brain was suspect. This was before the days of any careful realization of the usefulness of allometrical analysis. More recently, Uylings and van Eden (1990) have claimed that the prefrontal cortex in humans has shown an allometric increase beyond that of other primates. While the amount of prefrontal cortex does scale positively to the total amount of cerebral cortex (the slope when plotted with isocortex volume is 1.069), the slope when the prefrontal cortex is plotted against total brain volume is 1.108, and this is reported as significantly different from 1.0. This positive allometry led the authors to suggest that the human prefrontal cortex was proportionately larger than in apes. The rat, marmoset, macaque, orang-utan, and human all fall nicely on the same straight log–log regression lines. In other words, the 'positive' allometric increase from rat to marmoset, then to macaque, and then to orang-utan, is proportionately the same as that from orang-utans to humans. To me, this signals that human prefrontal cortex is exactly what would be expected for a primate with a human brain weight. Is this the same as saying that humans have relatively more prefrontal cortex than other primates? I don't believe so; but this does not diminish the importance of the frontal lobe, either with regard to its size or its organization.

Another very important topic is that of the surface convolutions of the brain. While the human brain is in actuality some 3–4 times heavier than the chimpanzee brain, there is considerable similarity between the two species with regard to the convolutional details (see Armstrong *et al.* 1991 in particular, as well



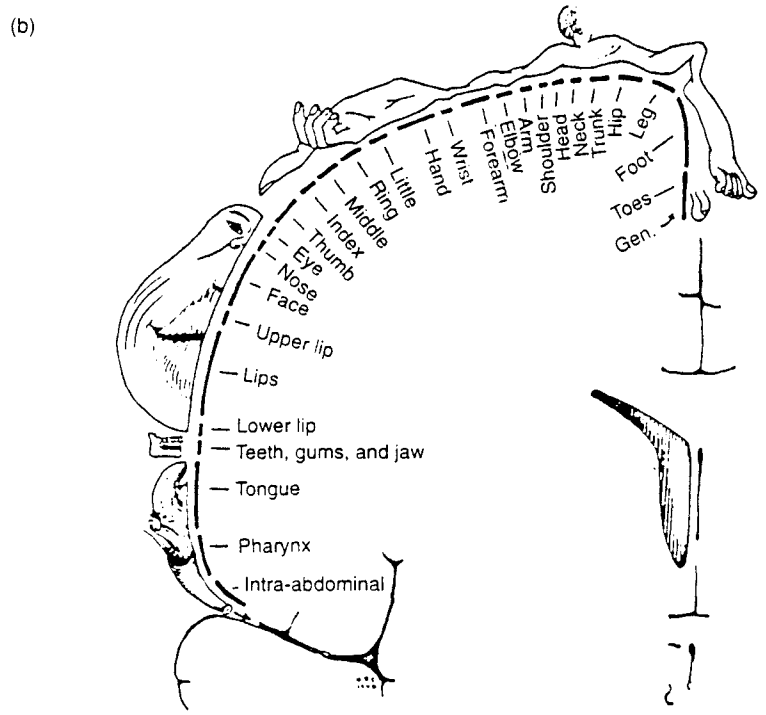


Fig. 4.4 Gross functional areas of the cerebral cortex [eds]. (a) The location of several functional areas: the representation of body parts on the primary motor and somatic sensory cortices includes the head (H), upper externity (UE), trunk (T), and lower extremity (LE), numbers represent areas of Brodmann. (b) Diagram showing the relative sizes of the parts of the central cortex from which sensations localized to distant parts of the body can be elicited on electrical stimulation in many (from Penfield and Rasmussen (1950)).

as my (Holloway 1992) critique regarding australopithecine brain endocasts). Although the human brain has more convolutions (a fact which is related to brain weight), and very considerable variation of its gyri and sulci, particularly in the parietal and frontal lobes, the primary and secondary gyri (the hills) and sulci (the valleys) are very similar and often the same between hominoid species. Of considerable interest to those studying the palaeoneurology of our fossil ancestors are the sulci labelled the lunate, the intraparietal, the Sylvian, and the lateral calcarine (see for example Holloway 1983*b*; see Fig. 4.5). In apes, such as the chimpanzee, the lunate sulcus is always present, and is the anterior boundary of primary visual striate cortex (area 17 of Brodmann), which subserves visual functions. Furthermore, in apes the intraparietal sulcus, in its posterior part, always terminates against the lunate sulcus, and divides the parietal portion of cerebral cortex into superior and inferior lobules. The calcarine fissure always runs medial from the occipital pole to a lateral position, but terminates before it reaches the lunate sulcus. Thus these sulci should not be confused with each other, but taken together represent an important neuroanatomical unit. The lunate sulcus of a human brain is in a very posterior position relative to where it can be found in apes (see Connolly 1950 and Holloway 1985*a* for a review of the history of this sulcus and its significance to human brain evolution). As the figures for the volume of visual striate cortex previously discussed indicate, the human brain has relatively less of this cortex making up its cerebrum than those of the apes. This means that the relative amount of parietal 'association' cortex has increased in the human species. The challenge is to document when such changes 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 motoric anterior gyrus and the posterior sensory gyrus. Both the inferior third frontal

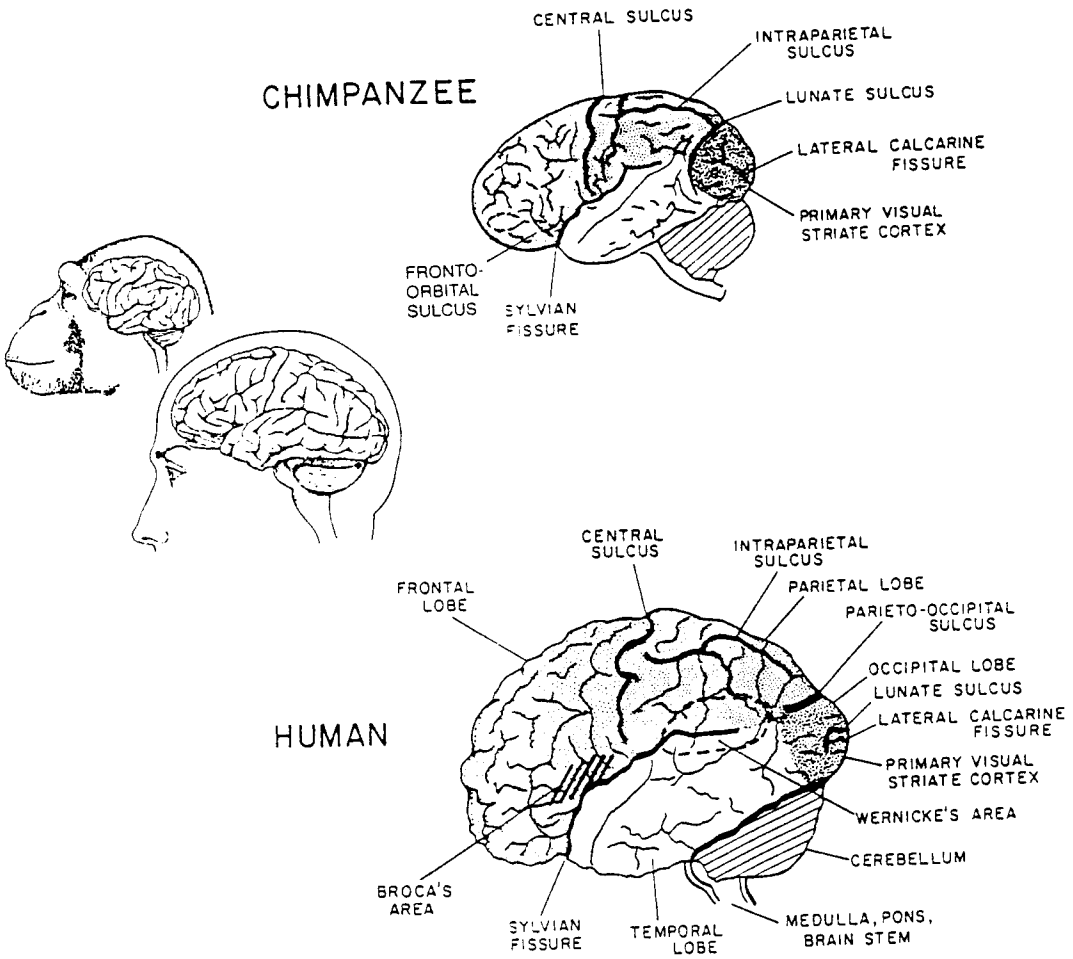


Fig. 4.5 The brains of chimpanzee and human in lateral view (after Passingham (1982) *The human primate*. Freeman, San Francisco) [eds].

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 linguistic communication. These particular regions are seldom well preserved on fossil endocasts, and are quite variable with regard to tertiary convolutions (for the finest details see for example Connolly 1950), and are areas of considerable interpretative controversy among palaeoneurologists.

Figure 4.6 (cf. Holloway 1983*a*) attempts to depict a few possibilities that might help to explain human brain evolution (see Section 4.4), in which brain size, reorganization, differences in 'wiring' of components, and asymmetries can be seen as phenotypic manifestations of changes in unknown parts of the underlying genetic code. Figure 4.7 provides a model (Holloway 1979) that attempts to synthesize the different viewpoints between those who stress mass or size, and those who stress reorganization. Brain size is simply the most obvious and reliably measured of such possible phenotypic windows on evolutionary changes. As one can see, many important changes enhancing hominid behavioural adaptations (see for example Holloway 1970, 1983*a*) *could* have taken place without necessarily involving brain-size increase. This is meant as a distinct warning to those who would simply plot brain size against time and conclude the brain was showing evidence for 'stasis' between hominid populations (for example Eldredge and Gould 1972; Eldredge and Tattersall 1982; Cronin *et al.* 1981). Many other events could have taken place that were important factors in human

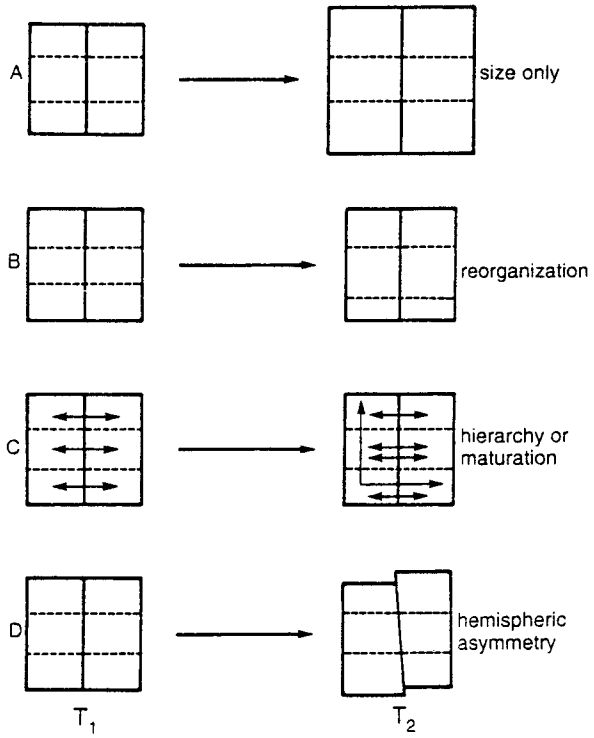


Fig. 4.6 Some evolutionary possibilities for hominid brains (adapted from Holloway 1983.) Four different (but not necessarily exclusive) possibilities of brain evolutionary change through time (T_1 to T_2). In A, the brain is represented with two hemispheres (left and right). The two dotted transverse lines are representations of the central or Rolandic sulcus (top) and the lunate sulcus (bottom). The change in time is simply an increase in absolute brain size, with or without concomitant body-size increase, and *without* any changes in the size of the cerebral components or the connections between them. This change could have occurred isometrically or allometrically. An example might be the change from *Homo erectus* in Indonesia to the later forms of the same species in China.

In B, the change from T_1 to T_2 does not necessarily, involve any change in brain size. Instead, *there is a change in the relative size of the components*. In this case, the lunate sulcus has moved back posteriorly, increasing the relative size of the parietal association cortex. This is a *reorganizational* model. An example could be the change from a pongid pre-australopithecine precursor to *Australopithecus afarensis*, or to *A. africanus*. (Combining A and B might be an example of the evolutionary change from a primitive *Australopithecus* to early *Homo*.)

Model C shows changes in the development of interconnections between cerebral components (hierarchical development, see Holloway 1979), *without any necessary change in absolute or relative brain size*. The arrows represent different fibre systems maturing at different rates and/or increasing in number between different cortical regions through the corpus callosum.

In model D, the absolute brain size remains constant from T_1 to T_2, but a more human type of hemispheric asymmetrical pattern develops (that is, a left-occipital right-frontal torsion pattern). For example, the change in brains from *Homo erectus* to *Homo sapiens* might have involved minimal increase in size, but changes in both hierarchy or maturation rates *and* hemispheric asymmetry.

It is important to note that these four models hardly exhaust the possibilities of different brain changes through time, and all of these changes and particular combinations of them may have been realized in human brain evolution. In addition, model B could be a true case of 'punctuated equilibrium' (as could A, C, or D), and thus be overlooked in hominid evolution. The change in A, rather than being a case of 'punctuated equilibrium', could be a simple matter of allometry, i.e., due to an increase in body size, without any substantial behavioural differences between T_1 and T_2.

