2007 Handbook of Palaeoanthropology, Vol. 2: Primate Evolution and Human Origins (Eds: W. Henke, & I. Tattersall), *Springer-Verlag, p. 133-1162.*

(1) Evolution of the Primate Brain

Dean Falk
Department of Anthropology
Florida State University
Tallahassee, FL 32306-7772
dfalk@fsu.edu

(12.) 1 Introduction

The mammalian order of primates is known for a variety of species that are lively, curious, social, and intelligent. Nonhuman primates are of special interest to people, not only because they are appealing and entertaining to watch, but also because certain species (e.g., of macaques or baboons) are genetically close to humans, which makes them excellent animal models for medical research. As curious primates ourselves, we wonder about our evolutionary origins. One way to address this topic is to study and compare species from living primates that are thought to approximate broad stages (or grades) that occurred during some 65 million years of primate evolution. Thus, one may compare particular anatomical structures or behaviors across appropriate representatives from the series prosimian-> monkey-> ape -> human. When possible, such a *comparative method* should be supplemented with the *direct method* of studying fossil primates, which adds elements of specificity and time to the picture.

Within this broader context, we are also interested in the more specific question of how humans came to be, not only the largest-brained primate, but also the most intelligent species on Earth. In order to address this question, one must study primate brain evolution. From our general understanding of primate evolution, we know that certain major adaptations occurred in some groups and that these changed and sculpted evolving brains during many millions of years. For example, the anthropoid ancestors of living monkeys, apes and humans became diurnal, and this shift from night-living to day-living dramatically impacted the lives and nervous systems of their descendants forever after. Thus, brains of diurnal primates have relatively enhanced visual compared to olfactory 'modules.' Another broad shift that greatly impacted the nervous system occurred when very early primates shifted from primarily ground living to living in trees. This newfound arboreal life underscored the adaptive value of keen vision with depth-perception and also led to improvements in sensory/motor coordination in conjunction with a variety of locomotor patterns that evolved in different arboreal species. More recently, some of these species shifted back to terrestrial living and this, too, left its imprint on their nervous systems.

As with many groups of mammals (Jerison 1973, Radinsky 1979), relative brain size (the ratio of brain to body size) increased during the course of primate evolution. Some years ago, Radinsky (1979: 24) noted that "elucidation of the factors responsible for the widespread evolutionary trend of increase in relative brain size in mammals, and for the extreme to which that trend was carried in humans, remains a fascinating unsolved problem." Even before Radinsky's observation, Jerison was pondering the laws that governed the evolutionary increase in brain size

for various groups of primates (and other animals) and partitioning the respective total increases into two parts: those associated with allometric scaling expected for given body sizes, and any remaining increases (or decreases) in brain size, known as 'residuals.' Other workers, most notably Holloway (Holloway 1974, 1979), emphasized the evolutionary importance of neurological reorganization that alters the quantitative relationships between brain nuclei, fiber tracts, and neuroreceptor sites (Holloway et al. 2004), thus allowing for rewired and altered neurochemistry in brains of similar (or different) size. Although the debate about the respective importance of brain size versus neurological reorganization is a false dichotomy (Gould 2001) (both are important, of course), it continues today (Falk and Gibson 2001). Bringing welcome balance, Holloway et al. (2004) note that the concept of reorganization in brain evolution is of less concern when one is examining broad genetic and evolutionary conservatism between large numbers of taxa (Finlay and Darlington 1995, Finlay et al. 2001, Jerison 1973, Kaskan and Finlay 2001), but more important when one attempts to explain species-specific differences in behavior (Holloway 2004, Preuss 2001).

(12.) 1.1 General methods for studying primate brain evolution

The *direct method* of studying fossilized braincases and casts of their interiors (endocranial casts or endocasts) is the bread and butter of palaeoneurology (literally 'old' neurology). Cranial capacities that approximate brain volume in cm^3 (and also brain mass in grams) may be measured from skulls by traditional methods such as filling braincases with mustard seed that is then measured in a graduated cylinder, or by obtaining volumes electronically from braincases (skulls) that have been subjected to three-dimensional computed tomography (3DCT). Indeed, because 3DCT is able to resolve small density differences such as those between fossilized bone and attached rock matrix, it is particularly good for investigating fossils (Spoor et al. 2000), and has become useful as a noninvasive method for visualizing 'virtual endocasts,' e.g., by flood-filling the virtual braincase (Falk 2004b). Although brain size is actually slightly smaller than cranial capacity because of the fluids, vessels, and brain coverings (meninges) that occupy the braincase along with brain tissue, the difference is insignificant compared to other sources of intraspecific variation in brain size (according to Hofman 1983, cranial capacity = 1.05 brain size), and the two variables are frequently used interchangeably. An advantage of using cranial capacities across the board in comparative studies is that, unlike actual brains, cranial capacities may readily be obtained from available skulls of fossil and extant primates.

Endocasts sometimes occur naturally under propitious geological conditions (such as those that exist in parts of South Africa) or, more often, are prepared artificially from skulls using liquid latex (see Falk 1986 for details). Over the past twenty years, the use of 3DCT data for reconstructing and measuring virtual endocasts has undergone numerous validation studies (Conroy and Vannier 1985, Conroy et al. 1990, 1998, Spoor et al. 2000) and is rapidly becoming a preferred method (Falk 2004b). Physical endocasts may be measured to determine cranial capacity, e.g. by displacing them in water (see Holloway et al. 2004 for details) and, as noted, the volumes of virtual endocasts may be measured electronically. Additionally, both kinds of endocasts (depending on their quality) may reveal positions of vessels and cranial nerves; details of suture closure, venous sinuses, and emissary veins (foramina); information about cortical asymmetries including brain shape (petalia) patterns; and information about sulcal patterns. Curiously, the most detailed endocasts are produced from skulls of relatively young individuals

within a species (Connolly 1950), and from skulls of smaller-brained species within a group of related species (Radinsky 1972). The former may relate to the timing of suture closure during development, while the latter may explain why some of the South African australopithecine natural endocasts reproduce a good bit of detail (Falk 1980a,b).

By comparison, those using the *indirect method* of comparing neuroanatomical structures among living species have a veritable arsenal of methods at their disposal. Specific cortical areas may be investigated using currently available histochemical and immunocytochemical techniques (Preuss 2001), in addition to relying on classic cytoarchitectural studies (Amunts et al. 1999). Questions can therefore be asked about the types, sizes, density, distribution, and connections pertaining to individual neurons, cell columns, or layers of the cerebral cortex (within and across particular regions). The comparative neuroscientist is able to ponder whether or not (and how) additional cortical areas have been 'added' during primate evolution, and the extent to which they might be associated with enlarged brains (Felleman and Van Essen 1991, Preuss and Goldman-Rakic 1991). Whereas CT is ideal for imaging fossil material, magnetic resonance imaging (MRI) is more suitable for imaging the soft-tissue structures that comparative neuroscientists study and may be performed non-invasively and *in vivo*. (Instead of relying on an X-ray source, MRI uses pulses of radiofrequency energy to map specimens that have been subjected to a strong magnetic field.) Even better, positron emission tomography (PET) and functional MRI (fMRI) are now commonly used to study functional processing in living human brains, and these techniques are beginning to be applied to nonhuman primates (Semendeferi 2001).

Although the increasingly-sophisticated information gleaned from comparative brain studies is indispensable for interpreting palaeoneurological data, the logistics of synthesizing findings from the *direct* and *indirect methods* for studying primate brain evolution remain tricky:

Deep disciplinary approaches: structural, functional and developmental, have started to coalesce whereby brain structures can be seen developing and functioning through the many new noninvasive imaging techniques that are available today. All this allows better understanding of not only how the brain works in terms of movement and sensation but also how it functions during sleep, during preparation for action, during thinking, and during emotions. These lines of investigation, however exciting, and with such major implications for normal human brain function and in disease, employ more and more complex methods and reveal the workings of smaller and smaller brain components. Consequently, the logistical problems of carrying out such studies in an evolutionary perspective and time-scale loom ever larger. Oxnard (2004:1128-9)

Quantifying Primate Brain Size

Certain allometric factors govern the general external and internal morphology of primate brains. Larger primate (indeed, mammalian) brains are characterized by more convolutions (gyri and sulci) than smaller ones (Radinsky 1975), which appears to be a mechanism for maintaining the ratio of surface (cortex) area to brain volume as brains enlarge (Jerison 1982, Falk 1980b). (This is not to say that sulci and convolutions are never associated non-allometrically with specialized features. Sometimes they are [Falk 1982], e.g. brains of prehensile-tailed New World monkeys

have tail representations that are delimited by special sulci.) Neuronal density decreases with increased brain size, although mean neuronal size does not appear to scale allometrically with brain volume (Haug 1987). Compared to other mammals, the primate cerebral cortex is thicker and its layer IV is highly granulated (Haug 1987). The volume of gray matter is basically a linear function of brain volume, whereas the mass of interconnections that form the underlying white matter increases disproportionately with brain size (Hofman 2001, Ringo 1991). Curiously, women have relatively more gray matter than men (Haug 1987, see Falk 2001 for details regarding sexual dimorphism in primate brains).

Absolute brain size is hugely variable across living primates. Cranial capacities of living prosimians, monkeys, and gibbons overlap and together range between 1-205 cm^3, which is separate from the great ape range of 275-752cm^3 (Falk 1986) (Fig. [12.]1). The human range is above that for great apes and extends from around ~ 1100-1700 cm^3, excluding extreme outliers for purposes of comparison. But there's a problem here. The world's smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*), has a body weight of approximately 30 g (~ 1 oz), so how can we possibly compare its tiny brain size to those of larger primates, such as the great apes? Clearly, a more meaningful parameter would be the ratio between brain size and body size, known as relative brain size (RBS). However, RBS is itself confounded by certain very powerful allometric scaling constraints that apply ontogenetically as individuals develop from smaller-bodied babies to adults (Passingham 1975b) and in interspecific comparisons of smaller-bodied with larger-bodied primates (Schultz 1956) (Fig. [12.]2). Allometric scaling is why human babies appear to have such relatively big heads (brains) compared to adults despite the fact that their absolute brain sizes are smaller, and it is why we should not be particularly impressed by the fact that little squirrel monkeys have an average RBS of about .02, which is equivalent to that of humans (Falk and Dudek 1993).