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brain and behavioural evolution that did not effect brain size *per se*. Punctuated equilibria and stasis models based on brain size alone never take these possibilities into account.

This does not mean that brain size should be ignored, or was unimportant during hominid evolution. It simply means that we should cast our nets wider for other phenotypic measures that pertain to the brain and how it works, both within and between species.

4.3 Lines of evidence regarding human brain evolution

There are three lines of evidence available to us for studying the evolution of the human brain: (1) palaeoneurology; (2) comparative neuroanatomy; and (3) both the products of behaviour resulting from past hominid activity and the fossil remains of cranial and postcranial anatomy. The first is a direct line of evidence; the others provide indirect evidence.

Palaeoneurology involves the study of endocasts, which are limited to only the surface features of once-living brains. The data available from such studies of casts made of the interiors of fossil crania include endocranial volume, convolutional details of the cerebral cortex, traces of meningeal vessels which may have some taxonomic if not functional significance, and the shape and asymmetries of the cerebral cortex.

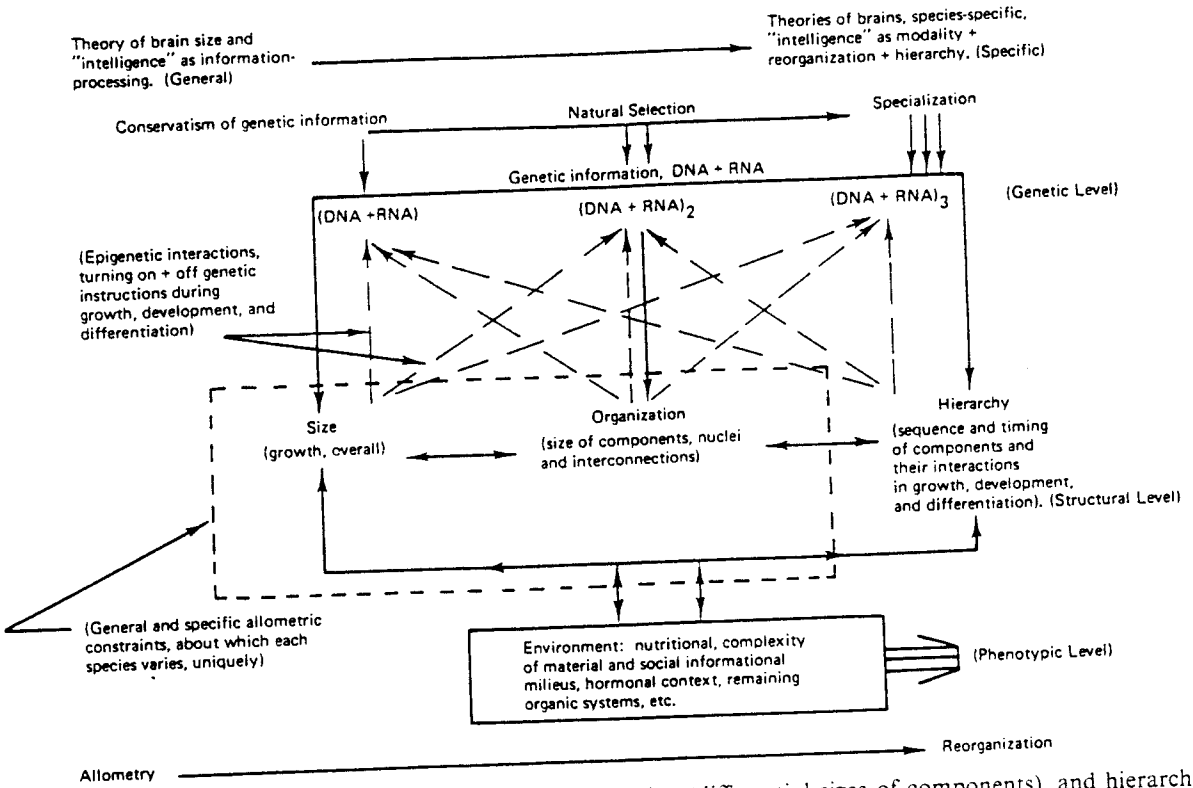


Fig. 4.7 A model of how brain size (absolute), reorganization (differential sizes of components), and hierarchy might be conceived. The 'phenotypic level' toward the bottom right portion of the diagram is almost exclusively regarded as brain size by most authors, but in this model is meant to include more than absolute size. For allometrists, only the left side appears to be of interest, the rest being 'trivial'. For anyone concerned about species-specific brain-behavioural evolution, i.e., *Homo sapiens*, the left portion cannot explain the totality that is the human brain (or any other animal's brain), as allometry is only the constraint around which other species vary, and brain size alone cannot be related to species-specific repertoires of behaviour, or unique evolutionary histories. This model explicitly regards the final phenotypic level as a complex orchestration between the neural events which unfold through the interaction of structural and regulatory genes, with natural selection operating upon at least three realms of genetic information (Holloway 1983*a*: adapted from Holloway 1979, where a fuller discussion can be found).

Unfortunately, in life the brain is covered with three meningeal tissues—dura, arachnoid, and pia mater—which tend to obscure the imprinting of underlying cortical gyri and sulci on the internal table of cortical bone, to say nothing of the effects of the cerebrospinal fluid. This means that it is extraordinarily rare for all cortical convolutions to be preserved on endocasts. Interpretations of what *is* preserved are thus often controversial; and hence it is the size of the brain and possible asymmetries of the cortex that provide the most reliable evidence of evolutionary changes.[2]

The study of *comparative neuroanatomy* provides evidence regarding the size and organization of the brains of living animals, each of which is a terminal end-product of its own evolutionary development, and not a living stage, as it were, of human evolution. This first line of indirect evidence is absolutely essential for understanding how neural nuclei, fibre tracts, and cortical cytoarchitecture vary in different animals, and how these variations relate to species-specific behaviour. While the present living chimpanzee (*Pan troglodytes* or *Pan paniscus*) is not a true stage in human evolution, most neuroscientists seem to believe that modern *Pan* is probably similar in many ways to the line from which the earliest hominids diverged 5 to 8 million years ago. Thus *Pan* is a useful comparative foil for providing quantitative data regarding neural organization, against which we can compare human brains. To a lesser extent the same applies to *Macaca* monkeys, although these are *the* favoured

primates for comparisons with the human brain, and the species on which much of modern neuroscience is done. For example, Heilbroner and Holloway (1988, 1989) have shown that there is Sylvian fissure asymmetry favouring the left side, and thus the temporal lobe as a whole, in *Macaca*, *Saimiri*, and *Callicebus*—results consistent with those reported by Falk *et al.* (1986). Our second study (1989) found less compelling evidence in other regions of the cortex and limbic system. It is also within this type of comparative evidential base that the study of allometry has become a valuable tool of studies of the brain (see Section 4.2 above).

The second line of indirect evidence relies upon the *products* of behaviour *resulting from past hominid activity* (see especially Chapters 9, 10, and 11 by White, Wynn, and Conkey respectively, of the present volume). This includes stone tools made to both non-standardized and standardized forms, and the palaeoarchaeological sites which have preserved past patterns of hominid activity, such as gathering, stone tool-making, scavenging, butchering, and hunting. Another aspect of this line of evidence relates to the actual *skeletal remains* of the hominids themselves (see Marzke, this volume, Chapter 5), which provide information regarding their locomotory patterns (bipedalism), their manipulatory capabilities (hand bones), and their other anatomical characteristics, including details of accidents and pathology. While all these provide only the most indirect of clues, major patterns of locomotory adaptations and complicated cognitive processes such as tool-making cannot evolve in a neural vacuum. The central nervous system has an intimate, if not a controlling, relationship with musculo-skeletal organization. Certainly, hominid evolution has been mosaic (McHenry 1975, 1982, 1988; White 1980), but there have been mosaics within the mosaic (Armstrong 1983; Holloway 1970, 1983*a*; Holloway and Post 1982). Empirically, the brain did become significantly larger in size *after* bipedalism developed; but size refers to but one phenotypic manifestation of the brain, and it is surely premature to ascribe a terminal role to brain evolution, i.e., to treat the brain as the last organ to evolve. Thus, Toth's suggestion (1985) that early stone tools show signs of having been made by right-handers is an important piece of possible evidence that can be related to the asymmetrical organization of the cerebral cortex in early *Homo* (see Section 4.4.2.3 below), and thus to handedness and other possible cognitive specializations.

Given the scarcity of truly empirical evidence regarding brain evolution, the challenge is to use all three of the above lines of evidence judiciously, synthesizing the best, and hopefully framing hypotheses that are capable of being refuted later. This is no easy task. While there is convincing evidence from the neurosciences in general relating to asymmetries of the human brain, and the relationships between handedness and language, or the hippocampus and memory, or the organization of the cerebral cortex into both serial and parallel processing devices (with unequal representations of cortical regions such as Broca's or Wernicke's areas), it is very difficult to relate this knowledge directly to poorly preserved, fragmentary endocast portions of fossil hominid crania.

The above discussion places the problems of attempting to understand human brain evolution in a fuller light. It is now time to approach these evidential bases more thoroughly.

4.4. Palaeoneurological evidence

4.4.1 *Brain size*

4.4.1.1. *Absolute brain size*

Table 4.1 (and see also Editorial appendix I—[eds]) provides a listing of the brain volumes (endocranial volumes) presently known for the major fossil hominid finds. Starting more than three million years ago with *Australopithecus afarensis*, there has been an increase in brain volume within the Hominidae from about 400 ml to roughly 1400 ml. That evolutionary gain in size, 1000 ml, is coincidentally approximately equivalent to the total known variation in normal human beings, based on large population sizes (see for example Dekaban and Sadowsky 1978; and Table 4.8b of Appendix I to this chapter—[eds]). Specific individual cases would include such old anthropological 'chestnuts' as Anatole de France, with roughly 1000 ml, and Jonathan Swift, with more than 2000 ml. Until recently, no reliable evidence has ever been presented that this variation in size has any meaningful relationship to behaviour in humans, either of a quantitative or qualitative nature, aside from known pathological conditions such as microcephaly, hydrocephaly, etc.: there are, for example, no published accounts of 'geniuses' with brain sizes in the range of pongids, i.e., 275 ml (lower limit of female pygony chimpanzee) to 752 ml (upper limit of male gorilla). (Values taken from Tobias (1971*b*) = Table 4.8b of Editorial appendix I to this chapter.) Recently, using MRI scans, Andrensen *et al.* (1993) have shown that there are strong correlations between the Wechsler Adult Intelligence Scale and various volume estimates of parts of the brain, with correlation coefficients of between 0.3 and 0.5. These are relatively high for a within-species sample of 67 volunteers.

Realizing that human pathologies have their limitations in discussing evolutionary trends, it is still intriguing to reflect on microcephaly. There are recorded

Table 4.1. Endocranial brain volumes of reconstructed hominids

Specimen		Region	Endocranial volume (ml)	Method	Eval.
Taung	*A. africanus*	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	*A. robustus*	"	530	A	1
OH5	*A. boisei*	E.A.	530	A	1
ER406	"	"	525	D	2
ER407	"	"	510	A	1
ER732	"	"	500	A	1
ER1805	*H.?*	"	582	A	1
ER1813	"	"	510	A	1
ER1470	*H. habilis*	"	752	A	1
OH7	"	"	687	B	2
OH13	"	"	650	C	2
OH24	"	"	590	A	2–3
OH9	*H. erectus(?)*	"	1067	A	1
ER3733	"	"	848	A	1
ER3883	"	"	804	A	1
HE1 (1892)	"	Indonesia	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	"	Morocco	880	A	1
SPY I	*H. sapiens (N)*	Europe"	1305	A	1
SPY II	"	"	1553	A	1
La Chapelle	"	"	1625		X
La Ferassie I	"	"	1640		X
Neandertal	"	"	1525	X	2
La Quina	"	"	1350	X	1
Jebel Irhoud1	"	Morocco	1305	A	1
AL 333–45	*A. afarensis*	Ethiopia	485**	C	2
AL 162–28	"	"	375–400**	est.	2
AL 333–105	"	"	310–320**	C	2

Some selected cranial capacities for different hominids that the author has examined. Method A, direct water displacement of either a full or a 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 the total endocast; D, determination from regression formulae. X refers to previously published values now confirmed by the author. An evaluation of 1 indicates the highest reliability; 3 the lowest, depending on the completeness of the specimen, distortion, and the author's techniques. An asterisk * refers to estimated adult volume from a juvenile or a child's endocast. The double asterisked items **, confined to the Hadar, Ethiopian *Australopithecus afarensis* materials, are 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.

cases of humans born with this condition who nevertheless have been claimed to develop and use 'language' via 'arbitrary symbol systems' though their brain sizes are less than those of some chimpanzees and gorillas (see the references below). True, their intelligence is subnormal, and many do not speak. Nevertheless, this pathology indicates that it may be possible for a brain with less volume than that of some apes to be organized in some distinctly human fashion. (Discussions of this condition have been more extensively treated by Seckel 1960; Lenneberg 1967; Yakovlev 1960; and Holloway 1964, 1966, 1968.)