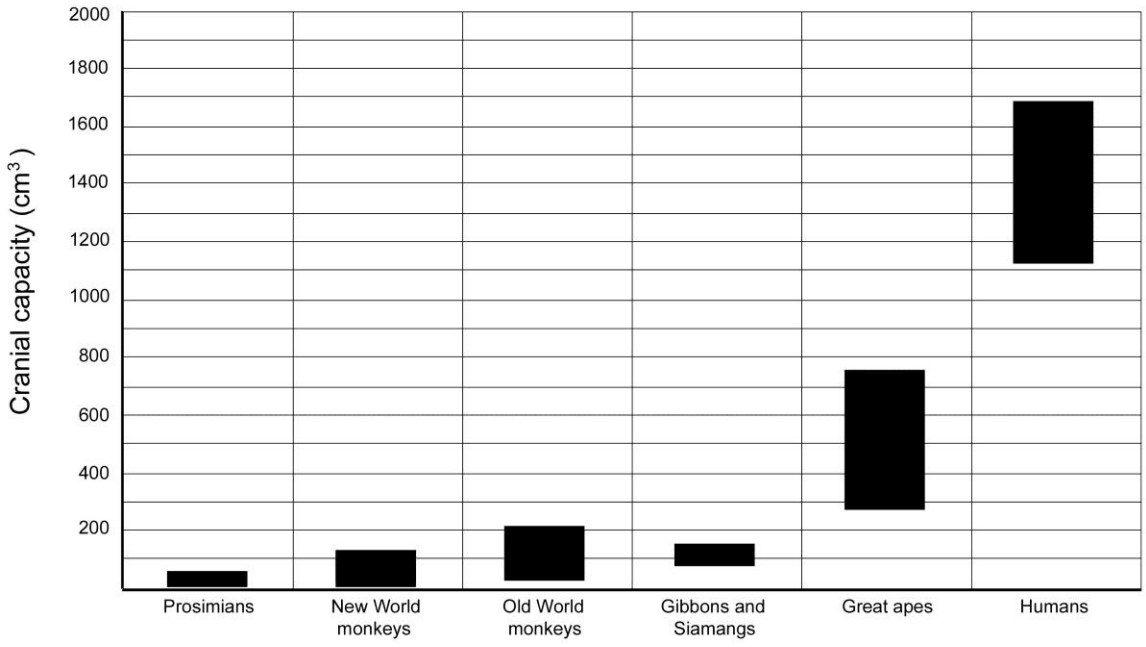


Fig. (12.) 1 ***Ranges of cranial capacities in living primates, excluding far-reaching extremes in humans for comparative purposes (modified from Falk 1986).***

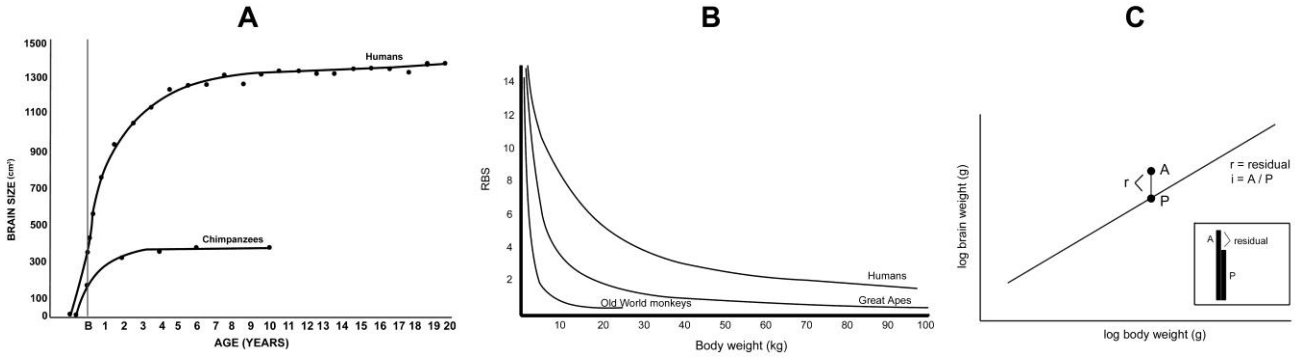


Fig. (12.) 2 ***Brain size and relative brain size (RBS) in humans and other primates. A, brain size growth in humans and chimpanzees. Brain growth in humans is at a higher rate after birth (B), which results in larger cranial capacities (and brain masses) for humans than chimpanzees at any given age (or body weight) (modified after Passingham 1975b). B, Relative brain size (RBS, brain size/body size) plotted against body weight for humans, great apes, and Old World monkeys. The shape of these curves are inverse to those on the left and, again, are stacked because of different rates of postnatal brain growth in the three groups. At any given body weight (and age), humans have RBS above those of apes, which are above those of monkeys. At smaller body weights (and therefore ages), primates have greater RBS (which is why human infants appear to have big heads) (modified from Schultz 1956). C, simple schematic that illustrates indices of relative brain size (i), the names of which vary (EQ, IP) with the reference group for the linear regression. When transformed to logarithms, brain size versus body size data (such as those in A) have a linear relationship (the straight line, or linear regression shown in C). P, is the mean value for brain size predicted by the regression for a species at a given mean body weight; A, is the actual mean value of brain size for that species. The index of RBS (or encephalization), i, is the ratio of A to P. The difference between P and A, the residual (r), is the extra (or reduced) mean brain size that a species has compared to a species of similar mean body size in the reference group. The reference group (be it composed of mammals, insectivores, or just monkeys) is very important for interpreting indices.***

In order to 'subtract' the effects of allometric scaling, comparative studies of primate brain size have traditionally relied on quotients that express 'residual' factors after the effects of body size have been removed from palaeoneurological data (Falk 1980b). Thus, Bauchot and Stephan (1966, 1969) and Stephan (1972) developed the index of progression (IP) by using brain weight/body weight data from basal insectivores and calculating the regression equation:

$$\log h = 1.632 + 0.63 \log k \qquad \textbf{(12.1)}$$

where h = brain weight, k = body weight. From this equation, 'basal' brain weight (BG) can be predicted for a given primate species by substituting its mean body weight into the equation. The ratio between actual mean brain weight of the species ('progressive size' = PrG) and the predicted 'basal size' (BG) equals IP, the index of progression,

$$IP = PrG/BG \qquad \textbf{(12.2)}$$

Jerison's (1973) famous encephalization quotient (EQ) is similar, but uses brain weight/body weight data from living mammals rather than insectivores to establish the baseline regression and resulting classic formula:

$$EQ = E_i/0.12P_i^{.67} \qquad \textbf{(12.3)}$$

where E_i = actual brain size, and P_i = predicted brain size

(Like other workers [Martin 1982, 1990], Jerison now uses a regression equation with an exponent of 0.75 instead of 0.67 [Jerison 2001].) It should be noted, however, that the comparative results of EQ studies depend very much upon the group selected for the baseline data (Holloway and Post 1982) and that there is an artifactual tendency for encephalization to be overestimated for smaller-bodied species but underestimated for larger ones (Radinsky 1982). One may also utilize similar regressions to estimate residual numbers of extra neurons (Jerison's extra neuron index, Nc) or to determine how 'encephalized' particular parts of the brain are. Toward these ends, Stephan, Bauchot, and Andy's (1970) widely-cited data for primate brains have been a gold mine for evolutionary studies.

(12.) 2 The evolution of primate brain size

Compared to basal insectivores, primates evolved enlarged brain size/body size ratios (Radinsky 1975). Cranial capacity estimates for a dozen available Eocene and Oligocene prosimian skulls are all under 11 cm^3, and their EQs suggest that the Eocene lemuriforms *Smilodectes*, *Adapis* and *Notharctus* were relatively smaller-brained that modern prosimians, and those for tarsiiforms (for which there is a brief series) increased through time (Gurche 1982, Radinsky 1975). By about 45 ma, some prosimians appear to have RBS at the lower end of modern ranges (Radinsky 1975). Radinsky (1974) noted that an Oligocene anthropoid, *Aegyptopithecus*, had a cranial capacity of approximately 32 cm^3, but had nevertheless attained an anthropoid level of RBS. The Miocene hominoid *Proconsul* had a comparatively whopping endocranial volume of 167 cm^3 and an estimated body weight of ~ 11 kg, giving it a relatively bigger brain than modern monkeys of comparable body size (Walker et al. 1983). Over a quarter of a century ago, Radinsky (1974) summarized his findings from the 'scanty' fossil record of primate brain evolution by observing that increased RBS dramatically distinguishes human brains from those of other primates, and he further suggested that this increase occurred relatively recently, beginning no more than 4 to 5 million years ago (Radinsky 1975).

Although most modern anthropoids have brains that are relatively larger than those of modern prosimians (Bauchot and Stephan 1969), caution must be exercised when using EQs or similar

indices to assess cognitive capacities. Despite the fact that EQs correlate to some degree with primate feeding behaviors (frugivorous primates are more encephalized than folivorous ones [Jerison 1973, Clutton-Brock and Harvey 1980, Milton 1988] and nonhuman primates that are omnivorous extractive foragers generally have higher IPs than the others [Gibson 1986]), such indices fail to predict relative cognitive capacities. Gibson (2001) argues persuasively that, compared to monkeys, great apes possess greater mental constructional capacities and cognitive abilities in realms once thought to be uniquely human. Using a test for mental flexibility that separates apes from monkeys (the Transfer Index), she demonstrates that absolute brain size, body size and extra neurons all correlate with performance, while EQ does not. Gibson therefore suggests that "the most practical measure for distinguishing intelligence and predicting the presence of human-like mental skills in hominid fossils is absolute brain size" (Gibson 2001:92).

The relationship between primate brain size and cognition may also be explored by investigating the interaction between life history adaptations, brain growth, and cognitive levels ('primate cognitive ecology,' [Garber 2004]). In one study, postnatal brain growth patterns were found to be highly variable among anthropoids (Leigh 2004). Leigh discerned two alternate life-history strategies that concern the metabolic costs of infant brain growth. In one, favored by Old World monkeys, relatively large-bodied mothers mature late and give birth to infants that require relatively little postnatal brain growth. This strategy requires high maternal metabolic investments during pregnancy. In the second strategy, exploited by tamarins, females mature especially early and produce offspring with brains that grow for a relatively long period of time during the postnatal period, which shifts some of their metabolic costs away from the mother and to others (including the offspring). Leigh notes that chimpanzees and humans are difficult to categorize in terms of these two strategies, and adds that differences in patterns of brain growth should be viewed as part of a more general complex of life-history traits, rather than as direct pace-setters of life histories. Citing comparative studies on the cognitive abilities of squirrel monkeys, tamarins, and baboons, Leigh concludes that life-history strategies may have coevolved with cognitive abilities in association with evolutionary changes in brain development.