Given the above, brain size taken alone presents something of a conundrum for interpreting the significance of the large increase in brain size from the fossil record. Intuitively, the more than trebling of brain size (even taking body-size increases into account through allometry) over three million years must have been important; but *where* is the evidence that brain-size increase in small increments is useful in some adaptational sense? Does this mean that one *Homo erectus* with a brain size of 749 ml was at a behavioural disadvantage compared to a sibling with 751 ml? Does it mean that the latter could 'talk' but the former couldn't (assuming that the famed 'Rubicon' *à la* Keith for symbolic language is 750 ml)? One thousand ml divided by three million years is an increase of 0.0003 ml per year, or with a generation span of 20 years, an increase of 0.0066 ml per generation. Thus it takes about 1000 generations to aggregate only about 6 ml of brain-size increase. It can be argued that this example mistakenly mixes analyses of population variability with evolutionary changes; but the point remains that in order to describe evolutionary changes in organs sensibly we must have some knowledge relating structural to functional variability. This is very much lacking for the brain. This is one reason, for example, why Dunbar's (1993) ideas regarding the relationships between group size, social grooming, and communication and neocortical size are difficult to accept. In fact, modern Europeans probably have less neocortex than did large-brained Neanderthals, and Australian Aborigines, famous for social complexity that has challenged many a social anthropologist, have demonstrably less neocortex than caucasians (Klekamp *et al.* 1987) but there is scant sign of any rush to conclude on the basis of this evidence that the Neanderthals must therefore have had a more sophisticated social structure and language than do modern humans.

Nevertheless, as Table 4.1 indicates, it would appear that the australopithecines had ape-sized brains, and retained them for perhaps two million years; and it is not until the first fossil evidence for the genus *Homo* (*H. habilis*, about 1.8 million years ago, using KNM-ER-1470, with about 752 ml in brain volume, for data) that we have evidence for a dramatic increase in brain size.[3]

In my view it is difficult to explain how and why hominid brains evolved after *Homo habilis*: that is, from *Homo erectus* at roughly 1.7 million years ago to the present. In this matter, the brain increases roughly twofold: from about 750 ml in late *Homo habilis* to 1500 ml in late Pleistocene *Homo sapiens sapiens* (for example, Cro-Magnon), while body size increases (or decreases?) only a small amount, if at all. (See Walker and Leakey (1993) for estimates of body size in early *H. erectus*—[eds]) This could appear to rule out simple allometry as a causal explanation.[4] Indeed, both Neanderthals and late Pleistocene specimens have, on the average, larger cranial capacities than the mean for recent *Homo sapiens*. Neanderthal brain volumes on average are slightly larger than those of modern *Homo*.

4.4.1.2 *Encephalization quotients*

Encephalization once meant only that the cerebral cortex had taken on more functions during the course of evolution, and that coritical organization is more specialized in advanced than in primitive animals. A more recently developed meaning given to encephalization is purely quantitative—the encephalization quotient, or EQ. In this latter sense, one is referring to a ratio, where an animal's brain weight is divided by an allometric equation derived from a particular taxon.

The equation below:

$$EQ = \frac{\text{brain weight (grams)}}{0.09908 \times (\text{body weight, grams})^{0.76237}}$$

is an example where the denominator is derived from the allometric equation for 88 species of primates, where the log (base 10) values for brain weights and body weights were regressed together (Martin 1983). In this example, using an average brain weight for *Homo sapiens* of 1330 grams, and a body weight of 65 000 grams, tne EQ is 2.87. The chimpanzee and gorilla values, respectively, would be 1.14, and 0.75. If the allometric equation for basal insectivores is used (*per* Stephan *et al.* 1970), the human, chimpanzee, and gorilla values would be 28.8, 11.3, and 6.67 respectively.[5]

Two important points emerge from EQ studies: first, the human animal always has the highest EQ whatever denominator value (or allometric equation) is used. Secondly, the EQ values and their relative values for different species can vary by as much as 20 per cent, and Spearman rank-ordering between species can vary, i.e., the correlations are less than perfect. In other words, there is a definite 'relativity' to relative brain sizes, depending on the taxonomic groups used to

generate the denominator (see Holloway and Post (1982) for other examples of this phenomenon).

It is important to underline the fact that when this quantitative approach is used with fossil hominids, the relative closeness to modern *Homo* or other primates (such as the chimpanzee or gorilla) will vary considerably depending on the equation chosen. There is no consensus at present regarding which equations to use—all vertebrates (Jerison 1973), all mammals, all primates, all basal insectivores (Stephan *et al.* 1970, 1981), the Anthropoidea, or the Pongidae (see also Martin 1983 for discussion).

One way around this dilemma is simply to take a '*Homo*centric' approach (since we humans have the highest EQ) and measure other animals' EQs to a standard in which the EQ for modern *Homo sapiens* is regarded as 1.0 or 100 per cent. This is achieved by using the average brain and body weight for the species as one point, and the 'origin' (i.e., 0 brain weight and 0 body weight) as the other point. The denominator then becomes body weight raised to the 0.64906 power, with a constant of 1.0. The advantage of this equation is that all other animal EQs are expressed directly as a percentage of *Homo*. In this case, the chimpanzee is 0.39, and the gorilla, 0.23. The disadvantage, of course, is that this approach is blatantly '*Homo*centric', and thus something of a matter of taste; but then again, so are all other EQ equations, and the purpose is almost always a comparison between ourselves and other animals.

Holloway and Post (1982) provided ten empirical allometric equations and some 20 examples of australopithecine brain and body-weight combinations (from low to heavy) and the resulting EQs, and compared these to modern *Homo* and *Pan*. High brain and low body weights for fossil hominids naturally provide higher EQs as a percentage of modern *Homo*, as compared to *Pan*, but the percentage can vary from about 40 per cent to 50–65 per cent of the modern *Homo* value *depending on the basal equation used*. Obviously, the evolutionary implications for early hominid brain evolution, and the interpretations of these, will vary considerably depending upon the provisional EQ established. All of this assumes, moreover, that we possess accurate estimates of the body weights of our fossil ancestors. This, again, is dubious and highly controversial (see for example McHenry 1975, 1982, 1988, who, however, continues to ignore the relative nature of these EQs). More solid data regarding fossil hominid brain and body weights (see McHenry 1992 for more recent estimates of body weights) and some consensus regarding the most appropriate allometric equations to be used in generating EQ scores are needed before any clear conclusions can be drawn.

4.4.2 *Organization of the brain*

As a palaeoneurologist, I look for *three indications* of brain reorganization. First, can one find a reduction in the relative amount of primary visual striate cortex, usually delimited anteriorally by the *lunate sulcus*? Secondly, can one 'make a case' for the third inferior frontal convolution's being human rather than ape-like? Thirdly, does the endocast show evidence of cortical asymmetries that follow the well-known right-frontal, left-occipital torsion petalial patterns (to be discussed below) described by LeMay and her colleagues (LeMay 1976, 1985; LeMay *et al.* 1982)? As the literature and following discussion will attest, the first two questions are highly controversial.

4.4.2.1 *Relative increase in parietal lobe association cortex*

The position of the lunate sulcus is one feature that is very different between ape and human brains (see Fig. 4.5, p. 84). All apes show the lunate sulcus in a relatively forward position; in humans, the position is much more posterior, if it occurs at all (see G. E. Smith 1904*a,b*; Levin 1937; Connolly 1950; Holloway 1983*b*, *c*). The importance of this fact is as follows: the lunate sulcus in apes is the anterior boundary of primary visual striate cortex, and the posterior boundary of parietal lobe 'association cortex', where major cross-modality integration is performed (see for example Geschwind 1965). (I am referring here to the role of posterior parietal cortex in mediating perceptions of spatial relationships among objects and places, as well as the cross-modal aspects made clear in Geschwind's famous 1965 papers on 'disconnection syndromes', which he claimed were an important foundation for human language). In humans, part of the posterior parietal cortex includes Wernicke's area, an important receptive and integrative zone for decoding and understanding speech. To state the fact that the amount of primary visual striate cortex is relatively reduced in humans is tantamount to saying that the relative amount of parietal lobe association cortex is larger. The comparative evidence for this is indisputable.

The human animal has roughly 121 per cent *less* primary visual striate cortex than would be expected for a primate of its brain size (as calculated from the data of Stephan *et al.* 1981).[6] Thus the correct identification of the lunate sulcus as an anatomical landmark on early hominid endocasts is an essential first step toward discerning any cortical reorganization in early hominid evolution. Consequently, if a hominid endocast (such as that of the Taung or Hadar A.L. 162–28 specimens) were to show the lunate sulcus to

be in a posterior position, it would be indicative of some cortical reorganization toward a more human-like pattern as having taken place early in hominid evolution, whatever the size of the brain. Conversely, if the lunate sulcus appears in a relatively anterior pongid-like position, one can infer that cortical reorganization of this area was not present during early hominid evolution: that is, early hominids, such as australopithecines, would be seen as having retained a primitive pongid-like cortical organization of this area of the brain. Obviously, these two alternative possibilities will have an important bearing on how one interprets the behavioural capacities of early hominids and their possible mosaic evolution.

There are two endocast portions that play a predominant role in the discussion of these questions. These are, first, that from the famous Taung specimen, named *Australopithecus africans* and described by Dart in 1925 and 1953 (and by Broom and Schepers 1946; cf. Connolly 1950); and, second, that from the more recently discovered Hadar (Ethiopia) A.L. 162–28 specimen of *Australopithecus afarensis*, the latter appearing to date from between 3.0 and 3.3 million years ago.[7]

My own interpretation (Holloway 1969*a*, 1972*a*, 1975*a,b*, 1981*b,c*, 1983*c*, 1984, 1985*a*, 1992, in press *a*; Holloway and Kimbel 1986; Holloway and Shapiro 1992) of these is that while early hominid brains were small, and within ape-sized limits, the organization of the cerebral cortex had already altered toward a more human-like pattern, in that there was a relative increase in posterior parietal 'association' cortex, and a relative reduction of primary visual sensory cortex. Falk's (1980*b*, 1983*a,b*, 1985*a,b*, 1986) position is that this reorganizational change is not present in these australopithecines. Tobias (1987, 1991) does not take a position, except to agree with me that one cannot demonstrate where the lunate sulcus is, but only show where it is not—a position I have long made public in my articles (in particular, see Holloway 1985*a* for a historical review of this matter).

The Hadar AL 162–28 *Australopithecus afarensis* endocast supports further comment, since the posterior end of the intraparietal sulcus is in a posterior position when the endocast is correctly oriented (cf. Falk 1986). Most recently, Holloway and Shapiro (1992) have shown that the squamous suture on all hominids has a relatively high arching pattern compared with that of all pongids. The remnant of the squamous suture on the AL 162–28 cranial fragment shows an arched configuration (Kimbel *et al.* 1982), well above the cranial landmark, the asterion, when the cranial fragment is approximated to a *norma lateralis* orientation. In addition, and most importantly, the distance from the occipital pole to the posterior end of the intraparietal sulcus (Falk and I apparently agree on this landmark) is one half (*c.*0.5) the distance on chimpanzee brain casts, which are usually *smaller* than the endocranial capacity of AL 162–28 (Holloway 1983*b*; Holloway 1988*b*; Holloway 1995; Holloway and Kimbel 1986). If there was a lunate sulcus at the position where the posterior part of the intraparietal sulcus was, then it was in a very un-pongid-like position, suggesting that by this early phase in hominid evolution there had already been significant cerebral reorganization, providing an expansion of the posterior parietal cerebral cortex beyond that of apes *prior* to any major expansion of the brain.

Unquestionably, this controversy is far from finished (in particular see Armstrong *et al.* 1991, who have not used the above measurements, and Holloway 1992); but the goals of testable hypotheses still remain well worth the effort, despite the sometimes acrimonious discussions. Needless to say, only more discoveries of better-preserved and more complete crania of early hominids are likely to settle this issue. Finally, in this palaeoneurological context, it is important that more investigators study these specimens (both fossil and extant) and come forth with new suggestions and hypotheses capable of quantitative testing to take us out of the present situation, where there are so few scientists studying these problems within the context of palaeoneurology.

Finally, it is necessary to point out that hominid endocasts subsequent to those known as australopithecine, such as those of *Homo habilis* and *Homo erectus* and late Neanderthalspecimens, are unhappily devoid of clear convolutional details, thus making it impossible to be certain about possible reorganizational changes within our own genus.

4.4.2.2 *A more human-like third inferior frontal convolution*

As for the frontal lobe and a Broca's area, none of the australopithecine endocasts show enough morphological convolutional relief to be satisfactory, despite Falk's (1980*b*, 1983*a*) claims of a pongid-like frontoorbital sulcus in Taung. The specimens in question are either damaged in these regions, retain matrix, or have the area missing (for example Taung, STS 60, STS 5). None of the adult Hadar *Australopithecus afarensis* specimens have the anterior portions available.

The exception to this state of affairs is the famous KNM-ER 1470 habiline (see Fig. 4.8), with a cranial capacity of 752 ml and dating at *c.*1.9 million years ago.