Other studies investigate the perplexing question of how primates (including humans) were energetically able to grow relatively large brains that are metabolically 'expensive' to maintain compared to the whole body. The maternal energy hypothesis (MEH) proposes that the mother's relative basal metabolic rate (BMR) during an infant's gestation determines its neonatal brain mass, and that subsequent maternal investment while the infant is nutritionally dependent is also an important factor for developing big brains (Martin 1996). The MEH is sometimes contrasted with the expensive tissue hypothesis (ETH), which proposes that relatively encephalized primates are able to maintain their brain's metabolic requirements because there has been an evolutionary trade-off in which brain tissue has increased at the expense (decrease in mass) of other metabolically expensive tissues such as guts, heart, liver, or kidney (Aiello and Wheeler 1995, Aiello et al. 2001). The two hypotheses should be viewed as complementary rather than contradictory because the MEH focuses on maternal energetics invested in offspring during gestation and lactation, while the ETH picks up from there by focusing on metabolic dynamics of brain growth and maintenance after weaning (Aiello et al. 2001). While the wider applicability of both hypotheses to mammals has been challenged by findings for bats (Jones and MacLarnon 2004), the recent trend toward studies that explore physiological and metabolic constraints on

brain size and development is welcome and dovetails nicely with primate life-history studies. (Another constraint hypothesis about brain size evolution, the radiator hypothesis, concerns the evolution of vascular anatomy in response to brain temperature regulation combined with selection for bipedalism [Falk 1990, 2005].)

Parsing Brain Size Evolution

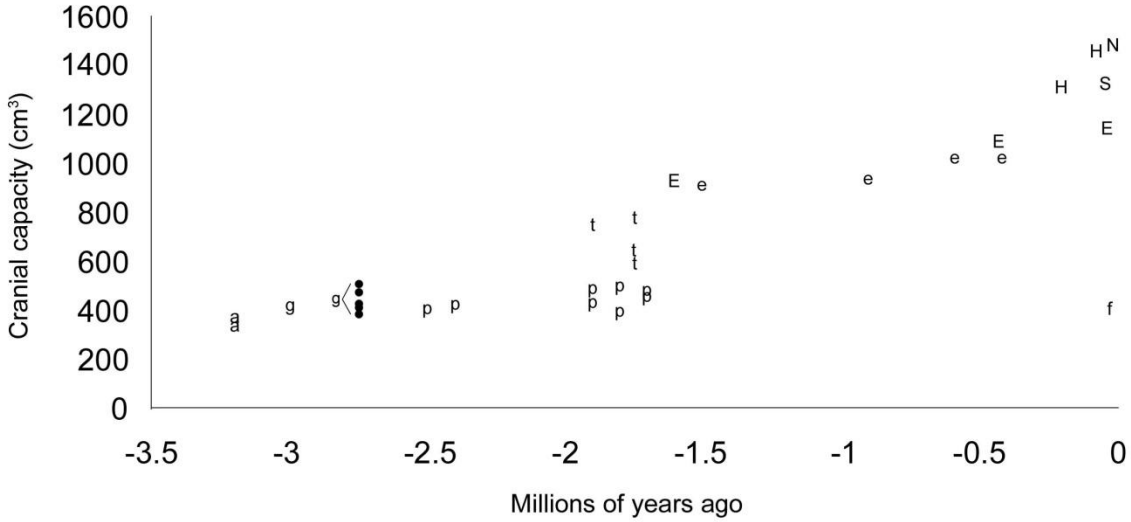
But what are the possible neurological correlates of increased brain size during primate evolution? To address this, Finlay and colleagues concentrated on critical factors that drove mammalian (including primate) brain size, especially the manner and number of neurons generated during development (Finlay and Darlington 1995, Finlay et al. 2001). They found that the longer cytogenesis is prolonged for a given structure (based on timing of the peak in 'neuronal birthdays'), the larger the structure will ultimately be. Since mammalian neurogenesis of brain parts proceeds uniformly (i.e., the order is conserved), "by far the most useful predictors of structure sizes are the sizes of other brain structures" (Finlay et al. 2001:268). (It should be noted, however, that olfactory bulbs (and medulla) are an exception to this rule because they are smaller overall in anthropoids than prosimians and may map onto nocturnal versus diurnal niches [Barton et al. 1995]). A result of this regularity is that most parts of mammalian brains enlarged together, which led Finlay et al. to suggest that enlarged isocortices could have been by-products of structural developmental constraints ('spandrels') that were only later co-opted for specific functions. The suggestion that the sizes of different brain structures is a consequence of overall brain size has perhaps received more controversy than it should have (Barton and Harvey 2000, Barton 2001, Oxnard 2004) because the Finlay et al. model, in fact, accommodates independent variation of individual brain parts that may be associated with specific behavioral advantages (e.g., foraging ability). Generally, this latter type of brain growth, which makes up the unaccounted-for variance in Finlay et al.'s model, underlies a small (but presumably evolutionarily crucial) variation of individual structure size on the order of two- to threefold (Finlay et al. 2001).

(12.) 2. 1 Evolution of brain size in hominins

As noted, cranial capacities may be obtained for fossil hominins by measuring the endocasts (actual or virtual). Error may be introduced, however, because fossil endocasts are rarely whole and, thus, usually require partial reconstruction. Because morphological differences were found to distinguish the frontal lobes and temporal poles of robust and gracile (*Australopithecus africanus*) australopithecines, new endocast reconstructions were provided for four *Paranthropus* specimens, which reduced the mean cranial capacity for the genus to the point where it approximated that of *A. africanus* (see Falk et al. 2000 for details). These new cranial capacities and others appear in Table (12.)1 and Fig. (12.)3. (For more extensive data, the reader is referred to Appendix 1 of Holloway et al. [2004].)

Species	Date (Ma)	Specimen	Adult cm³	Cm³ Reference
Australopithecus				
A. afarensis	~3.2	AL 333-105	343	Falk 1987b
-	~3.2	AL 162-28	375	Falk 1985
A. africanus	~3.0	MLD 37/38	425	Conroy et al. 1990
-	~2.75	Sts 60	400	Holloway et al. 2004
-	-	Sts 71	428	Holloway et al. 2004
-	-	Sts 5	485	Holloway et al. 2004
-	-	Sts 19	436	Holloway et al. 2004
-	-	Stw 505	515	Conroy et al. 1998
Paranthropus				
P. aethiopicus	~2.5	KNM-WT 17000	410	Walker et al. 1986
P. boisei	~2.4	Omo L339y-6	427	Holloway et al. 2004
-	~1.9	KNM-ER 23000	491	Brown et al. 1993
-	~1.8	KNM-WT 17400	400	Holloway et al. 2004
-	~1.8	OH 5	500	Falk at al. 2000
-	~1.9	KNM-ER 407	438	Falk at al. 2000
-	~1.7	KNM-ER 732	466	Falk at al. 2000
P. robustus	~1.7	SK 1585	476	Falk at al. 2000
Australopithecus/Homo?				
-	~1.9	KNM-ER 1470	752	Holloway et al. 2004
-	~1.75	D2700	600	Vekua et al. 2002
-	-	D2282	650	Gabunia et al. 2000
-	-	D2280	780	Gabunia et al. 2000
Homo erectus				
Java (Sangiran)	~1.6	n=6	Mean=932	Holloway et al. 2004
Africa	~1.5	KNM-WT 15000	909	Walker and Leakey 1993
Java (Trinil)	~0.9	Trinil 2	940	Holloway et al. 2004
China (Beijing)	~0.585	Skull D1	1020	Weidenreich 1943
China (Beijing)	~0.423	n=3	Mean=1090	Weidenreich 1943
Hexian	~0.412	-	1025	Wu et al. 2005
Java (Solo)	~0.027	n=6	Mean=1149	Holloway et al. 2004
Homo				
European	~0.2	-	Mean=1314	Hofman 1983
Neandertals	~0.07	-	Mean=1487	Hofman 1983
European	~0.04	-	Mean=1460	Hofman 1983
H. sapiens	~0.01	-	Mean=1330	Holloway et al. 2004
Homo floresiensis	~0.018	LB1	417	Falk et al. 2005

Table (12.)1 ***Cranial capacities for various adult hominins. Following Holloway et al. (2004), the chronological data are approximate middle values of the ranges for estimated dates (see also Falk et al. 2000). See Fig. 3 for plots of data.***



a	*Australopithecus afarensis*	g	*Australopithecus africanus*
p	*Paranthropus*	t	*Australopithecus/Homo?*
e	*Homo erectus*	E	*Homo erectus* (mean)
H	*Homo* (mean)	N	Neandertal (mean)
f	*Homo floresiensis* (LB1)	S	*Homo sapiens* (mean)

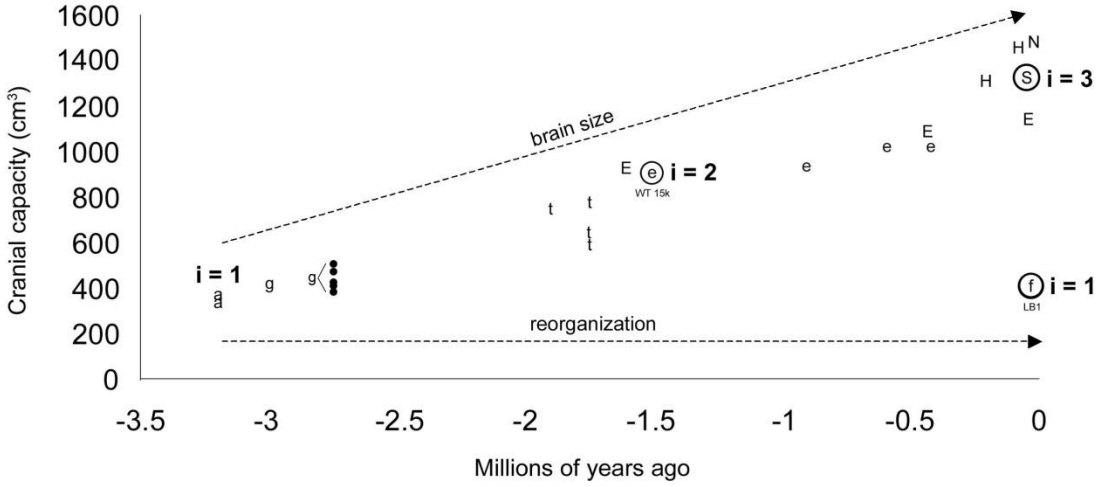


Fig (12.)3 ***Cranial capacities of select hominins plotted against time; data from Table 1. Above, plot includes capacities for robust australopithecines (Paranthropus). The trend for brain size increase appears flat until around 2.0 ma, and then begins to increase in Homo. Below, the same plot, but without the Paranthropus specimens (generally thought not to be ancestral to Homo). The trend toward brain size increase now appears to increase from before***

3.0 ma. Part of the reason for this is the recently described 'transitional' specimens from Dmanisi, Republic of Georgia (listed under Australopithecus/Homo in Table 1). The earliest australopithecines and relatively recent LB1 (Homo floresiensis) have brain sizes expected for apes of equivalent body sizes (i=1); Homo erectus from Nariokotome (KNM-WT 15000) has a brain that is twice the size expected for similarly-sized apes (i=2); and contemporary Homo sapiens' mean brain size is three times that expected for apes of equivalent body size (i= 3). This figure illustrates the trends for increasing brain size (vertical axis) and ongoing neurological reorganization (horizontal axis).