The ER 1470 endocast does indicate a somewhat more complex and modern-human-like third inferior frontal convolution containing Broca's area related to motor control of vocalization (Holloway 1976*a*,

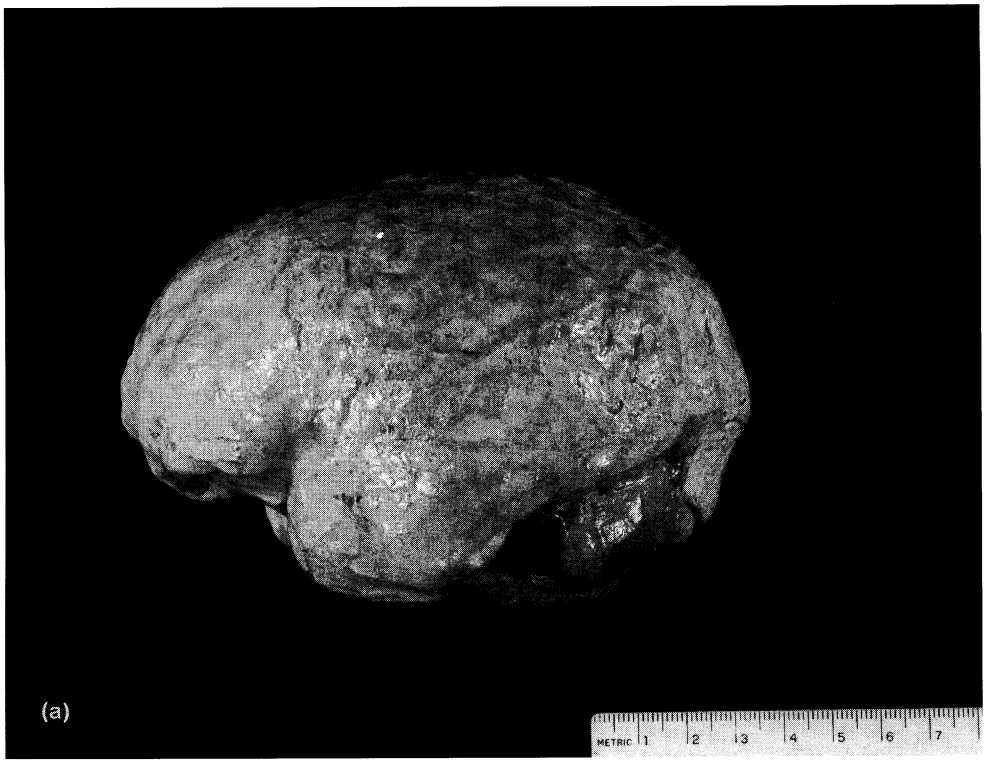
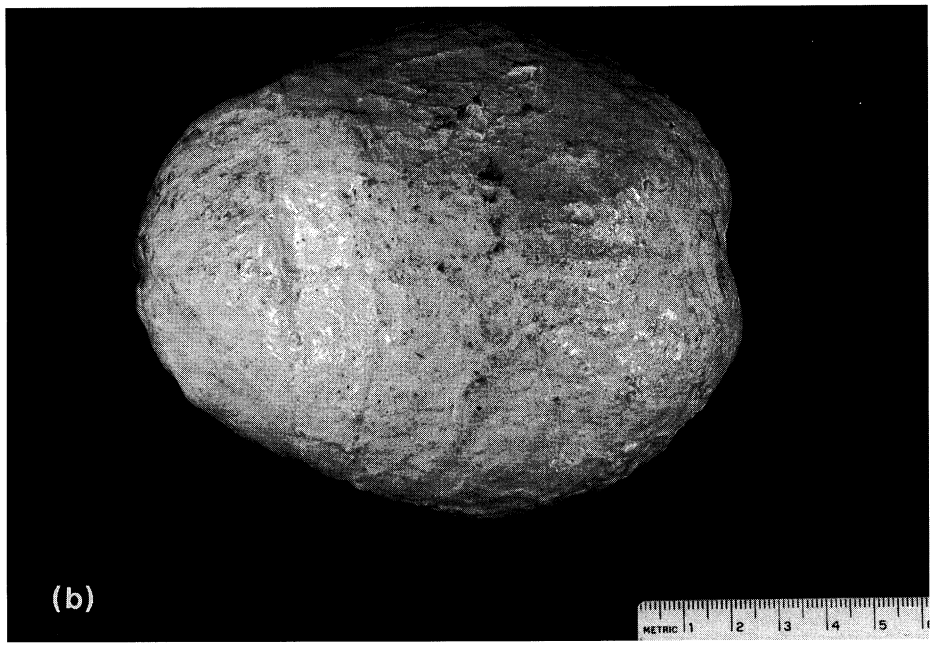


Fig. 4.8 Endocast of KNM-ER 1470.
(a) left lateral view. The third inferior frontal convolution, or Broca's area, appears *Homo*-like.



(b) dorsal view, showing typical *Homo* right-handed petalial pattern of a protruding left occipital lobe and a wider right frontal lobe.

1983*b*; Falk 1983*b*). Unfortunately, the posterior parietal region, the anterior occipital zone, and the superior portion of the temporal lobe of fossil endocasts do not provide enough cortical details to prove that a human-like receptive and associative Wernicke's region was present at that time, nor can one assess the position of the lunate sulcus, if indeed there was one.

In the chimpanzee the inferior prefrontal portion of the frontal lobe is structurally homologous to Broca's region in living *humans*, at least cytoarchitectonically, although the degree of macroscopic convolutedness is not as great, and one cannot really parcellate the *Pan* region into strict *Homo* homologues. The same applies to Wernicke's area, although in this case it is not really clear whether the cytoarchitectonic evidence proves homology. As for functions, fortunately no ablation research has been (or is) being published which can bear on the problems of functional homology between *Pan* and *Homo*, and one can only hope that this situation remains the same. Radical neurosurgery on chimpanzees, simply to see if their motoric vocalization (Broca's) suffers or their receptive understanding of sounds (Wernicke's) diminishes, as it does in aphasic humans, would be criminal. It seems safest to conclude that while the human precursors for such specialized tissue may be nascent in *Pan*, they are fully evolved in living *Homo*, and would appear to be present in *Homo habilis*, at about 2.0 million years ago, judging by ER 1470.

Recently, Tobias (1987) has claimed that language began with *Homo habilis*, an opinion based mainly on the ER 1470 endocast that I originally prepared in Nairobi in the mid-1970s. As Leakey (1981) and Leakey and Lewin (1977) indicated, I was then of the opinion that the endocast showed a human third inferior frontal convolution, with a good example of Broca's area (see also Holloway 1976*a*). I believe Tobias is correct, but this is hardly a new position.[8]

Unfortunately, later hominid endocasts from *H. habilis* to the present seldom show the sulcal and gyral patterns faithfully. It thus becomes impossible to test whether or not there had been further cortical reorganization from *H. habilis* times to the present, for instance in either Broca's or Wernicke's areas.[9]

Broca's and Wernicke's areas are not discrete structures, and are defined better by function than as precise anatomical locations with particular sulcal boundaries. In general, Broca's area in humans includes the third inferior frontal gyrus, including the *pars orbitalis*, *pars triangularis*, and *pars opercularis*. From numerous neurophysiological studies, it is known that this region of the frontal lobe in humans has a close relationship to the motor control of vocalization, and one presumes, to the serialization of motor sequencing. Lesions in this region, particularly on the dominant side (which is the left cerebral cortex in right-handers) often lead to motor aphasia, an inability to articulate language through speech. Wernicke's area is even more difficult to localize in any exact neuroanatomical sense. In general it is in the posterior half of the human brain, behind the sensorimotor cortex, and involves the inferior parietal and superior temporal lobes in the region of the Sylvian fissure. This region appears to be strongly related to receptive functions of speech and language, and lesions in this region (both sides, but it appears more lateralized in males to the left side) produce receptive *aphasias*, an inability to understand spoken and sometimes written language. (These descriptions are oversimplified, and the reader is encouraged to consult a good neuropsychology text—for example Kolb and Whishaw 1985—and Ojemann's (1991) article on the cortical organization of language.)

These two regions can seldom be recognized *unambiguously* on endocasts. Broca's area is somewhat easier to demonstrate than Wernicke's area on endocasts because of the more distinctive human morphology of the third inferior frontal convolution, particularly with its *pars triangularis*. Indeed, the ER 1470 endocast of *Homo habilis* shows a human-like shape and morphology in this region, in contrast to monkeys and apes, which show very little differentiation of this region, as I demonstrated in 1974 to Richard Leakey. Lesions in these zones, however, in both monkeys and apes, can disrupt cognitive processes related to communication. There is some indication that even in macaques (see Dewson 1977) there is some auditory lateralization in what might be roughly analogous to Wernicke's area in humans. Deacon's (1988*a*) paper on language circuits and homologies in the fibre systems in the brain challenges us all to understand what differs neurologically between ourselves and our pongid cousins.

4.4.2.3 *Asymmetries of the brain and laterality*

Observations regarding cerebral hemispheric asymmetries extend back into the nineteenth century, but have only been fully corroborated and certified within the last decade.[10] The topic has an enormous literature and is very complicated, being wholly relevant to handedness, hemispheric specialization, left–right brain differences, sexual dimorphism in the corpus callosum and behaviour, symbolic abilities, linguistics, comparative behaviour, and certainly human brain evolution. The neurological literature is very rich, but the comparative and evolutionary records are not, and, as with any neurologically-based subject, are still controversial.

Basically, there is considerable evidence that differing degrees of cognitive competence exist between the cerebral hemispheres with regard to symbol comprehension and manipulation (left hemisphere in the overwhelming majority of right-handers) and visuospatial integration and emotional appreciation of context (right hemisphere) (see especially Witelson 1977, 1982, for further commentary). Of particular interest is Scheibel's (1990) finding that neurons in the left Broca's region tend to have more dendritic branching than on the right side.

Asymmetries in brain structures are *not* limited to the human animal. Asymmetries have been found in chimpanzees (Yeni-Komshian and Benson 1976), monkeys (Dewson 1977; Falk 1978; Falk *et al.* 1986; Heilbroner and Holloway 1988, 1989), and rats, fish, and amphibians (Denneberg 1981; Diamond *et al.* 1981), and have been beautifully demonstrated in certain bird species (see for example Nottebohm 1977). Other anthropologically-oriented investigators such as Marshack (1976) and Jaynes (1976) have relied upon some of the above neurological literature to discuss aspects of human brain and cultural evolution, taking the point of view that true human symbolic behaviour did not emerge until hemispheric specialization took place, or until one has examples of explicit symbolic depictions, such as in cave art, or inscribed artefacts. The fossil hominid endocasts clearly show the kind of asymmetry associated with hemispheric specialization, but are not archeologically associated with any art.

While cerebral (and subcortical) asymmetries appear widespread throughout the animal kingdom, it remains a possibility that the patterns of asymmetries and their quantitative extent could differ in important ways between different species or taxonomic levels. Certainly, handedness, the ability to throw objects with force and accuracy (Holloway 1976*a*, *b*, 1983*a*; see W. H. Hall 1983 and Calvin 1983 for a much more expanded analysis), and systematic tool-making in standardized stylistic forms, as well as the use of arbitrary symbol systems, do appear confined to the human species. Further comparative work with different primate species could well upset this notion. At present, however, there is no reliable evidence for any of these behavioural patterns in other species.

It was really the work of LeMay (1976; see also LeMay *et al.* 1982 and LeMay 1985 for more extensive citations and recent findings) on petalias (asymmetrical projections of occipital and frontal cortex, anterior and posterior, as well as laterally) that opened up the possibility of establishing relationships between external cortical morphology and handedness, and trying to find such patterns in different species and in the fossil record. Basically, right-handers show a left-occipital petalia combined with a torsional right-frontal petalia, while mixed- and left-handers tend to show the opposite configuration. Such asymmetries were shown by LeMay and her colleagues to be strongly correlated with handedness. (The correlations are strong but not 100 per cent, which is why LeMay and her colleagues have emphasized that such petalial configurations are *not totally obligatory*.)

Brain endocasts of apes have been studied for petalial configurations and asymmetries. LeMay *et al.* (1982) and LeMay (1985) continue to find petalial asymmetries in pongids based on fairly small sample sizes, with the gorilla showing the strongest degree of petalial differences between right and left occipital lobes. Holloway and de Lacoste-Lareymondie (1982) studied some 190 endocasts, with chimpanzee and gorilla species numbering roughly 40 each. In general, we found, on the basis of *ordinal* observations, that (1) asymmetries were clearly present in pongids, most strongly in the gorilla; but (2) the combination of left-occipital/right-frontal petalias was fairly rare in pongids, including the gorilla; yet (3) strong in modern humans, and certainly present in early *Homo*. LeMay *et al.* (1982), LeMay (1985), and Geschwind (1984) conclude that pongids show asymmetries in the same direction as *Homo*. Our study suggests that while asymmetries certainly exist in pongids, neither the pattern nor direction is anywhere near as strong as in *Homo*.