A number of observations regarding the evolution of absolute brain size in hominins are suggested by Fig. (12.)3. Although brain size remained conservative during the evolution of *Paranthropus*, it increased in *Australopithecus* and between the latter and specimens that lived more recently (~ 1.7-1.9 ma) in Africa and the Republic of Georgia. The overall morphology of these more recent specimens is transitional enough so that some workers place them in *Australopithecus* while others include them in early *Homo* (Balter & Gibbons 2002, Wood and Collard 1999). If, indeed, these specimens are transitional, then the received wisdom that brain size suddenly 'took off' in the genus *Homo* around 2.0 mya needs serious reevaluation (Falk 2004b, Falk et al. 2000). Thus, rather than there being a jump in cranial capacity in early *Homo*, cranial capacity may have begun increasing in the *Australopithecus* ancestors of *Homo* a million years earlier (Falk et al. 2000). With the redating of Java sites (Swisher et al. 1994, Huffman 2001) pushing certain cranial capacities further into the past, there is no longer the discontinuity in the trend for increasing cranial capacity (Falk 1987b, 1998) that once contributed to the suggestion that brain size evolution underwent 'punctuated' events (Hofman 1983, Ruff et al. 1997, Leigh S, 1992). Rather, the recent discovery of LB1, the small-brained type specimen for *Homo floresiensis* (Brown et al. 2004, Morwood et al. 2004), lends an entirely new perspective to the study of hominin brain size evolution (Falk at al. 2005): From australopithecines through extant *Homo*, upward selection widened the range of brain-size variation, while australopithecine-sized brains may have continued to provide the lower boundary (at least, until very recently). Thus, to some extent, Fig. (12.)3 encapsulates the interplay between selection for brain size (vertical vector) and selection for neurological reorganization (horizontal vector).

But what about the evolution of RBS in hominins? After all, LB1 was tiny, only about a meter in stature (Brown et al. 2004), which must certainly account for much of the recent variation in brain size. Although many workers have estimated EQs for fossil hominins, these estimates must be taken with a grain of salt because of the difficulty of determining surrogates for body mass. Without an associated skull, how does one identify the species of postcrania such as femurs that are often used to predict body mass or stature? Needless to say, the few known hominin partial skeletons are extremely important in this endeavor. Conservatively, we know exactly this much about encephalization in hominins: Living people have brains and (separately) neocortices that are approximately three times as large as expected for nonhuman primates of the same body size (Passingham 1973, 1975a; Passingham and Ettlinger 1974; Stephan et al. 1970) and, surprisingly, this is true using regression equations based on all nonhuman primates, just monkeys and apes, or just apes (Stephan 1972, Falk 1980b). Turning to the hominin fossil record, there are two skeletons that provide important data. First, there's approximately 3'6"

Lucy (AL 288-1), dated to a bit over 3.0 ma. Although a definitive cranial capacity could not be obtained from this specimen, hominin cranial capacities of less than 400 cm^3 were not uncommon at that time and place (Table (12.)1), so it is safe to say that small-bodied australopithecines from Hadar, Ethiopia had ape-sized body masses that were probably associated with ape-sized brains (giving them a RBS index of i =1). Fast forwarding to ~1.5 ma, the *Homo erectus* skeleton from Nariokotome, Kenya (KNM-WT 15000) paints quite a different picture. By the time he reached adulthood, it was projected that this 'lad' would have reached a stature of over six feet and a cranial capacity of 909 cm^3 (Walker and Leakey 1993). That capacity is twice the means for both *A. africanus* and *Paranthropus* (Table (12.)1), and roughly twice the means for living great apes (490 cm^3 for gorillas, 375 cm^3 for common chimpanzees and for orangutans [Falk 2000b:312]). It is also 2/3 of 1364 cm^3, which is very close to the oft-cited world mean for contemporary *Homo sa*piens of 1350 cm^3. It therefore looks as if African *H. erectus* that lived ~1.5 ma may have had a brain mass that was twice the size predicted for a living nonhuman primate of equivalent body mass (i = 2) or, put another way, that *H. erectus* was two-thirds as encephalized as *H. sapiens*. These few data provide nice 1-2-3 estimates for indices of RBS at ~3.0 ma, ~1.5 ma, and today (Fig. [12.]3). Beyond this, conjecture about the past evolution of hominin encephalization remains just that.

One can, however, make reasoned conjectures about future brain size evolution. In a fascinating paper, Hofman (2001) applies the design principles and operational modes (including energetic and neural processing constraints) that underlie information processing in primate brains to the task of modeling the limits of future brain size evolution in *Homo sapiens*. His model predicts that, as brain size increases beyond a certain critical point, subcortical volume (cerebellum, brain stem, diencephalon, etc.) would decrease in conjunction with increasing white matter. The net result would be that hominins with brains enlarged beyond that critical point would have a declining capability for neuronal integration despite an increased number of neurons. The critical point is approximately 3500 cm^3, beyond which "any further step in the evolution of intelligence will then have to take place outside our nervous system, in a technological world where the selection mechanisms and forces are radically different from those operating in nature" (Hofman 2001:125). Although Hofman's model does not incorporate anatomical constraints that govern head size and parturition, perhaps the technological world he envisions will, indeed, make it possible for women to bear (presumably) bigger-brained neonates!

(12.) 3 The evolution of neurological reorganization

Despite the enormous energy that palaeoneurologists have devoted to studying primate brain size evolution, there remains a conviction that size alone is not enough to account for the observed diversity in primate behavior, and that circuitry, neurochemistry, and subsystems (modules) must have become reorganized within brains to accommodate evolving behavioral repertoires (Preuss 2001, Holloway et al. 2004). Preuss, in fact, goes so far as to suggest that "the cortex is a veritable hotbed of evolutionary reorganization" (2001:140). Although reorganization was undoubtedly important, deciphering the details of internal brain evolution is much more difficult than studying the gross phenomenon of brain size. Nevertheless, information yielded by both *direct* and *indirect methods* sheds some light on at least the broad aspects of neurological reorganization that occurred during primate evolution.

Comparisons of brains of basal insectivores and living primates suggest early evolutionary trends in primates that included not only the larger brain size/body size ratios noted above, but also relatively enlarged neocortices for brain size, a decrease in the relative size of the olfactory bulbs, an increase in the amount of visual cortex, and development of a central sulcus in anthropoids rather than the coronal sulcus seen in prosimians (Radinsky 1975). At histological levels, layer 4 of the posterior cingulate cortex appears to be less densely packed with small cells in prosimians than anthropoids (Zilles et al. 1986), a finding that has now been extended to include much of the parietal and temporal cortices (Preuss and Goldman-Rakic 1991). The fossil record of prosimian endocasts helps pin down the approximate dates when some of these primate specializations occurred (Radinsky 1974, 1975; Gurche 1982). Thus, visual and temporal cortices had expanded to comparable modern levels in some ancestral tarsiiform and lemuriform primates by ~ 55ma (early Eocene), but frontal lobes were still relatively small except in the line leading to *Adapis* (Gurche 1982, Radinsky 1975). Analysis of the fossil record of anthropoid endocasts, particularly partial endocasts of *Aegyptopithecus*, reveals that by ~25 to 30 ma (Oligocene), olfactory lobes had reduced and visual cortices had expanded compared to prosimians. Although its frontal lobes appeared to be small compared to modern anthropoids, *Aegyptopithecus* had an anthropoid-like central sulcus instead of a longitudinally oriented fissure, the coronal sulcus, which separates head from forelimb representations in primary somatosensory cortices of prosimians (Radinsky 1975). The oldest record of an anthropoid endocast of modern appearance is that of ~ 18 ma *Proconsul* (Walker et al.1983, Falk 1983). Regarding neurological reorganization during primate evolution, Radinsky summarized:

Since *Aegyptopithecus, Dolichocebus* and *Apidium* are among the oldest known pongids, ceboids and cercopithecoids respectively, it is likely that elaborations of visual abilities and reduction of olfaction were among the features involved in the initial emergence of higher primates from prosimians. It is interesting that those same features, although not as extensively developed, appear to have been among the key adaptive features at the base of the great Eocene prosimian radiations. (Radinsky 1974:25)

A comparative study of endocasts from extant New and Old World monkeys describes various cortical specializations that were independently evolved in both groups as well as similarities that were retained from a common ancestor (Falk 1981). Within Old World monkeys, cercopithecine sulcal patterns appear to be more derived than colobines as manifested in relative expansion of prefrontal, and inferior temporal integration cortices (Falk 1978). Radinsky (1974) showed that a cercopithecoid endocast from *Mesopithecus*, dated to ~ 9 ma, exhibits the typical colobine pattern and is similar to the brain of ~ 6 ma *Libypithecus*. Thus, the modern colobine sulcal pattern, which appears to represent the more primitive condition, had occurred by at least 9 ma. He also noted that the derived cercopithecine sulcal pattern had appeared by ~ 2 ma in *Paradolichopithecus*.

The addition of new cortical areas may have provided an opportunity for the evolution of new behavioral capacities (Allman 1990, 1977; Kaas 1987, 1995; Felleman and Van Essen 1991, Preuss and Goldman-Rakic 1991). To date, primates are known to possess 50-100 cortical areas, and it has been hypothesized that many of these may be higher-order areas that are unique such as dorsolateral prefrontal, posterior parietal, and inferotemporal cortices (Preuss 2001). Preuss also notes that higher-order association regions of primates are strongly connected with each

other and these regions are all connected with a prominent thalamic structure, the medial pulvinar, which has no obvious counterpart in other mammals. He further suggests, "not only do primates possess primate-specific higher-order cortical territories, but these territories form a distinctive connectional system" (Preuss 2001:153). The suggestion that new cortical areas constitute a natural by-product of increasing brain size is consistent with Ringo's (1991) mechanistic observation that enlarging brains would become swamped with white matter without neurological reorganization that increased the number of local (as opposed to longer corticocortical) connections and therefore areas (Hofman 2001).

Relatively recent comparative work also suggests that the cerebellum, long known to be important for motor coordination and now thought to contribute to higher cognitive functions in humans (Fiez 1996, Muller et al. 1998), underwent neurological reorganization during primate evolution. Thus, the lateral cerebellar system is relatively large in chimpanzees and gibbons, while a central nucleus (the dentate nucleus, the output of which influences the cerebral motor cortex) is larger in humans than apes (Matano et al. 1985, Mantano and Hirasaki 1997). This is particularly interesting in light of the fact that the human cerebellum appears to be smaller than expected for an ape brain of human size (Semendeferi and Damasio 2000).

It is important to keep in mind that a part of the brain does not need to be 'new' or grossly enlarged for reorganization to occur. For example, Armstrong (et al. 1987) investigated which thalamic nuclei changed in volume relative to the rest of the thalamus and found that, after controlling for the size of the brain, anthropoids that lived in single-male societies had more anterior principal thalamic neurons than primates that lived in multi-male societies. Since limbic structures are known to be important for social life, it is not surprising that the sizes and reorganizations of limbic structures may link more than those of other structures to specific behaviors and niches (e.g., the relationship of olfactory bulbs with nocturnal and diurnal niches) (Finlay et al. 2001). (Along somewhat related lines but focusing on gross brain size rather than reorganization, the "social brain" (or Machiavellian Intelligence) hypothesis incorporates data showing that neocortical size correlates with social group size and proposes that large primate brains evolved in response to living in complexly bonded social groups [Dunbar 1998, 2003; Falk and Dudek 1993; Byrne 2000].)

While complex social life may, indeed, have contributed directly or indirectly to selection for large primate brains, partitioning the types of internal reorganization that characterize different groups hones in on other aspects of lifestyle. In an important follow-up to Finlay et al.'s research, de Winter and Oxnard (2001) performed similar multivariate analyses on a greatly enlarged data set that confirmed earlier findings (Finlay and Darlington 1995), and extended earlier multivariate analyses to include a series of brain-part ratios that partly reflected in-put/out-put relationships within the brain. Rather than grouping primates according to phylogenetic relationships, however, the groups that emerged from the comparisons were based on similar lifestyles, such as lower-limb dominated lifestyles that involve much leaping (tarsiers, indriids, galagos, mouse lemurs), and four-limb dominated lifestyles (some strepsirrhines, New and Old World monkeys) (Oxnard 2004, de Winter and Oxnard 2001). Genera with upper-limb dominated lifestyles involving hang-feeding in arboreal habitats and escaping by upper-limb acrobatics (*Ateles*, *Lagothrix*, *Hylobates*, *Pan* and *Gorilla*) also emerged as a cluster:

The brain organization that is involved in the trend along the axis towards the fore-limb dominant species is increasing expansion of the neocortex, striatum, cerebellum and diencephalon relative to medulla. This particular pattern of brain organization could involve brain functions based on expansion of higher levels of voluntary sensory and motor control. In turn, they could relate to a trend towards creatures with greater degrees of complex voluntary behavior and increased capacity to plan strategically and to control complex motor actions. (Oxnard 2004:1147)

Significantly, similar multivariate analyses separate humans from chimpanzees to a degree that rivals the extent of separation within all Old World monkeys and apes, which is not only contrary to the much-cited close genetic relationship between *Pan* and *Homo* but also implies that the internal organization of the human brain is quantitatively different from any other living primate (Oxnard 2004). Further, the differences between chimpanzees and humans are not related to brain size alone, and may relate to the existence of internal functional interactions, loops or modules (ibid).

(12.)3.1 Neurological reorganization in hominins

In light of the theoretical emphasis neurological reorganization has been given in the literature, surprisingly little precise information is available about its nature during hominin evolution. However, recent work by a few workers provides a glimpse of what might have happened. Contrary to earlier notions about 'mosaic evolution,' the research of Finlay, Oxnard, and colleagues discussed above suggests that major steps in neurological reorganization (i.e., as opposed to, say, fine tuning of individual nuclei) rarely, if ever, entailed isolated structures within the brain but, instead, were probably distributed across multiple structures (or modules) within the brain. This hypothesis is concordant with functional imaging studies that indicate that higher-order cognitive tasks engage numerous cortical areas that are dispersed across the cortical mantle (Frackowiack et al. 1997). For this reason, I remain respectfully skeptical about the suggestion (based on controversial identifications of the lunate sulcus) that early australopithecines with otherwise ape-like cortical morphologies were reorganized in posterior parietal association cortices (Holloway et al. 2004). That said, I agree with my colleagues that dramatic neurological reorganization can occur separately from brain enlargement, but hypothesize that it is likely to be manifested more globally.

Recent research of Semendeferi and colleagues (Semendeferi 2001, Semendeferi and Damasio 2000, Semendeferi et al. 1997) sheds light on neurological reorganization in hominins at the level of large sectors including whole lobes. Semendeferi and Damasio (2000) obtained MRI scans of brains from nearly 30 living humans and apes, processed the data to obtain volumes of the various lobes, and performed comparative statistical analyses of the absolute and relative volumes of each lobe. Although the overall relative sizes of the lobes of the brain changed little after the phylogenetic split of hominins from great apes, this study revealed that the temporal lobe (involved in recognition and memory) may have differentially enlarged during hominin evolution, while the human cerebellum is significantly smaller than expected from allometric predictions. The insula (which processes autonomic functions, internal stimuli, taste, and speech articulation [Dronkers 1996]) may also be somewhat enlarged in humans. Contrary to Semendeferi's (2001) finding of no increase beyond allometric expectations for the large parieto-

occipital sector of the human brain, those of another study (utilizing geometric morphometrics) suggest that modern humans are characterized by relatively great development of the parietal lobes (Bruner 2004), a conclusion that awaits further confirmation.

Equally important, by analyzing 3D-MR reconstructions of brains from living apes and humans (Semendeferi et al. 1997) in conjunction with comparative histological sections from postmortem specimens, Semendeferi and her colleagues have helped dispel old myths (indeed, some might even say 'received wisdom') about the evolution of human frontal lobes. Until recently, many believed that higher cognitive abilities in humans evolved in conjunction with differentially enlarged frontal lobes. Semendeferi's comparative imaging work dispelled this notion, however, by quantifying the allometric nature of human frontal lobe enlargement (i.e., they are the size one would expect in ape brains enlarged to the size of human brains).

Turning to the important question of neurological reorganization within larger sectors, comparative cytoarchitectonic studies suggest that human frontal lobe evolution entailed internal rewiring and enlargement in some areas (e.g., Brodmann's area 10, Semendeferi et al. 2001, 2002) and a decrease in others (Brodmann's area 13; Semendeferi et al. 1998), rather than an increase in overall frontal lobe size. It was therefore concluded that area 13 of the posterior orbitofrontal cortex, a part of the limbic system that is involved in emotional reactions to social stimuli, is a conserved feature in brain evolution, whereas the relative size of area 10 that forms the frontal pole in ape and human brains and contributes to planning and the undertaking of initiatives did increase during hominin evolution. A remarkable increase in the proportion of white matter volume of the human precentral cortex was also found (Semendeferi et al.1997), which again speaks to the fact that human frontal lobes are better wired rather than relatively larger than those of their ape cousins.

Recent work also suggests that the visual system was reorganized during human evolution (Preuss et al. 1999), which surprised even the investigators because "it is axiomatic among neuroscientists and psychologists that the visual abilities of humans and monkeys are virtually identical" (Preuss 2001:156). Specifically, the authors report histological evidence suggesting that the human primary visual area differs from that of apes and monkeys in the way that information is segregated from layers of the lateral geniculate nucleus. Interestingly, they suggest that humans have enhanced capacities for analyzing moving stimuli and speculate that these changes may have occurred in response to the challenge of visually decoding rapid mouth movements entailed in speech and its accompanying manual gestures (Preuss 2001).

Neurological Reorganization Related to Language, Handedness, and Music

It is tempting to hypothesize that the expansion of the human cortex was accompanied by the addition of new areas, and that the classic language areas in the left hemisphere (Broca's speech area [Brodmann's areas 44 and 45] and Wernicke's language receptive area [Brodmann's areas 21, 22 plus, when defined more broadly, 37, 39, 40]) are neomorphic structures (Preuss 2001). However, Preuss notes that "at the present time, there is no good evidence that humans possess species-specific cortical areas" (Preuss 2001:155). Indeed, cytoarchitectonic studies on macaques suggest that the inferior limb of the arcuate sulcus contains homologs of areas 44 and 45 (Galaburda and Pandya 1982, Deacon 1992, Preuss 2000), and homologs of posterior language

areas (Wernicke's area) have been identified in the macaque superior temporal and inferior parietal lobes (Galaburda and Pandya 1982, Preuss 2000) (Fig 4). Simple movements of the mouth and hands activate ventral premotor cortex in monkeys, as they do its likely homolog, Broca's area, in humans (Colebatch et al. 1991, Gallese et al 1996, Petersen et al. 1988, Rizzolati et al. 1996), and these 'mirror neurons' also discharge when similar actions are observed in others (Rizzolati et al 1996). Because of their discovery in human and nonhuman primates, mirror neurons are hypothesized to be part of an action-perception network that facilitates gestural (manual and orofacial) communication in apes and humans as well as linguistic communication in the latter (Falk 2004c,d). From a functional perspective, it is also interesting that, like humans, macaques are thought to be left-hemisphere dominant for processing certain socially meaningful (as opposed to neutral) vocalizations (Petersen et al 1978, 1984; Heffner and Heffner 1984, 1986).