It remains, therefore, an intriguing possibility that cerebral cortical asymmetries have evolved independently in several primate species, or are part of a common evolutionary heritage, but are more pronounced in hominids, and particularly modern humans, although weaker asymmetries appear presaged in the earlier and later australopithecines (Holloway 1976*a*, 1983*b*; Holloway and de Lacoste-Lareymondie 1982). The KNM-ER 1470 early *Homo* specimen shows a very strong left-occipital and right-frontal petalial pattern (Holloway and de Lacoste-Lareymondie 1982). In the light of Toth's (1985) marginal evidence for right-handedness based on stone-tool analyses, this correlation provides a tantalizing glimpse offering both a structural and a functional synthesis between some of the palaeoneurological, modern neurobiological, and archaeological lines of evidence. Obviously, such interpretations, which try to link handedness, stone-tool-making, and endocasts, not to say language, together, are highly speculative.[11] Once again, correlations are *not proof* of causal connections, and it would be healthy to remain sceptical of such interpretations. Nevertheless, this is one set of findings, which, with further research, might prove promising in coming to a better understanding of how

and when the human brain and its associated behavioural elements evolved.

Thus another morphological aspect, asymmetry between left and right hemispheres, becomes an important focus in studying the human brain. While this question is still being studied, Holloway and de Lacoste-Lareymondie (1982) have suggested that the degree of asymmetry may increase with later hominids—i.e., those later than *H. habilis*, although it is not clear whether the greater amount of asymmetry, which favours the left hemisphere and current models of right-handedness, could be explained allometrically. Other descriptions of some of the fossil hominid endocasts may be found in Holloway 1983*c*.

In the early Pleistocene East African *Homo erectus* specimens, KNM-ER 3733 and ER 3883, the internal table of bone has been damaged, but each shows a pattern of cerebral asymmetry suggestive of right-handedness, i.e., with left-occipital and right-frontal endocast petalias. The degree of these asymmetries is somewhat less strong than in ER 1470, but certainly within the modern *Homo* range. Both *Homo erectus* and fossil *H. sapiens* have hemispheric asymmetries well within the range of variation for living *Homo sapiens*. Indeed, some of the Upper Palaeolithic specimens of *H. sapiens*, such as Predmostí, show petalial asymmetries at the stronger end of the human distribution, while *Homo erectus* would be at the weaker end. This suggests some possible evolutionary change of *degree* in brain organization between *Homo erectus* and *Homo sapiens sapiens*, although the very small sample sizes of such specimens preclude proof of this assertion.

The australopithecine evidence is very scanty given its fragmentary preservation, seldom of both sides in the same individual. The SK 1585 endocast (Holloway 1972*b*) does show considerable asymmetry of the occipital petalias, suggesting a right-handed pattern. Earlier australopithecine endocasts that possibly led to the robust line show very small asymmetries, if any (Holloway 1988*b*).

4.4.2.4 *Towards a synthesis*

Tables 4.2, 4.3, and 4.4 provide a synthesis between the direct evidence of brain endocasts and the reorganizational and size changes that occurred during the evolution of the hominid brain.

There are four major reorganizational changes that have occurred during hominid brain evolution, viz.: (1) reduction of the relative volume of primary visual striate cortex area, with a concomitant relative increase in the volume of posterior parietal cortex, which in humans contains Wernicke's area; (2) reorganization of the frontal lobe, mainly involving the third inferior frontal convolution, which in humans contains Broca's area; (3) the development of strong cerebral asymmetries of a torsional pattern consistent with human right-handedness (left-occipital and right-frontal in conjunction); and (4) refinements in cortical organization to a modern human pattern, most probably involving tertiary convolutions. (This last 'reorganization' is inferred; in fact, there is no direct palaeoneurological evidence for it.)

Integrated with the first three reorganizations are no less than five episodes of brain-size change, all positive except for the last (present?) episode. These changes in size have been regarded as either allometric or not, the criterion being whether or not there has been a significant increase in body size. This is a judgemental process, and these judgements could prove erroneous in reality. For example, the brain-size increase from *A. afarensis* to *A. africanus* is judged to be small, on the basis of only three fragmentary *A. afarensis* endocasts, all of which have required considerable reconstruction, and on little in the way of postcranial remains, in a situation in which sexual dimorphism in body size is likely to have been very high in *A. afarensis*. The increase could of course be a statistical artefact; but it could also be a combination of allometric and non-allometric increments. The fossil record simply does not allow any finer-grained analysis as yet.

Similarly, the increase from *A. africanus* to *Homo habilis* opens the thorny issue of *which* specimens are habiline! Are OH 24, OH 13, OH 16, and OH 7 habilines, or a more advanced species of *Australopithecus*? I frankly do not know; but in this proposed scheme I mean by *Homo habilis* something akin to ER 1470 or OH 7. Depending on which one chooses, the brain-size increase will be differently proportioned between allometric and non-allometric increases.

These details will only emerge with more specimens of a less fragmentary nature. Still, despite these and other problems, I suggest that the evolution of the hominid brain has been a reticulated process of reorganizational and phasic allometric and non-allometric increases in brain size, and that it is highly unlikely that these processes were independent. At least two forms of dependence are likely: (1) reorganization and size-increase could involve each other—i.e., as reorganization of the brain occurs, so does an overall size-increase (see Armstrong *et al.* 1991 and my critique, Holloway 1992); and (2) an increase in size could alter succeeding selection pressures for reorganization and vice versa. I think it is foolhardy to suggest that all selection pressures were of a constant (for example, brain-size and intelligence) nature. Why should the brain-size increase between *A. africanus* and early *Homo* be for the same reasons or involve exactly the same selection pressures as between *Homo*

Table 4.2 Reorganizational changes in the evolution of the human brain (Holloway 1995)

Brain changes (*Reorganization*)	Taxa	Time (m.y.a.)	Evidence
(1) Reduction of primary visual striate cortex (area 17); and relative increase in posterior parietal cortex	*A. afarensis*	3.5 to 3.0	AL 162–28 brain endocast
(2) Reorganization of frontal lobe (third inferior frontal convolution, Broca's area)	*Homo habilis*	2.0 to 1.8	KNM-ER 1470 endocast
(3) Cerebral asymmetries, left occipital, right frontal petalias	? *Homo habilis*	2.0 to 1.8	KNM-ER 1470 endocast
(4) Refinements in cortical organization to a modern *Homo* pattern	? *Homo erectus* to Present ?	1.5 to 0.10	*Homo* endocasts (*erectus, neanderthalensis, sapiens*)

Table 4.3 Brain-size change in human evolution (Holloway 1995)

Brain changes (brain-size related)	Taxa	Time (m.y.a.)	Evidence
(1) Small increase, allometric*	*A. afarensis to A. africanus*	3.0 to 2.5	Brain endocasts increase from 400 ml to 450 ml.
(2) Major increase, rapid, both allometric and non-allometric	*A. africanus to Homo habilis*	2.5 to 1.8	KNM-1470, 752 ml (*c.*300 ml)
(3) Modest allometric increase in brain size to 800 ml–1000 ml (assumes *habilis* is KNM-ER 1470-like)	*Homo habilis to Homo erectus*	1.8 to 0.5	*Homo erectus* brain endocasts and postcranial bones, e.g., KNM-ER 17000
(4) Gradual and modest size increase to archaic *Homo sapiens*, non-allometric	*Homo erectus to Homo sapiens neanderthalensis*	0.5 to 0.075	Archaic *Homo* and Neanderthal endocasts 1200 to 1700– ml
(5) Small reduction in brain size among modern *Homo sapiens*	*Homo s. sapiens*	0.015 to the present	Modern endocranial capacities

* *Note*: Allometric means related to body-size increase.

Table 4.4 Major cortical regions in early hominid evolution

Cortical regions	Brodmann areas	Functions
posterior occipital striate cortex	17	primary visual
posterior parietal and anterior occipital (peri-and parastriate cortex)	18, 19	secondary and tertiary visual; integration with area 17
posterior parietal, superior lobule	5, 7	secondary somatosensory
posterior parietal, inferior lobule (mostly right-side. Left-side processes symbolic–analytical)	39	angular gyrus: perception of spatial relations among objects
posterior parietal, inferior lobule (mostly right-side. See above)	40	supramarginal gyrus: spatial ability
posterior superior temporal cortex	22	Wernicke's area, posterior superior temporal gyrus: comprehension of language
posterior inferior temporal	37	polymodal integration, visual, auditory; perception and memory of objects' qualities
anterior prefrontal cortex	44, 45 (also 8, 9, 10, 46)	Broca's area: motor control of vocalization, language

habilis and *Homo erectus*? In my 1980 paper on within-species variation I questioned the need for a homogeneous explanation for all brain-size increases, and suggested instead that the brain could have increased in size for different reasons at different times. I see no reason to withdraw that suggestion.

Thus this reticulated process is hypothesized not to have involved constant selection pressures for some general 'intelligence' except at particular times; and it is doubtful that these could ever be reconstructed from the fossil and archaeological records.

Finally, as Table 4.4 indicates, a major portion of the reorganizational changes involved posterior parietal and anterior occipital cortex. In humans these regions (Brodmann's 18, 19, 5, 7, 39, 40) are mostly involved with visuo-spatial relationships, while the adjacent area 22, mostly Wernicke's area, is involved with comprehension of communication (language), whereas area 37, the inferior temporal cortex, is involved with polymodal integration and the perception of, and memory of, an object's qualities. In particular, see Holloway (1995).

Each of these are rather specific kinds of intelligence that integrate to become a major adaptive mode for humans: expanding the world in which we live and the materials we utilize to secure an existence in which to reproduce and evolve. If there is one common denominator in all of these complexities, it is (for me, at least) that all relate to social behaviour: hence my insistence over the years that our brains are the product of varying selection pressures for different aspects of social behaviour, of which, incidentally, tool-making is but one small portion, albeit the greatest from the standpoint of the archaeological evidence (Holloway 1981*a*). At this point, perhaps it will now become evident why there is an Appendix I on the sexual dimorphism of the corpus callosum. This structure, after all, particularly in its posterior or splenial portion, is the structure that unites the two posterior parietal cerebral cortices, left and right. I believe that the sexual dimorphism to be described is the result of natural selection's operating to maximize a complemental strategy of male and female behaviours supporting offspring that remain immature for longer periods of time, and thus dependent on a complemental social order requiring some gender based differentiation of behavioural and economic roles. I am not so sure that this differentiation is particularly adaptive now . . .

4.5 Conclusion

It is difficult not to admire that Gallic opinion that once relegated such discussions as that on the origins of human language to non-scientific audiences as totally untestable, and proscribed them from open discussion in scholarly gatherings during the nineteenth century. Thus I prefer to take the position that while there is no palaeoneurological evidence that can prove the presence or absence of speech and the use of a symbol system, certain combinations of evidence do increase the probability that either signed or spoken proto-language was an early hominid invention, based on changes in the evolution of the brain from some more primitive hominoid precursor. I doubt that language was present in the australopithecines, but I do believe their brains were organized differently from like-sized ape brains in important ways that relate to visuo-spatial integration and communication, and that they were more social-behaviourally adapted toward a human direction than are the present living apes. I certainly believe that some form of primitive language was present in early *Homo*, and that stone tools made to standardized patterns are the best chances we have of learning about early hominid cognitive behaviour.

To me social behaviour and its evolution was of considerable importance in the evolution of the human brain, and vice versa. For me the two cannot be dissociated from each other, as I have tried to explain in previous publications (for example 1964, 1967, 1970, 1972*a*, 1975*a*, *b*, 1981*a*, 1983*b*, in press *a*). This is, of course, a perspective which weights social behaviours as prime interactive agents in human brain evolution somewhat more heavily than other explanations, such as bipedalism, hunting and/or gathering *per se*, or tool-using and making.[12] I specifically *do not* mean that these were unimportant factors contributing to the totality of pressures which eventually shaped human brains. Rather, our humanness resides mostly in our brains, endowed with symbolic abilities, which have permitted the human animal extraordinary degrees of control over its adaptive powers in both the social and material realms. Conceivably, these powers may eventually themselves become powerless to undo many of the human-generated conditions that terrify us all. Given the resurgence of 'ethnic cleansing' (Bosnia), the killing fields of Cambodia, the omnipresent anti-Semitism and xenophobia (to mention but a few horrors), and all the disastrous environmental waste and destruction still manifested by human-kind, despite the grim lessons of the Second World War and more than ample evidence regarding ecology, I feel rather pessimistic about the future of human evolution. These things are products of human brains and social structures *in concert*. More optimistically perhaps, it is also conceivable that a better understanding of how we became what we are, and how our brains and

behaviour were shaped during millions of years of evolution, would allow our socially-derived brains to control those very inventions (conceived and designed through the use of symbols) which so threaten ourselves and all other forms of life on this planet. First, we must cope with ourselves . . .

Appendix: Sexual dimorphism and the brain

Associated with the cerebral asymmetries discussed above in Section 4.4.2.3 is growing evidence that the brains of many animals are sexually dimorphic, and that structures other than those related to reproductive functions (for example, the preoptic nucleus of the hypothalamus) *might* also be sexually dimorphic. Sexual dimorphism in brain structures related to reproduction is not surprising when one considers the vast amount of variation in the sexual behaviour and courtship patterns that exists among sexually reproducing animals. Nevertheless, the possibility that the human species *might* evidence inherent sexual dimorphism in their brains that is unrelated to reproduction (see Swaab and Fliers (1985) on the preoptic nucleus), with associated cognitive differences (at least in *degree*) between females and males, is regarded as a heresy in current anthropological (and social-science) circles.

While some nineteenth-century and early twentieth-century neuroanatomists were deeply concerned with the topic, and claimed many differences in cerebral morphology and behavioural functioning (see both Mall 1909 and Papez 1927 for excellent reviews of some of these early works), the topic is extraordinarily controversial. There has been a discernible shift in the last decade that recognizes some dimorphism between male and female brains (beyond brain weight, which is well known, but functionally empty—see for example Holloway 1980), and it has become an almost-respected line of inquiry today, in contrast to the situation just a decade ago, as described for example in McGlone's fine 1980 review. Indeed, an entire volume of *Progress in Brain Research*, edited by DeVries *et al.* (1984) is devoted to the topic.[13]

We have found significant differences in the midline area of the corpus callosum and particularly in the posterior splenial portion of this structure (de Lacoste-Utamsing and Holloway 1982; Holloway and de Lacoste 1986, Holloway *et al.*, 1993.). It is the corpus callosum which interconnects the two cerebral hemispheres, and the splenial portion carries fibres which interconnect the posterior portions of the cerebral cortex, particularly the parietal lobes. Our research indicates that in females the average total area of the corpus callosum is roughly the same or slightly smaller than in males, but not significantly so. Relatively, however, i.e., correcting for brain weights (significantly higher in males), the corpus callosal area is statistically significantly larger in females. The same applies, but more strongly so, to the posterior portion, the splenium, as measured by its dorsal–ventral width. The two early papers (1982, 1986) were on small, but independent samples (n=16 in the latter reference), and we did find that the *absolute* area of the corpus callosum was larger in females, a finding not replicated in a recent study (Holloway *et al.* 1993). These results, on a sample of over 100 brains, roughly equally divided between males and females, show statistically strong differences in the *relative* size of the corpus callosum and the splenium in favour of females. Baack *et al.* (1982) and, recently, de Lacoste *et al.* (1986) have shown that these differences are apparent by the age of 26 weeks prenatal. Papez (1927), in his classic work on the brain of Helen Gardener, found differences in a small sample of males and females; but unfortunately the necessary statistical methods were not used for in-depth analyses of those differences. It must be remembered that these are average relative differences (differences of sample means), and while statistically significant, are based on small sample sizes. There is certainly overlap in the values, both absolute and relative. Only larger samples will be adequate for accurately assessing the degree of overlap. Earlier, Witelson (1985) had argued that her data did not show sex differences; rather, she claimed the difference was related to handedness. Our analysis of her data, however, leaves her finding exciting but doubtful (Holloway and de Lacoste 1986). More recently Witelson suggests that there is a sex difference in the so-called isthmus of the splenium (Witelson 1989).

Since we wrote our replication study (Holloway and de Lacoste 1986) a number of papers have appeared attempting to prove that there is no significant sexual dimorphism in the human corpus callosum (see below). Reviews of this literature may be found in Holloway (1990), Holloway *et al.* (1993), Peters (1988), and Clarke *et al.* (1989). These last authors, while finding partial support for sexual dimorphism in human corpora callosa, have failed to consider brain weight correctly in either their post-mortem (autopsied) samples or those from MRI (Magnetic Resonance Imaging). Unfortunately, at the present time it is not feasible to obtain accurate brain volumes from MRI materials, although de Lacoste (pers. comm.) has found some linear measurements that correlated with brain size to roughly $r = 0.94$.

More recently, some additional support for our original findings has been published by Allen *et al.* (1991) and Steinmetz *et al.* (1992, 1995), particularly

with regard to the splenial portion of the corpus callosum's being larger and more bulbous in females.

It is interesting to consider some of the reports claiming no sexual dimorphism in the corpus callosum. For example, Weber and Weis (1986) used a sample with an average age of 74.7 years, and a male average brain weight of 1029 grams and 890 grams for females. This is a rather high average age, and the brain weights are obviously on the low side, reflecting the known fact that brain weight decreases with age. The standard deviations for the callosal measures were roughly 1/4 the value of the mean, which is very high, and yet the average values for the corpus callosal area and splenium were roughly equal between the two sexes. No attempt was made to correct for brain size, despite the large average difference between male and female brain weights. MRI studies by Bleier *et al.* (1986), Byne *et al.* (1988), Kertesz *et al.* (1987), Oppenheim *et al.* (1987), Weis *et al.* (1988), and Yoshii *et al.* (1986), do *not* provide brain-size data, but find that the values between male and female measurements on the corpus callosum are roughly equal. Demeter *et al.* (1988) claim from autopsied material that there is no significant sexual dimorphism, even though splenial area is identical between males and females while male brain sizes go as high as 1700 cc, and their Fig. 4 (p. 222) shows great dimorphism in brain size, with practically no overlap between 22 males and 12 females. Yet they adamantly dismiss brain size as relevant in their studies!

All of the above papers have ignored the point that my colleague and I attempted to make, which is that *it is the relative size of the corpus callosum and its splenial portion that is dimorphic between human females and males*. In fact, many of these reports suggest that if brain size were correctly taken into account, the relative size of the corpus callosum would be larger in females. (In particular, see Appendix I in Holloway *et al.* 1993) Unfortunately, most of the studies were done using MRI techniques, which do not allow for easy assessment of brain size.

The dimorphism of the corpus callosum *contrasts* remarkably with all other regions of the brain (Holloway *et al.* 1993). For example, if one takes the cerebellum, hippocampus, pulvinar, putamen, pallidum, ventricles, or amygdala and compares their volumes between human males and females, one finds that there is a significant size difference favouring males. If one looks at brain size, there is also a significant difference favouring males. If one then corrects for brain size, the ratios of these structures divided by brain volumes *show no significant differences between males and females*. This pattern is in complete contrast to the corpus callosum, where the female sizes either equal or are larger than in males, and the relative sizes are statistically significantly larger in females.

It is interesting to recall the monumental task that Maccoby and Jacklin (1974) undertook in exposing so much of the current and past psychological literature on sex differences in behaviour related to symbolic and language skills and visuo-spatial integration, exposing sexual biases and poor experimental design. Even so, they were left with an essential core of differences that they believed could not simply be explained away as cultural artefacts. Those 'residua' were repeated findings about 'rough and tumble play', mathematical and visuo-spatial integration, and language (symbolic competence) abilities, in which males on average consistently scored higher in the first two components, and females in the third. Hall's (1984) book, reviewing sex differences in non-verbal behaviour, also found consistent average differences in the same directions. It would appear from the above-mentioned studies on the corpus callosum that a neuroanatomical basis might exist, in so far as these data suggest that males are perhaps on average more lateralized and asymmetrical than females with regard to the posterior part of the cerebral cortex. With regard to the frontal lobe, however, it is possible that females may be on average more lateralized than males for motor control of vocalization, according to recent research published by Kimura (1980, 1983, 1992) and Kimura and Harshman (1984).

Using an experimental technique of measuring sex differences in test responses to visual images, either words or faces, Pollack (1987) has demonstrated that human females score on average fewer errors and with shorter reaction times than males. Her models and tests were based on a callosal model to test our previous anatomical findings (de Lacoste-Utamsing and Holloway 1982). As her samples' sizes were 25 of each gender, and many of the results were statistically significant between the two, male–female differences should be consistently tested cross-culturally.

If such results prove replicable, we must eventually face the questions of whether there is some true causal relationship between brain structure and functioning, and then of how these dimorphic brain differences came about. As these differences in the corpus callosum appear by the age of 26 weeks prenatal, this suggests that purely cultural influences can be ruled out. Furthermore, common sense, as well as everyday experience (not to mention many scientific studies) indicates that *even if* such differences exist, they do not necessarily become biologically-determined fates for individual members of the two genders. With training and equal access to opportunities, whatever inherent differences might exist would appear to be

highly malleable. My interest in this issue, however, is not the present or future, but rather the past evolution of hominid brains and behaviour.

It is my own conviction (Holloway 1983*c*, Holloway 1990, Holloway *et al.* 1993) that these differences are evolutionarily-derived residua, based on past selection pressures for female precocity in neural and behavioural development, and upon a complemental social and cognitive structuring of intellectual and sensorimotor tasks that were related to a stronger degree of sexual division of labour than currently exists. Obviously, *palaeoneurology cannot provide any evidence relating to these speculations*. Given that at some time in past hominid evolution there necessarily occurred an increased period of social and material nurturance of longer-growing offspring with increased dependency times, I believe a complemental behavioural adaptation between males and females was necessary to support such a change successfully. Perhaps the palaeoanthropological record could help in this regard, if it were more complete.[14] In other words, understanding human evolution really requires an analysis that includes the differential cognitive abilities of males and females that complement each other and together enabled the species to be more successful in its social-behavioural adaptations, particularly those associated with the nurturance and education of offspring with prolonged learning periods gained through a delay in maturation. In this model males are regarded as having (on average) superior visuospatial integrative abilities (including orientation in space relative to distant food and water resources), and these would have complemented the female's superior abilities at social communication and the nurturance of children.

I also believe that the sexual dimorphism in the human corpus callosum may be species-specific, as there appears to be no solid evidence from prosimians and monkeys (either Old or New World) of any dimorphism in this structure (Heilbronet and Holloway 1989). An earlier report by de Lacoste and Woodward (1988) regarding a dimorphism in the Great Apes is based on averaging small numbers of each sex, and needs replication, particularly on a large sample of chimpanzees. These data are, for the time being, almost impossible to get.

Notes

1. Most neurobiologists speak of endocranial volume and brain size as the same things. Brain size, as measured by its volume, is very close to endocranial volume, as the specific gravity of brain tissue is essentially 1.0. Brain *weight*, however, is always somewhat less than brain *volume*, but the difference is seldom more than 10 per cent, which is roughly the amount of the meninges which surround the brain, and which are often included in brain volume. In this chapter, I am taking the liberty, except where noted, of using these terms interchangeably.

2. A case in point is a recent publication by Falk *et al.* (1989), which claims to have traced the sulci on the Taung infant brain endocast, and, by comparing the lengths of the sulci with a formula established by Jerison (1982) based on comparative (adult animals) work by Elias and Schwartz (1969), to conclude that Taung definitely had an ape-like brain. Unfortunately, there are no agreements as to which sulci and gyri are actually on the Taung endocast (see for example Connolly 1950; Holloway 1981*b*, 1983*b*, 1984, 1985*a*, 1988*b*).

3. The majority of palaeoanthropologists would consider specimens KNM-ER 1813 and 1805 to be smaller-brained versions of *Homo habilis*. (Falk (1982) appears to be alone in considering ER 1805 an australopithecine.) But both of these specimens, while relatively complete, are very puzzling to those emphasizing the importance of brain size to taxonomy. It is far from clear whether these are *H. habilis* or perhaps an advanced version of *Australopithecus*, given their relatively small cranial capacities. See Wood (1992) for a recent discussion of these hominids and the possible diversity of species of early *Homo*. (Wood follows Groves (1989) in placing ER 1470 in the species *H. rudolfensis*—[eds])

4. Although it is possible to suggest that as the tool industries become more complex from *H. habilis* to the late Pleistocene, so does the brain, it remains conceptually difficult causally to connect brain-size increase with technological advances solely related to tool-making and use. In essence, the relationship between behavioural and brain complexity (as measured by size) is a correlational, rather than causal one. After all, stone-tool-making is but one subset of the totality of social behaviour.

5. The equations used for the Primates (or indeed, any other taxon) will depend on the number of species used and the values selected to represent brain and body weights. In the example provided above for 88 primate species drawn from the list in Stephan *et al.* (1970) list (see also Bauchot and Stephan 1969), *Homo* was excluded. If *Homo* is included the equation becomes EQ = brain weight (grams) ÷ (0.09 × body weight (grams), exp. 0.77531). The correlation coefficient for the first equation is 0.97062, while for the latter equation it is 0.96863. Whether *Homo* is included or not, the correlation between the $\log_{10}$ of brain weight and $\log_{10}$ body weight is very high. This

example is included to give some idea of how one point out of 88, i.e. *Homo*, can affect the equations. It should be noted that the exponent for the power equation between brain and body weights is of the order of 0.76–0.77, and not the value of 0.66 which Jerison (1973) claimed. Jerison's (1973) formula was not an empirical one based on the actual data for the primates, but rather a perceived 0.66 slope was put through an array of mammalian data (Jerison's 'polygon') to satisfy Jerison's (1973) preconceived notions regarding a 0.66 (2/3) scaling factor. However, some physical anthropologists, such as McHenry (1988) and Tobias (1987), continue to use Jerison's (1973) equation of EQ = brain weight (grams) × 0.12 body weight (grams), exp. 0.66 (see Holloway 1988*a* for additional comments). Given the incorrectness of Jerison's (1973) equation for mammals and for the primates in particular, it is erroneous that Tobias (1971, 1987, 1991) continues to calculate 'extra neurons' from Jerison's equations. As I have indicated elsewhere (Holloway 1966, 1968, 1974), these numbers are fictitious, whether they occur in Jerison (1973) or in Tobias's works. These numbers are calculated from a formula which doubles the exponent of 0.66, and is biased toward higher body weights.