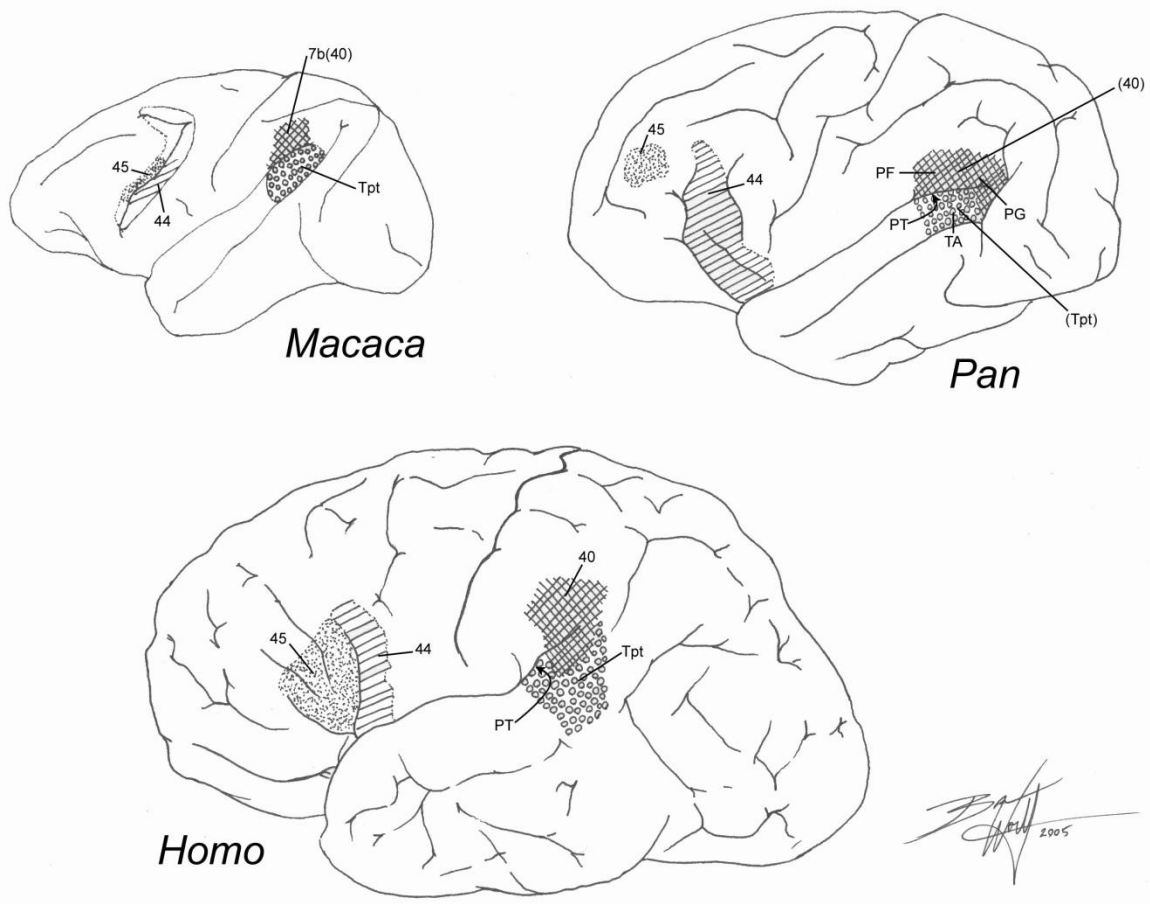


Fig. (12.) 4 ***Gross language areas in humans and their proposed homologs in macaques and common chimpanzees. In the left hemispheres of humans, Brodmann's areas 45 (pars triangularis) and 44 comprise Broca's speech area, while areas Tpt (temporoparietal), PT (planum temporale, buried within depths of Sylvian fissure), and Brodmann's area 40 are parts of Wernicke's receptive language area. Human area 40, macaque area 7b, and chimpanzee area PF/PG are proposed homologs, as are human and macaque areas Tpt and***

chimpanzee area TA. The proposed homologs are based on cytoarchitectonic and functional similarities and should be viewed as tentative. Data from Preuss (2000); Amunts et al. (1999); Gannon et al. (1998); Aboitz and Ricardo (1997); Galaburda and Pandya (1982); Crosby, Humphrey and Lauer (1962); Jackson et al. (1969); Bailey et al. (1950); von Bonin (1949).

Palaeoneurologists have long speculated about whether a chimpanzee-like frontal lobe in early hominins could have given rise to a humanlike Broca's area, but these efforts have been hampered by a lack of consensus about the identities of homologous sulci and gyri in great apes and humans, which were traditionally proposed mainly on the basis of relative positions of sulci rather than on cytoarchitectonic grounds (Connolly 1950). Unlike frontal lobes of humans, a fronto-orbital sulcus (*fo*) of chimpanzees typically incises the lateral border of the dorsal frontal lobe and extends onto its orbital surface where it courses caudally to the temporal pole (Connolly 1950). The bulge delimited by *fo*, or so-called orbital cap, represents Brodmann's area 44 (Bailey 1948, Bailey et al. 1950, Connolly 1950, Jackson et al. 1969) (Fig. 4) and to varying degrees the addition of part of area 45 (Sherwood et al. 2003) in chimpanzees. Sherwood et al (2003) explored the relationship of sulci to cytoarchitectural areas 44 and 45 in brains from five adult chimpanzees and found that, just as the border between cytoarchitectonic areas 44 and 45 of humans is not always defined by sulci (Amunts et al 1999), the border between the two areas in chimpanzees does not always coincide with the surface of the fronto-orbial sulcus. Rather, intersubject variability was high and area 45 tended to spill over caudally into the presumed domain of area 44 in both species. It is also important to stress that the similar bulge that appears at the level of the temporal pole in humans, the orbital cap (or so-called "Broca's cap"), is *not* homologous to that of chimpanzees because it contains areas 45 and 47 rather than the areas located in the chimpanzee cap – namely, area 44 (Connolly 1950) and (sometimes) 45 (Sherwood et al. 1999). Although it has recently been suggested that area 44 is larger in the left than the right hemisphere of chimpanzees (Cantalupo and Hopkins 2001) as is the case for humans (Amunts et al. 1999), for methodological reasons the jury is still out on whether or not the homolog of Broca's area in great apes exhibits humanlike asymmetry (Sherwood et al. 2003).

There is more agreement about asymmetry in the chimpanzee homolog of at least part of Wernicke's area. Gannon and colleagues (1998, 2001) investigated the homolog of the planum temporale (PT) in 18 chimpanzee brains and determined that the left PT was significantly larger in 17 of the18 brains (94%). This region is a component of Wernicke's area in the left hemisphere of humans, in whom it manifests a similar anatomical pattern and left hemisphere size predominance. The authors concluded that human language may have been founded on this basal anatomic substrate and that it may have been lateralized to the left hemisphere in the common ancestor of chimpanzees and humans millions of years ago (Gannon 1998).

Thus, more than a century after Broca's area was identified, it is recognized that it has certain nonlinguistic functions and that the act of speech activates wider areas of the cerebral cortex. Nevertheless, the importance of this area for speech and Wernicke's area for human language reception cannot be denied, and the evolutionary details of their coordinated neurological reorganization (including with other parts of the brain) remain open to investigation (Sherwood et al 2003, Holloway et al 2004).

One may, however, engage in reasoned speculation about the evolution of a suite of unique behaviors in hominins and their underlying interconnected and reorganized neurological structures. We know, for example, that people are more neurologically lateralized than other primates and that certain cortical asymmetries underpin behaviors that are unique to the human primate (Falk 1987a), such as the universally high frequency of right-handedness, symbolic language, and humanlike creative abilities related to music, art, and technology (Falk 2000a, 2004a). One may explore the evolution of brain lateralization by studying shape asymmetries in endocasts of fossil hominins (Holloway et al. 2004), since in living people these petalias (which exist to a lesser extent in nonhuman primates [LeMay et al. 1982]) are statistically associated with handedness patterns and sex (LeMay 1977, Bear et al. 1986). We also know that men and women differ in the anatomies of their brains, and that these differences are hypothesized to have evolved as correlates of different reproductive strategies (Falk 1997, 2001, Falk et al. 1999). Although a review of the literature on primate brain lateralization is beyond the scope of this paper, it is worth noting that Hofman's (2001) exploration of design principles that govern the evolution of large brains led him to conclude that large brains tend to increase the number of distinct cortical areas in order to maintain processing capacity, and that this may be related to the high degree of brain lateralization in humans:

Large-brained species may develop some degree of brain lateralization as a direct consequence of size. If there is evolutionary pressure on certain functions that require a high degree of local processing and sequential control, such as linguistic communication in human brains, these will have a strong tendency to develop in one hemisphere (Aboitiz, 1996). (Hofman 2001:123)

(12.) 4 Conclusion

Primate nervous systems became more variable over the course of evolution. During the Eocene, brain sizes were all small. Today, there are still small-brained species, but also larger-brained ones due to a widening range of variation as the Cenozoic progressed. The same can be said for RBS. Over thirty years ago, Radinsky (1974) pointed out that elaboration of visual abilities and reduction of olfaction were among the features involved at the base of prosimian radiations and, again, in the later emergence of higher primates from prosimian stock. The broad visual and limbic systems that subserve these features were (and are) extremely important for primate species-specific communication. Over time, the various neurological components of these systems became variably elaborated and reorganized within different groups. Preuss' (2001) suggestion that the 'surprisingly' reorganized human visual system may have evolved in response to the challenge of visually decoding rapid mouth movements entailed in speech and its accompanying manual gestures underscores the ongoing continuity of adaptations that occurred extremely early in primate evolution. Semendeferi's (2001) seminal work on hominoid prefrontal cortices (Brodmann's areas 10 and 13) illustrates that executive parts of the cerebral cortex eventually got into the act and were also subjected to evolutionary reorganization (Semendeferi et al. 2001).

The arguments about the relative evolutionary merits of brain size versus neurological reorganization are unnecessary (Gould 2001). The suggestion by Finlay and colleagues (Finlay and Darlington 1995, Finlay et al. 2001, Kaskan and Finlay 2001) that the sizes of different brain structures is a consequence of overall brain size, not only in primates but also in other mammals,

is an important contribution to our understanding of ontogenetic brain development and brain evolution. What has sometimes been lost is that Finlay's model leaves room for evolution of the kinds of neurological specializations that interest palaeoneurologists. Oxnard and de Winter's models for parsing brain size evolution are no less elegant and shed light on the evolution of broad (but presumably intertwined) subsections of the nervous system that subserve very different lifestyles, separate from phylogenetic considerations (de Winter and Oxnard 2001, Oxnard 2004). These findings extend, rather than contradict, those of Finlay and colleagues. Add to the mix, neurological reorganization that can take place with, or without, an increase in brain size and the potential for evolving internal functional interactions, loops or modules (Oxnard 2004) becomes realized. Primate cortices may, indeed, represent "veritable hotbed(s) of evolutionary reorganization" (Preuss 2001:140)! As students of palaeoneurology have discerned, however, the high intelligence of today's primates flowered from trends in primate brain evolution that reach back into deep time (Radinsky 1974). Given the complexities involved in disentangling the evolutionary dynamics of increasing brain size from the intricate (and often hidden) subtleties of neurological reorganization, that insight is somehow very satisfying.