6. This was shown by Holloway (1976*a*, 1979) on four independent samples, confirming Passingham's (1982) and Passingham and Ettlinger's (1973) observations. (Passingham *et al.* (1986) does not provide the percentage deviations of humans from a pongid base-line, and interprets *reorganization* somewhat differently.)

7. The Taung specimen includes a fossil endocast portion. Unfortunately, none of the other natural endocasts of *Australopithecus africanus*, such as STS 60, or the robust australopithecines, such as SK 1585, provide any confirming data, as these portions are either missing, as is the case with STS 60, or not visible, as in SK 1585 (see also Holloway 1972*a*, *b* [eds]). This area is also not visible on the constructed endocast of STS 5 (Ms. Ples.).

8. Tobias's claims regarding a *Homo*-like brain and language functions based on endocasts of *Homo habilis* fossil specimens differ from those of previous authors (for example Holloway or Falk) in being too adamant, and in including fossil specimens which are *extraordinarily incomplete* or *fragmented*, such as OH 16, OH 24, etc. These simply cannot be assigned to any taxon without controversy. Neither are they supporting evidence for strong *Homo*-like petalial asymmetries in purported habilines (*pace* Tobias 1987). OH 16 has been likened to a few bits of bone floating in sea of plaster. To describe petalias on such fragmentary specimens is probably quite erroneous. The OH 7 parietals were found flattened in Bed I at Olduvai Gorge. How one can claim a slightly larger parietal petalia on one side, as does Tobias, is beyond this writer. Additionally, OH 24 was found crushed in five layers before Dr Ron Clarke's excellent reconstructions of the crania. Any petalias found on this specimen are similarly suspect.

9. For example, the degree of replication of convolutions in Neanderthal specimens is simply horrible, making fine-grained statements about mental functioning in these hominids impossible. Still, there is nothing striking about Neanderthal brain casts in comparison to those of more recent *Homo sapiens* (for example, Cro-Magnon) suggesting any significant evolutionary change. (See also Holloway 1985*b*.)

10. For reviews of this literature, and more recent analyses, please refer to Corballis (1983); Damasio and Geschwind (1984); Helige (1983); Strauss *et al.* (1983); Witelson (1982); Young (1983); Kimura (1983); Kimura and Harshman (1984); and Geschwind and Galaburda (1984). More recent papers by some of the above authors may be found in Glick (1985). Kolb and Whishaw (1985) provide an excellent text for introducing the subject, and many of these topics can also be found in Kandel and Schwartz's (1981) textbook.

11. Also along these lines, Frost (1980) has argued that in hominid evolution lateralized representation was an evolutionary consequence of the requirement for asymmetrical employment of the forelimbs in the making and using of tools. The colateralization of language mechanisms was held to be a consequence of the coupling of these to the motoric mechanisms already lateralized at an earlier point in hominid evolution [eds].

12. In particular, the increased postnatal dependency period and the increased duration of growth appear to me as extraordinary evolutionary events, as they appear to imply an energetic shift toward nurturance that would require a more complemental set of behavioural patterns between the sexes. This implies a cohesive and co-operative adaptation within groups. To increase brain size threefold beyond pongid levels must surely have required socially cohesive adaptations.

13. For other reviews of this general topic, see Kimura 1980, 1983; Kimura and Harshman 1984; Kinsbourne 1978; McGlone 1980, with associated peer commentary; Witelson 1982; Arnold and Gorski 1984; J. A. Hall 1984; and Khan and Cataio 1984 for a wealth of references on human sexual dimorphism in general, but particularly the brain; for sexual differentiation of the brain, see Toran-Allerand 1986; Juraska 1986; and Kelly 1981 in Kandel and Schwartz. For a speculative account and an attempted

synthesis with the fossil record and hominid evolution, see Holloway 1983*c*, 1990, and Holloway *et al.*, in press).

14. I think it is worth stressing that considerable caution must be exercised regarding these preliminary findings. No one knows exactly what these dimorphisms mean in the modern context, and there is still much vital ethnographic and anatomical evidence to be collected regarding sexual dimorphism in brain and behaviour. I frankly do not know what the practical significance of such findings is within Western societies. Furthermore, the presence of an anatomical difference need not necessarily prove a functional difference. In this case, however, there is an overwhelming amount of clinical evidence suggesting that these differences in the corpus callosum might form a possible anatomical substrate to help explain such behavioural differences. This, in part, should explain my preference for regarding these differences as evolutionarily derived, and as another example of reorganization of the brain, involving important internal changes without necessarily creating an increase in brain size.

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Editorial appendix I: Endocranial volumes

In addition to the figures given in Table 4.1, there have been numerous published determinations of the endocranial volumes of many of the fossil specimens by a number of workers. Table 4.5 is probably not exhaustive, but lists those we have located. Table 4.6 gives summary statistics of the measures in Table 4.5. Table 4.7 is from Tobias (1987), and samples a different, though occasionally overlapping, population of specimens. Table 4.8*a* and *b*, the former by Holloway, the latter from Tobias (1971*b*), give comparative figures for extant hominoids. Given the material and methods involved in determining these volumes, we can at least conclude that hominid brain capacities have increased in the human evolutionary line, while noting (1) brain–body ratios need to be taken into account (see the discussion of encephalization quotients Section 4.4.1.2 above); (2) extant *Homo sapiens sapiens* figures appear to show smaller capacities than Neanderthals; and (3) exact capacities determined by any one researcher are more informative when viewed in the context of figures generated by several investigators over a period of years [eds].

Table 4.5 Hominid endocranial volumes [eds]

Taxon	Specimen	Country/Region	Endocranial volume (cm^3)	Reference
A. afarensis	AL 162–28	Ethiopia	350–400	Falk (1985)
			*c.*400	Holloway (1983*a*, *b*)
			375–400	Holloway (this chapter)[1]
	AL 333–45	Ethiopia	485–500	Holloway (1983*b*)
			485	Holloway (this chapter)[1]
	AL 333–105[2]	Ethiopia	352[3]	Falk (1985)
			343[3]	Falk (1987)
			310–320	Holloway (this chapter)[1]
			310–320; *c.*400[3]	Holloway (1983*b*)
A. africanus	MLD 1	S.A.	*c.*500	Holloway (1973)
	MLD 37/38	S.A.	435	Holloway (1970, 1973)
			480	Tobias (1971*a*)[4]
	STS 5	S.A.	485	Holloway (1970, 1973, 1981*a*)
			480	Tobias (1971*a*)[4]
	STS 19/58	S.A.	436	Holloway (1970, 1973)
			530	Tobias (1971*a*)[4]
	STS 60	S.A.	428	Holloway (1970, 1973)
			435	Tobias (1971*a*)[4]

Table 4.5 (*Contd.*)

Taxon	Specimen	Country/Region	Endocranial volume (cm^3)	Reference
A. africanus (cont.)	STS 71	S.A.	428	Holloway (1970, 1973)
			480–520	Tobias (1971*a*)[4]
	TAUNG[2]	S.A.	412[3]	Falk (1987)
			405; 440[3]	Holloway (1970)
			500; 540[3]	Tobias (1971*a*)[4]
A. robustus	SK 1585	S.A.	475	C. K. Brain (cited by Tobias 1971*a*)
			530	Holloway (1970, 1973)
A. boisei	OH 5	Tanzania	530	Holloway (1970, 1973)
			522	Holloway (1975)
			530	Tobias (1971*a*)
	L388y-6[2]	Ethiopia	427; 448[3]	Holloway (1981*d*)[5]
	ER 406	Kenya	*c*.510	Holloway (1973)
			525	Holloway (1983*b*)
	ER 407	Kenya	506	Falk and Kasinga (1983)
			510	Holloway (1983*b*)
	ER 732	Kenya	500	Holloway (1973)
	ER 13750	Kenya	450–480	Holloway (1988)
			c.530	Leakey and Walker (1988)
	WT 17000	Kenya	410	Walker *et al.* (1986)[6]
	WT 17400[2]	Kenya	390–400	Holloway (1988)
Homo habilis?	ER 1805	Kenya	582	Holloway (1978)
	ER 1813	Kenya	509	Holloway (1978)
H. habilis	OH 7[2]	Tanzania	687	Holloway (1978)
			700–750	Holloway (1980*a*)
			657;684[3]	Tobias (1971*a*)
			647;674[3]	Tobias (1987, 1991)
			690	Vaisnys *et al.* (1984)
			580–600	Wolpoff (1981)[7]
	OH 13[2]	Tanzania	650	Holloway (1973)
			639;652[3]	Tobias (1971*a*, 1975)
			673[3]	Tobias (1987, 1991)
	OH 16[2]	Tanzania	620;633[3]	Tobias (1971*a*, 1975)
			625;638[3]	Tobias (1987, 1991)
	OH 24	Tanzania	590	Holloway (1973)
			597	Tobias (1975)
	ER 1470	Kenya	752	Holloway (1978)
	ER 1590[2]	Kenya	810	Blumenberg (1985)[8]
H. erectus	ER 3733	Kenya	848	Holloway (1983*b*)
	ER 3883	Kenya	804	Holloway (1983*b*)
	WT 15000[2]	Kenya	880;909[3]	Begun and Walker (1993)
	OH 9	Tanzania	1067	Holloway (1975)
			1000[9]	Tobias (1971*a*)
	OH 12	Tanzania	727	Holloway (1978)
			750	Holloway (1980*a*)
	TRINIL 2 (Pith.I)	Java	940	Holloway (1981*c*)
			953	Holloway (this chapter)
			850	Tobias (1967)
			935	Weinert (cited by Weidenreich 1943)
	SANGIRAN 2 (Pith.II)	Java	815	Boule and Vallois (1957)
			813	Holloway (1981*c*)
			815	Holloway (this chapter)
			775	Weidenreich (1943)
	SANGIRAN 4 (Pith.IV)	Java	908	Holloway (1981*c*)
			900	Holloway (this chapter)
			750	von Koenigswald (1962)
			c.880	Weidenreich (1943)

Table 4.5 (*Contd.*)

Taxon	Specimen	Country/Region	Endocranial volume (cm^3)	Reference
H. erectus (cont.)	SANGIRAN 10 (Pith.V, also Skull 6)	Java	855	Holloway (1981*c*)
			975	Jacob (1966)
			975	von Koenigswald (1962)
	SANGIRAN 12 (Pith.VII)	Java	1059	Holloway (1981*c*)
			915	Tobias (1971*a*)[4]
	SANGIRAN 17 (Pith.VIII)	Java	1004	Holloway (1981*c*)
			1029	Sartono (1971)
	SOLO I (Ngandong)	Java	1143	Dubois (1937)
			1172	Holloway (1980*b*)
			1158	Oppenoorth (1937)
			1035	Weidenreich (1943)
	SOLO V (Ngandong)	Java	1284	Dubois (1937)
			1251	Holloway (1980*b*)
			1316[10]	Oppenoorth (1937)
			1255	Weidenreich (1943)
	SOLO VI (Ngandong)	Java	1087	Dubois (1937)
			1013	Holloway (1980*b*)
			1189[10]	Oppenoorth (1937)
			1040	Schaefer (1963)
			1035	Weidenreich (1943)
	SOLO IX (Ngandong)	Java	1135	Weidenreich (1943)
	SOLO X (Ngandong)	Java	1231	Holloway (1980*b*)
			1055[9]	Weidenreich (1943)
	SOLO XI (Ngandong)	Java	1090	Holloway (1980*b*)
			1095	Schaefer (1963)
			1060	Weidenreich (1943)
	LANTIAN	China	780	Woo (1966)
	ZHOUKOUDIAN II	China	1030	Weidenreich (1943)
	ZHOUKOUDIAN III[2]	China	915	Weidenreich (1943)
	ZHOUKOUDIAN X	China	1225	Weidenreich (1943)
	ZHOUKOUDIAN XI	China	1015	Weidenreich (1943)
	ZHOUKOUDIAN XII	China	1030	Weidenreich (1943)
	SALÉ[11]	Morocco	880	Holloway (1981*b*)
Archaic *H. sapiens*	BROKEN HILL (Kabwe)	Zambia	1280[9]	Day (1986)
			1325	Weidenreich (1943)
	FLORISBAD	S.A.	>1280?	Singer (cited by Beaumont *et al.* 1978)
	SALDANHA	S.A.	1200[9]–1250	Drennan (1953)
	LAETOLI, LH18	Tanzania	1200	Day *et al.* (1980)
	NDUTU	Tanzania	1070–1120	Holloway (pers. comm., cited by Rightmire 1983)
	OMO II	Ethiopia	1430	Day (1972)
			1435± 20	Day (1986)
	ARAGO XXI–XLVII	Europe	1100–1200	Holloway (cited by Day 1986)
	PETRALONA	Europe	1220	Poulianos (cited by Day 1986)
			1230	Protsch (pers. comm. cited by Stringer 1984)
			1190–1210	Stringer *et al.* (1979)
	STEINHEIM	Europe	1150–1175	Howell (1960)
			1070	Weinert (cited by Day 1986)
	SWANSCOMBE	Europe	1250–1300	Howell (1960)
			1325	Swanscombe Committee (cited by Day 1986)
	VÉRTESSZÖLLÖS II	Europe	± 1300	Thoma (1981)
			1115–1437	Wolpoff (1977)
	DALI	China	1120	Wu (1981)
			1200	Wu (pers. comm., cited by Day 1986)