References

Aboitiz F (1996) Does bigger mean better? Evolutionary determinants of brain size and structure. Brain Behav Evol 47:225-245

Aboitiz F, Ricardo GV (1997) The evolutionary origin of the language areas in the brain. A neuroanatomical perspective. Brain Research Reviews 25:381-396

Aiello LC, Wheeler P (1995) The expensive-tissue hypothesis; the brain and the digestive system inhuman and primate evolution. Cur Anthropol 36:199-221

Aiello LC, Bates N, Joffe T (2001) In defense of the expensive tissue hypothesis. In: Falk D and Gibson KR (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 57-78

Allman J (1977) Evolution of the visual system in the early primates. In: Sprague JM, Epstein AN (eds) Progress in Psychology and Physiological Psychology, Academic Press, New York, pp. 1-53

Allman J (1990) Evolution of neocortex. In Jones EG, Peters A (eds) Cerebral Cotex, Volume B: Comparative Structure and Evolution of Cerebral Cortex, Part II, Plenum, New York, pp. 269-283

Amunts K, Schleicher A, Bürgel U, Mohlberg H, Uylings HBM, Zilles K (1999) Broca's region revisited: cytoarchitectures and intersubject variability. J Comp Neurol 412:319-341

Armstrong E, Clarke MR, Hill EM (1987) Relative size of the anterior thalamic nuclei differentiates anthropoids by social system. Brain Behav Evol 30:263-271

Bailey P (1948) Concerning cytoarchitecture of the frontal lobe of chimpanzee (*Pan satyrus*) and man (*Homo sapiens*). In: The Frontal Lobes, The Williams & Wilkins Company, Baltimore, pp. 84-94

Bailey P, von Bonin G, McCulloch WS (1950) The isocortex of the chimpanzee brain. The University of Illinois Press, Urbana

Balter MA, Gibbons A (2002) Were 'little people' the first to venture out of Africa? Science 297: 26-27

Barton RA (2001) The coordinated structure of mosaic brain evolution (commentary). Behav Brain Sci 24:281-282

Barton RA, Harvey PH (2000) Mosaic evolution of brain structures in mammals. Nature 405:1055-1058

Barton RA, Purvis A, Harvey PH (1995) Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. Phil Trans Roy Soc London B 348:381-392

Bauchot R, Stephan H (1966) Données nouvelles sur l'encéphalisation des insectivores et des prosimiens. Mammalia 30:160-196

Bauchot R, Stephan H (1969) Encephalisation et niveau evolutif chex les simiens. Mammalia 33:235-275

Bear D, Schiff D, Saver J, Greenberg M, Freeman R (1986) Quantitative analysis of cerebral asymmetries. Fronto-occipital correlation, sexual dimorphism and association with handedness. Arch Neurol 43:598-603

Brown B, Walker A, Ward CV, Leakey RE (1993) New *Australopithecus boisei* calvaria from east Lake Turkana. Am J Phys Anthropol 91:137-159

Brown P, Sutikna T, Morwood MJ, Soejono RP, Jatmiko, Saptomo EW, Due RA (2004) A new small-bodied hominin from the late Pleistocene of Flores, Indonesia. Nature 431:1055-1061

Bruner E (2004) Geometric morphometrics and paleoneurology: brain shape evolution in the genus *Homo*. J hum Evol 47:279-303

Byrne RW (2000) Evolution of primate cognition. Cogn Sci 24:543-570

Cantalupo C, Hopkins WD (2001) Asymmetric Broca's area in great apes. Nature 414:505

Clutton-Brock TH, Harvey PH (1980) Primates, brains and ecology. J. Zool 190:309-323

Colebatch JG, Deiber MP, Passingham RE, Friston KJ, Frackowiak RSJ (1991) Regional cerebral blood flow during voluntary arm and hand movements in human subjects. J Neurophysiol 65:1392-1401

Connolly CJ (1950) External morphology of the primate brain. Charles C Thomas, Springfield, Illinois

Conroy GC, Vannier MW (1985) Endocranial volume determination of matrix-filled fossil skulls using high-resolution computed tomography. In: Tobias PV (ed) Hominid Evolution: Past, Present and Future, Alan R. Liss, New York, pp. 419-426

Conroy GC, Vannier MW, Tobias PV (1990) Endocranial features of *Australopithecus africanus* revealed by 2- and 3-D computed tomography. Science 247:838-841

Conroy GC, Weber GW, Seidler H, Tobias PV, Kane A, Brunsden B (1998) Endocranial capacity in an early hominid cranium from Sterkfontein, South Africa. Science 280:1730-1731

Crosby EC, Humphrey T, Lauer EW (1962) Correlative Anatomy of the Nervous System. The Macmillan Company, New York

Deacon TW (1992) Cortical connections of the inferior arcuate sulcus cortex in the macaque brain. Brain Res 573:8-26

de Winter W, Oxnard CE (2001) Evolutionary radiations and convergences in the structural organization of mammalian brains. Nature 409:710-714

Dronkers NF (1996) A new brain region for coordinating speech articulation. Nature 384:159-161

Dunbar RIM (1998) The evolution of the social brain. Evolutionary Anthropology 6:178-190

Dunbar RIM (2003) The social brain: Mind, language, and society in evolutionary perspective. Annu Rev Anthropol 32:163-181

Falk D (1978) Brain evolution in Old World monkeys. Am J Phys Anthropol 48:315-319

Falk D (1980a) A reanalysis of the South African australopithecine natural endocasts. Am J Phys Anthropol 53:525-539

Falk D (1980b) Hominid brain evolution: the approach from paleoneurology. Yrbk Phys Anthropol 23:93-107

Falk D (1981) Comparative study of the endocranial casts of New and Old World monkeys. In: Ciochon RL, Chiarelli AB (eds) Evolutionary Biology of the New World Monkeys and Continental Drift, Plenum, New York, pp. 275-292

Falk D (1982) Mapping fossil endocasts. In: Armstrong E, Falk D (eds) Primate Brain Evolution, Methods and Concepts, Plenum Press, New York, pp 217-226

Falk D (1983) A reconsideration of the endocast of Proconsul africanus. In: Ciochon RL, Corruccini RS (eds) New Interpretations of Ape and Human Ancestry, Plenum, New York, pp. 239-248

Falk D (1985) Hadar AL 162-28 endocast as evidence that brain enlargement preceded cortical reorganization in hominid evolution. Nature 313:45-47

Falk D (1986) Endocranial casts and their significance for primate brain evolution. Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy, pp. 477-490

Falk (1987a) Brain lateralization in primates. Yrbk Phys Anthropol 30:107-125

Falk D (1987b) Hominid paleoneurology. Yrbk Phys Anthropol 16:13-30

Falk D (1990) Brain evolution in *Homo*: the "radiator" theory (target article, commentaries and author's response). Behav Brain Sci 13:333-381

Falk D (1997) Brain evolution in females: An answer to Mr. Lovejoy. In: Hager (ed) Women in Human Evolution, Routledge, London, pp. 114-136

Falk D (1998) Hominid brain evolution: Looks can be deceiving. Science 280:1714

Falk D (2000a) Hominid brain evolution and the origins of music. In: Wallin NL, Merker B, Brown S (eds) The Origins of Music, MIT Press, Cambridge, pp. 197-216

Falk D (2000b) Primate Diversity. WW Norton, New York.

Falk D (2001) The evolution of sex differences in primate brains. In: Falk D and Gibson KR (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 98-112

Falk D (2004a) Braindance, Revised and Expanded Edition. University Press of Florida, Gainesville.

Falk D (2004b) Hominin brain evolution: New century, new directions. Collegium Antropologicum 28:59-64

Falk D (2004c) Prelinguistic evolution in early hominins: Whence motherese? (target article). Behav Brain Sci 27: in press.

Falk D (2004d) The *"Putting the baby down" hypothesis*: Bipedalism, babbling, and baby slings (response to commentaries). Behav Brain Sci 27, in press

Falk D (2005) Constraints on brain size: The radiator hypothesis. In: Preuss TM and Kaas JH (eds) The Evolution of Primate Nervous Systems. Elsevier, submitted

Falk D, Dudek B (1993) Mosaic evolution of the neocortex (commentary). Behav Brain Sci 16:701-702

Falk D, Froese N, Sade D, Dudek B (1999) Sex differences in brain/body relationships of rhesus monkeys and humans. J hum. Evol 36:233-238

Falk D, Gibson K (eds) (2001) Evolutionary Anatomy of the Primate Cerebral Cortex. Cambridge University Press, Cambridge. In: Falk D and Gibson KR (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 98-112

Falk D, Hildebolt C, Smith K, Morwood MJ, Sutikna T, Brown P, Jatmiko, Saptomo EW, Brunsden B, Prior F (2005) The brain of LB1, *Homo floresiensis*. Science 308:242-245

Falk D, Redmond JC Jr, Guyer J, Conroy GC, Recheis W, Weber GW, Seidler H (2000) Early hominid brain evolution: A new look at old endocasts. J hum Evol 38:695-717

Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex 1:1-47

Fiez JA (1996) Cerebellar contributions to cognition. Neuron 16:13-15

Finlay BL, Darlington RB (1995) Linked regularities in the development and evolution of mammalian brains. Science 268:1578-1584

Finlay BL, Darlington RB, Nicastro N (2001) Developmental structure in brain evolution. Behav Brain Sci 24:283-308

Frackowiak RSJ, Friston KJ, Frith CD, Dolan RJ, Mazziotta JC (1997) Human Brain Function. Academic Press, San Diego

Gabunia L, Vekua A, Lordkipanidze D, Swisher CC, Ferring R, Justus A, Nioradze M, Tvalchrelidze M, Anton SC, Bosinski G, Joris O, de Lumley MA, Majsuradze G, Mouskhelishvili A (2000) Earliest Pleistocene Hominid Cranial Remains from Dmanisi, Republic of Georgia: Taxonomy, Geological Setting, and Age. Science 288:1019-1025

Galaburda AM and Pandya DN (1982) Role of architectonics and connections in the study of primate brain evolution. In: Falk D and Armstrong E Primate Brain Evolution: Methods and Concepts, Plenum, NY, pp. 203-216

Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. Brain 119:593-609

Gannon PJ, Holloway RL, Broadfield DC, Braun AR (1998) Asymmetry of chimpanzee planum temporale: human like pattern of Wernicke's brain language area homology. Science 279:220-222

Gannon PJ, Kheck NM, Hof PR (2001) Language areas of the hominoid brain: a dynamic communicative shift on the upper east side planum. In Falk D and Gibson KR (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 216-240

Garber PA (2004) New perspectives in primate cognitive ecology. Am J Primatol 62:133-137

Gibson KR (1986) Cognition,brain size and the extraction of embedded food resources. In Else JG, Lee PC (eds) Primate Ontogeny, Cognition, and Social Behaviour, Cambridge University Press, Cambridge, pp. 93-103

Gibson KR (2001) Bigger is better; primate rain size in relationship to cognition. In Falk D and Gibson KR (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 79-97

Gould SJ (2001) Size matters and function counts. In: Falk D and Gibson KR (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp.xiii-xvii

Gurche JA (1982) Early primate brain evolution. In: Armstrong E, Falk D (eds) Primate Brain Evolution, Methods and Concepts, Plenum Press, New York, pp. 227-246

Haug H (1987) Brain sizes, surfaces, and neuronal sizes of the cortex cerebri: a stereological investigation of man and his variability and a comparison with some mammals (primates, whales, marsupials, insectivores, and one elephant). Am J Anat 180:126-142

Heffner HE, Heffner RS (1984) Temporal lobe lesions and perception of species-specific vocalizations by macaques. Science 226:75-76

Heffner HE, Heffner RS (1986) Effect of unilateral and bilateral auditory cortex lesions on the discrimination of vocalization by Japanese macaques. J Neurophysiol 56:683-701

Hofman MA (1983) Encephalization in hominids: evidence for the model of punctuationalism. Brain Behav Evol 22:102-117

Hofman MA (2001) Brain evolution in hominids: are we at the end of the road? In: Falk D and Gibson KR (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 113-127

Holloway RL (1974) On the meaning of brain size. A review of H. J. Jerison's 1973 Evolution of the Brain and Intelligence. Science 184:677-679.