Table 4.5 (*Contd.*)

Taxon	Specimen	Country/Region	Endocranial volume (cm^3)	Reference
H. sapiens neanderthalensis	LA CHAPELLE	Europe	1626	Boule (cited by Holloway 1981*b*)[12]
	LA FERRASSIE I	Europe	1689	Heim (1976)
			1641	Boule (cited by Holloway 1981*b*)[12]
	LA QUINA 5	Europe	1350	Boule (cited by Holloway 1981*b*)[12]
	LE MOUSTIER	Europe	1565	Olivier and Tissier (1975)
	MONTE CIRCEO I	Europe	1550	Olivier and Tissier (1975)
	NEANDERTAL	Europe	1525	Boule (cited by Holloway 1981*b*)[12]
	SACCOPASTORE I	Europe	1245	Olivier and Tissier (1975)
	SPY I	Europe	1305	Holloway (1981*b*)
	SPY II	Europe	1553	Holloway (1981*b*)
	AMUD I	Near East	1740	Ogawa *et al.* (1970)
	SHANIDAR I	Near East	1600	Stewart (1977)
	TABŪNIN I	Near East	1271	McCown and Keith (1939)
	JEBEL IRHOUD 1[13]	Morocco	1305	Holloway (1981*b*)
	JEBEL IRHOUD 2[13]	Morocco	1450	Olivier and Tissier (1975)
Early *H. sapiens sapiens*	JEBEL QAFZEH VI	Near East	1568[10]	Vallois and Vandermeersch (cited by Day 1986)Early *H. sapiens*
	SKHŪL I[2]	Near East	1150;1450[3]	McCown and Keith (1939)
	SKHŪL IV	Near East	1554[9]	McCown and Keith (1939)
	SKHŪL V	Near East	1450–1518	McCown and Keith (1939)
	SKHŪL IX	Near East	1587	McCown and Keith (1939)

[1] Provisional estimates from current research, see Table 4.1, in this chapter.

[2] Immature individual.

[3] Estimated adult volume from immature individual.

[4] These values from Tobias (1971*a*) are based on published figures of earlier authors.

[5] Holloway (1981*d*) has questioned the assignment of this specimen to *A. boisei.*

[6] WT 17000 has been reassigned by some authors to *A. aethiopicus* (e.g. Kimbel *et al.* 1988).

[7] See Tobias (1991) for critical notes on Wolpoff's methods.

[8] Blumenberg's (1985) value seems to be his own guesstimate. Specimen ER 1590, which is approximately the same stratigraphic age as ER 1470, is probably somewhat larger in cranial capacity, although given the incompleteness of the fragments a reliable endocranial capacity cannot be calculated (Holloway, pers. comm.). Also note that both ER 1470 and ER 1590 have been reclassified as *H. rudolfensis* by Groves (1989) and Wood (1992).

[9] Olivier and Tissier's (1975) morphometric analysis questions a quantity this low for this specimen.

[10] Olivier and Tissier's (1975) morphometric analysis questions a quantity this high for this specimen.

[11] The Salé specimen may be an early Archaic *Homo sapiens* (Hublin 1985).

[12] Volume estimate confirmed by Holloway, this chapter, Table 4.1.

[13] The Jebel Irhoud specimens should probably not be assigned to the Neanderthal clade (see references in Day 1986).

Table 4.6 Hominid Endocranial Volumes: Summary [eds]

Taxon	Specimen notes	*n*	Adult cranial volume estimates (range, cm^3)
Australopithecus afarensis	All are incomplete specimens requiring extensive reconstructions. Falk (1988) believes that the high value for AL 333–45 will decrease significantly once the frontal part of the endocast is reconstructed on the basis of new information gained from the endocast of WT 17000.	3	*c.*343 to 485
A. africanus	The range cited here is based on the most reliable estimates (see notes in Holloway 1975 and this chapter, Table 4.1). Falk (1987) gives a new adult estimate for Taung that would lower the range to 412.	3	428 to 485
A. aethiopicus sensu auctt.	Only one skull is available (WT 17000). The reconstructed endocast is pictured in Leakey and Walker (1988).	1	410
A. robustus	Only the estimated values for one specimen are available (SK 1585, a partial fossil endocast; see Tobias 1971*a*). The estimate cited here is considered to be reliable (see discussion in Holloway 1975).	1	530
A. boisei	There are three specimens with what are considered to be reliable estimates (see Holloway 1975, and this chapter, Table 4.1). Note that the value of 522 for OH 5 is taken from Holloway 1975.	3	500 to 522
Homo habilis sensu stricto	This range is based on the Olduvai specimens, all of which required extensive reconstructions (see notes in Holloway 1978, 1980*a*, and Tobias 1991). (If, following Wood 1992, we added ER 1813 to the *H. habilis* hypodigm then the observed range would be lowered to 509.)	4	590 to *c.*700 (?)
H. rudolfensis (cf. Groves 1989)	Only the value for one specimen is available (ER 1470), but that is considered reliable (see Holloway 1978). Another specimen assigned to this species (a calotte and partial fossil endocast, ER 3732) is similar in size and shape to ER 1470 (Wood 1991). The immature and fragmentary specimen ER 1590, also assigned to this species, probably had a somewhat larger endocranial volume (the conjoined parietal fragments fit over ER 1470: Holloway pers. comm.).	1(3)	752+
H. ergaster sensu Wood (1992)	This species contains ER 3733, ER 3883 and WT 15000, all of which provide reliable endocranial estimates.	3	804 to 909
H. erectus sensu stricto	This includes the Zhoukoudian specimens from China and the Trinil plus Sangiran specimens from Java. The range cited here is based on the most reliable estimates (see notes in Holloway 1975, and this chapter, Table 4.1, plus the notes in Weidenreich 1943, p. 113).	8	815 to 1225
H. sapiens neanderthalensis	For a broad range of reliable estimates we have those of Holloway, this chapter, Table 4.1. If we add Amud I (Ogawa *et al.* 1970) the upper value increases to 1740, and in so far as one can judge from text and photographs this seems to be a reliable estimate.	5(6)	1305 to 1640 (1740)
H. sapiens sapiens	The values cited here are based on the example of maximum normal variation provided by Hrdlička (1939), and may represent less than 1% of the non-pathological distribution in pre-industrial human populations. Tobias (1971*b*) gives a value of 800 for the lower part of the range.	1000s	(800) 910 to 2100

Table 4.7 Endocranial capacity values for various fossil hominid series (cm^3): means, standard deviations, coefficients of variation and 95 per cent population limits. From Tobias (1967), courtesy of P. V. Tobias.[a]

Taxon	*n*	Mean	SD	*V* per cent	95 per cent limits of population (rounded off to nearest cm^3)
A. afarensis	3	?413.5	—	—	352–?493[f]
A. africanus	6	441.2	19.60	4.44	391–492
A. robustus	1	530.0	—	—	—
A. boisei	4	513.0	11.49	2.24	476–550
A. robustus/A. boisei	5	516.4	12.52	2.42	482–551
H. habilis	6	640.2	82.23	12.85	429–852
H. erectus erectus[b]	7	895.6	93.57	10.45	667–1125
H. erectus erectus[c]	6	929.8	91.67	9.86	694–1165
H. erectus pekinensis	5	1043.0	112.51	10.79	731–1355
H. erectus (Asia and Africa)	15	937.2	135.48	14.46	647–1228
H. sapiens soloensis[d]	6	1090.8	75.39	6.91	897–1285
H. sapiens soloensis[e]	5	1151.4	99.51	8.64	896–1407

[a] In this table no attempt has been made to separate the series into presumptive male and female sub-sets.

[b] Based on Tobias's (1975) estimate, but with the incorporation of that author's new value for Trinil 2, based on Holloway's (1975) new value for Sangiran 2.

[c] Based on Holloway's (1981*b*) new values for six Indonesian specimens.

[d] Based on Weidenreich (1943). (Ngandong specimens [eds])

[e] Based on Holloway (1980*b*). (Ngandong specimens [eds])

[f] Observed range.

Table 4.8a Hominoid cranial volumes—means, ranges, SDs

Species	Sex	Sample size	Volume (mean)	SD	Range
Gibbon (*Hylobates lar*)					
	male	44	106.3	7.23	92–125*
	female	37	104.2	7.01	90–116
Siamang (*Symphalangus syndactylus*)					
	male	8	127.7	8.15	99–140†
	female	12	125.9	12.71	102–143
Chimpanzee (*Pan troglodytes*)					
	male	159	397.2	39.4	322–503‡
	female	204	365.7	31.9	270–450
Chimpanzee (*Pan paniscus*)					
	male	28	351.8	30.6	295–440§
	female	30	349.0	37.7	265–420
Orang-utan (*Pongo pygmaeus*)					
	male	66	415.6	33.6	334–502¶
	female	63	343.1	33.6	276–431
Gorilla (*Gorilla gorilla*)					
	male	283	535.5	55.3	410–715[11]
	female	199	452.2	41.6	345–553
Human (*Homo sapiens sapiens*)					
	male	502	1457.2	119.8	1160–1850**
	female	165	1317.9	109.8	1040–1615

From Tobias (1971*b*), by permission.

* The individual cases on which these statistics are based came from Dr A. Schultz's collection and were kindly provided to Dr Holloway by Dr D. Passingham.

† These figures are again based on Schultz's collections.

‡ The specimens summarized here are drawn from various collections.

§ These statistics are based on the individual specimens from the collection at Terveuren, Belgium, which were kindly provided to Dr Holloway by Dr D. Kramer.

¶ The orang values include values from the Smithsonian collection, the Cleveland Museum of Natural History, the American Museum of Natural History, and Schultz's collection.

‖ These values do not include the famous 752 cc case published by Schultz (1962), as Dr Holloway was never able to locate the proposed specimen in Zurich. Two 715 cc values come from the Powell–Cotton collection. These figures include specimens from the Powell–Cotton, Todd, American Museum of Natural History, and Schultz collections. We are grateful to Dr Bernard Wood for the Powell–Cotton data, and Dr W. Kimbel for the Todd collection values in the Cleveland Museum. These data were analysed using the SPSS^{X} statistical package. The values presented in this table are quite similar to those in Tobias (1971*b*) (see table 4.8*b*) but herein include the standard deviations.

** These cases are from Holloway (1980*c*), and are based on a culled Danish sample previously published by Pakkenberg and Voigt (1964). All pathological cases were removed, including extreme low and high body weights and statures. In fact, world-wide, the range of normal variation for the species *Homo* is roughly 1000–2200, the SD being roughly 10 per cent of the mean. There are ethnic variations in brain weight, but these appear to be mainly related to body size.

Table 4.8b Hominoid cranial volumes—means and sample ranges

Species	Size of sample	Mean volume (cm^3)	Range (cm^3)
Gibbon (*Hylobates lar*)			
Males	95	104.0	89–125 (=36)
Females	85	100.9	82–116 (=34)
Combined males and females	180	102.5	82–125 (=43)
Gibbon (*Hylobates agilis*)			
Combined males and females	21	98.8	81–120 (=39)
Siamang (*Symphalangus syndactylus*)			
Males	23	125.8	100–150 (=50)
Females	17	122.8	105–152 (=47)
Combined males and females	40	124.5	100–152 (=52)
Chimpanzee (*Pan troglodytes*)			
Males	163	398.5	292–500 (=208)
Females	200	371.1	282–460 (=178)
Combined males and females	363	383.4	282–500 (=218)
Pygmy chimpanzee (*Pan paniscus*)			
Males	6	356.0	334–381 (=47)
Females	5	329.0	275–358 (=83)
Combined males and females	11	343.7	275–381 (=106)
Orang-utan (*Pongo pygmaeus*)			
Males	203	434.4	320–540 (=220)
Females	199	374.5	276–494 (=218)
Combined males and females	402	404.8	276–540 (=264)
Gorilla (*G. gorilla gorilla*)			
Males	414	534.6	412–752 (=340)
Females	254	455.6	340–595 (=255)
Combined males and females	668	504.6	340–752 (=412)
Modern Human (*Homo sapiens sapiens*)			
Males	1000s	1345.0	900–2000 (=1100)
			800–2100 (=1300)

From Tobias (1971*b*) by permission.

References to Editorial appendix I

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Editorial appendix II: Evolution of the human vocal apparatus[1]

Introduction

The mammalian upper respiratory system is often informally referred to as the 'vocal tract'. It is composed of the larynx and pharynx, plus the nasal and oral cavities (see Fig. 4.9). In fact, this anatomical region is the crossroads of both our respiratory and our alimentary systems, as well as the site for the production of vocal sounds. In particular, the location of the larynx is very important in determining the way we breathe, swallow, and vocalize. Nineteenth-century anatomical studies noted that the larynx of mammals is placed high in the neck. Negus (1929, 1949, 1965), documented the high position of the larynx in many mammalian species, and

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