Hollway RL (1979) Brain size, allometry, and reorganization: toward a synthesis. In Hahn ME, Jensen G, Dudek BC (eds) Development and Evolution of Brain Size: Behavioral Implications, Academic Press, New York, pp. 59-88

Holloway RL, Broadfield DC, Yuan MS (2004) The Human Fossil Record Volume Three Brain Endocasts The Paleoneurological Evidence. Wiley-Liss, New York.

Holloway RL, Post DG (1982) The relativity of relative brain measures and hominid mosaic evolution. In: Armstrong E, Falk D (eds) Primate Brain Evolution, Methods and Concepts, Plenum Press, New York, pp 57-76

Huffman O (2001) Geologic context and age of the Perning/Mojokerto *Homo erectus*, East Java. J Hum Evol 40:353-362

Jackson WJ, Reite ML, Buxton DF (1969) The chimpanzee central nervous system: A comparative review. Primates in Med 4:1-51

Jerison HJ (1973) Evolution of the brain and intelligence. Academic Press, New York

Jerison HJ (1982) Allometry, brain size, cortical surface, and convolutedness. In: Armstrong E, Falk D (eds) Primate Brain Evolution, Methods and Concepts, Plenum Press, New York, pp 77-84

Jerison HJ (2001) The study of primate brain evolution: where do we go from here? In: Falk D and Gibson KR (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 305-337

Jones KE, MacLarnon AM (2004) Affording larger brains: testing hypotheses of mammalian brain evolution on bats. Am Naturalilst 164:E20-E31

Kaas JH (1987) The organization and evolution of neocortex. In: Wise SP (ed) Higher Brain Function: Recent Explorations of the Brain's Emergent Properties, John Wiley, New York, pp. 347-378

Kaas JH (1995) The evolution of isocortex. Brain Behav Evol 46:187-196

Kaskan PM, Finlay BL (2001) Encephalization and its developmental structure: how many ways can a brain get big? In: Falk D and Gibson (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 14-29

Leigh SR (1992) Cranial capacity evolution in Homo erectus and early Homo sapiens. Am J Phys Anthropol 87:1-13

Leigh SR (2004) Brain growth, life history, and cognition in primate and human evolution. Am J Phys Anthropol 62:139-164

LeMay M (1977) Asymmetries of the skull and handedness. Phrenology revisited. J Neurol Sci 32:243-253

LeMay M, Billig MS, Geschwind N (1982) Asymmetries of the brains and skulls of nonhuman primates. In: Armstrong E, Falk D (eds) Primate Brain Evolution, Methods and Concepts, Plenum Press, New York, pp 263-277

Martin RD (1982) Allometric approaches to the evoluton of the primate nervous system. In Armstrong E, Falk D (eds) Primate Brain Evolution, Methods and Concepts, Plenum Press, New York, pp 39-56

Martin RD (1990) Primate Origins and Evolution: A Phylogenetic Reconstruction, Chapman & Hall, London

Martin RD (1996) Scaling of the mammalian brain: the maternal energy hypothesis. News in Physiological Sciences 11:149-156

Matano S, Hirasaki E (1997) Volumetric comparisons in the cerebellar complex of anthropoids, with special reference to locomotor types. Am J Phys Anthropol 103:173-183

Matano S, Baron G, Stephan H, Frahm H (1985) Volume comparisons in the cerebellar complex of primates II. Cerebellar Nuclei. Folia Primatological 44:182-203

Milton K (1988) Foraging behavior and the evolution of primate intelligence. In: Byrne R, Whiten A (eds), Machiavellian Intelligence, Clarendon Press, Oxford, pp. 285-305

Morwood MJ, Soejono RP, Roberts RG, Sutikna T, Turney CSM, Westaway KE, Rink WJ, Zhao Jx, van den Bergh GC, Due RA, Hobbs, DR, Moore MW, Bird MI, Fifield LK (2004) Archaeology and age of a new hominin from Flores in eastern Indonesia. Nature 431:1087-1091

Muller RA, Courchesne E, Allen G (1998) The cerebellum: so much more. Science 282:879-880

Oxnard CE (2004) Brain evolution: Mammals, primates, chimpanzees, and humans. Int. J. Primatol 25:1127-1158.

Passingham RE (1973) Anatomical differences between the brain of man and other primates. Brain Behav Evol 7:337-359

Passingham RE (1975a) Changes in the size and organization of the brain in man and his ancestors. Brain Behav Evol 11:73-90

Passingham RE (1975b) What's so special about man's brain? New Scientist 68:510-511

Passingham RE, Ettlinger G (1974) A comparison of cortical functions in man and the other primates. In: Pfeiffer C, Smythies J (eds) International Review of Neurobiology, Academic Press, New York, pp. 233-299

Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1988) Positron emission tomographic studies of the cortical anatomy of single-word processing. Nature 331:585-589

Petersen M, Beecher M, Zoloth S, Moody D, Stebbins W (1978) Neural lateralization of species-specific vocalizations by Japanese macaques (*Macaca fuscata*). Science 202:324-327

Petersen MR, Beecher MD, Zoloth SR, Green S, Marler PR, Moody DB, Stebbins WC (1984) Neural lateralization of vocalizations by Japanese macaques: Communicative significance is more important than acoustic structure. Behav Neurosci 98:779-790

Preuss TM (2000) What's human about the human brain? In: Gazzaniga MS (ed) The New Cognitive Neurosciences, MIT Press, Cambridge, pp.1219-1234

Preuss TM (2001) The discovery of cerebral diversity: an unwelcome scientific revolution. In: Falk D and Gibson (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp.138-1164

Preuss TM, Goldman-Rakic PS (1991) Architectonics of the parietal and temporal association cortex in the strepsirhine primate *Galago* compared to the anthropoid primate *Macaca*. J Comp Neurol 310:475-506

Preuss TM, Qi H-X, Kaas JH (1999) Distinctive compartmental organization of human primary visual cortex. Proc Nat Acad Sci USA 96:11601-11606

Radinsky LB (1972) Endocasts and studies of primate brain evolution. In: Tuttle R (ed) The Functional and Evolutonary Biology of Primates, Aldine, Chicago, pp. 175-184

Radinsky LB (1974) The fossil evidence of anthropoid brain evolution. Am J Phys Anthropol 41:15-27

Radinsky LB (1975) Primate brain evolution. Amer Sci 63:656-663

Radinsky LB (1979) The fossil record of primate brain evolutoin (49th James Arthur Lecture). American Museum of Natural History, New York

Radinsky LB (1982) Some cautionary notes on making inferences about relative brain size. In: Armstrong E, Falk D (eds) Primate Brain Evolution, Methods and Concepts, Plenum Press, New York, pp 29-37

Ringo JL (1991) Neuronal interconnection as a function of brain size. Brain Behav Evol 38:1-6

Rizzolatti G, Fadiga L, Gallese V, Fogassi L (1996) Premotor cortex and the recognition of motor actions. Cognit Brain Res 3:131-141

Ruff CB, Trinkhaus E, Holliday TW (1997) Body mass and encephalizaiton in Pleistocene *Homo*. Nature 387:173-176.

Schultz AH (1956) Postembryonic age changes. In: Hofer H, Schultz AH, Starck D (eds) Primatologia Handbook of Primatology , S Karger, New York, pp. 887-964

Semendeferi K (2001) Advances in the study of hominoid rain evolution: magnetic resonance imaging (MRI) and 3-D reconstruction. In: Falk D and Gibson (eds) Evolutionary Anatomy of the Primate Cerebral Cortex, Cambridge University Press, Cambridge, pp. 257-289

Semendeferi K, Damasio, H (2000) The brain and its main anatomical subdivisions in living hominoids using magnetic imaging. J Hum Evol 38:317-332

Semendeferi K, Damasio H, Frank R, Van Hoesen GW (1997) The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. J Hum Evol 32:375-388

Semendeferi K, Armstrong A, Schleicher A, Zilles K, Van Hoesen GW (1998) Limbic frontal cortex in hominoids: a comparative study of Area 13. Am J Phys Anthropol 106:129-155

Semendeferi K, Armstrong E, Schleicher A, Zilles K, Van Hoesen GW (2001) Prefrontal cortex in humans and apes: a comparative study of Area 10. Am J Phys Anthropol 114:224-241

Semendeferi K, Lu A, Schenker N, Damasio H (2002) Humans and great apes share a large frontal cortex. Nat Neurosci 5:272-276

Sherwood CC, Broadfield DC, Holloway RL, Ganon PJ, Hof PR (2003) Variability of Broca's area homologue in African great apes: Implications for language evolution. Anat Rec 271A:276-285

Spoor F, Jeffery N, Zonneveld F (2000) Using diagnostic radiology in human evolutionary studies. J Anat 197:61-76

Stephan H (1972) Evolution of primate brains: a comparative anatomical investigation. In Tuttle R (ed) Evolutionary Biology of Primates, Aldine, Chicago, pp. 55-174

Stephan H, Bauchot R, Andy OJ (1970) Data on size of thebrain and of various brain parts in insectivores and primates. In: Noback CR, Montagna W (eds) Adv Primatol vol 1, The Primate Brain, Appleton-Century-Crofts, New York, pp. 289-297

Swisher C, Curtis G et al. (1994) Age of the earliest known hominids in Java, Indonesia. Science 263:1118-1121

Vekua A, Lordkipanidze D, Rightmire GP, Agusti J, Ferring R, Maisuradze G, Mouskhelishvili A, Nioradze M, Ponce de Leon M, Tappen M, Tvalchrelidze M, Zollikofer C (2002) A New Skull of Early Homo from Dmanisi, Georgia. Science 297:85-89

von Bonin G (1949) Architecture of the precentral motor cortex and some adjacent areas. In: Bucy PC (ed) The Precentral Motor Cortex, U of Illinois Press, Urbana-Champaign, pp 7-82

Walker A, Leakey R (1993) The Nariokotome *Homo Erectus* Skeleton, Harvard University Press, Cambridge.

Walker A, Falk D, Smith R, Pickford M (1983) The skull of *Proconsul africanus*; reconstruction and cranial capacity. Nature 305:525-527

Walker AC, Leakey RE, Harris JM, Brown FH (1986) 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. Nature 322:517-522

Weidenreich F (1943) The skull of *Sinanthropus pekinensis*: A comparative study on a primitive hominid skull. Paleontol Sinica, ns D 10:1-485

Wood B, Collard M (1999) The human genus. Science 284:65-71.

Wu X, Schepartz LA, Falk D, Liu W (2005) Endocranial cast of Hexian Homo erectus from South China. Am J Phys Anthropol, under review.

Zilles K, Armstrong E, Schlaug G, Schleicher A (1986) Quantitative cytoarchitectonics of the posterior cingulate cortex in primates. J Comp Neurol 253:514-524