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## (1) Evolution of the Primate Brain

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### (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<sup>3</sup> (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:

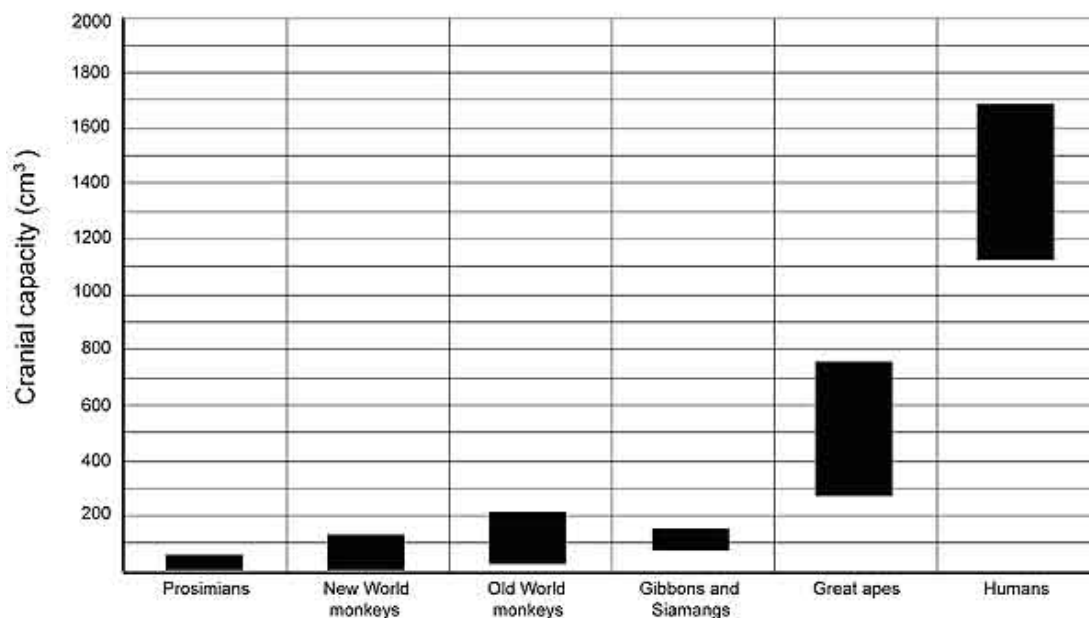
Deep disciplinary approaches: structural, functional and developmental, have started to coalesce whereby brain structures can be seen developing and functioning through the many new noninvasive imaging techniques that are available today. All this allows better understanding of not only how the brain 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

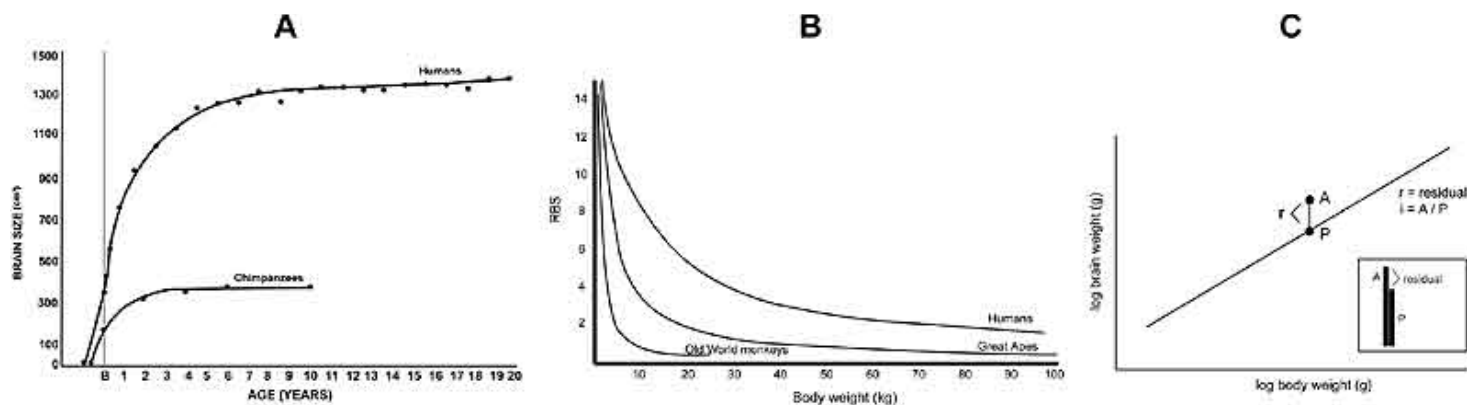
Certain allometric factors govern the general external and internal morphology of primate brains. Larger primate (indeed, mammalian) brains are characterized by more convolutions (gyri and sulci) than smaller ones (Radinsky 1975), which appears

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<sup>3</sup>, which is separate from the great ape range of 275-752cm<sup>3</sup> (Falk 1986) (Fig. [12.]1). The human range is above that for great apes and extends from around ~ 1100-1700 cm<sup>3</sup>, 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:

$$\log h = 1.632 + 0.63 \log k \quad (12.1)$$

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,

$$IP = PrG/BG \quad (12.2)$$

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:

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

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,  $N_c$ ) 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<sup>3</sup>, and their EQs suggest that the Eocene lemuriforms *Smilodectes*, *Adapis* and *Notharctus* were relatively smaller-brained than modern prosimians, and those for tarsiiiforms (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<sup>3</sup>, but had nevertheless attained an anthropoid level of RBS. The Miocene hominoid *Proconsul* had a comparatively whopping endocranial volume of 167 cm<sup>3</sup> 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).

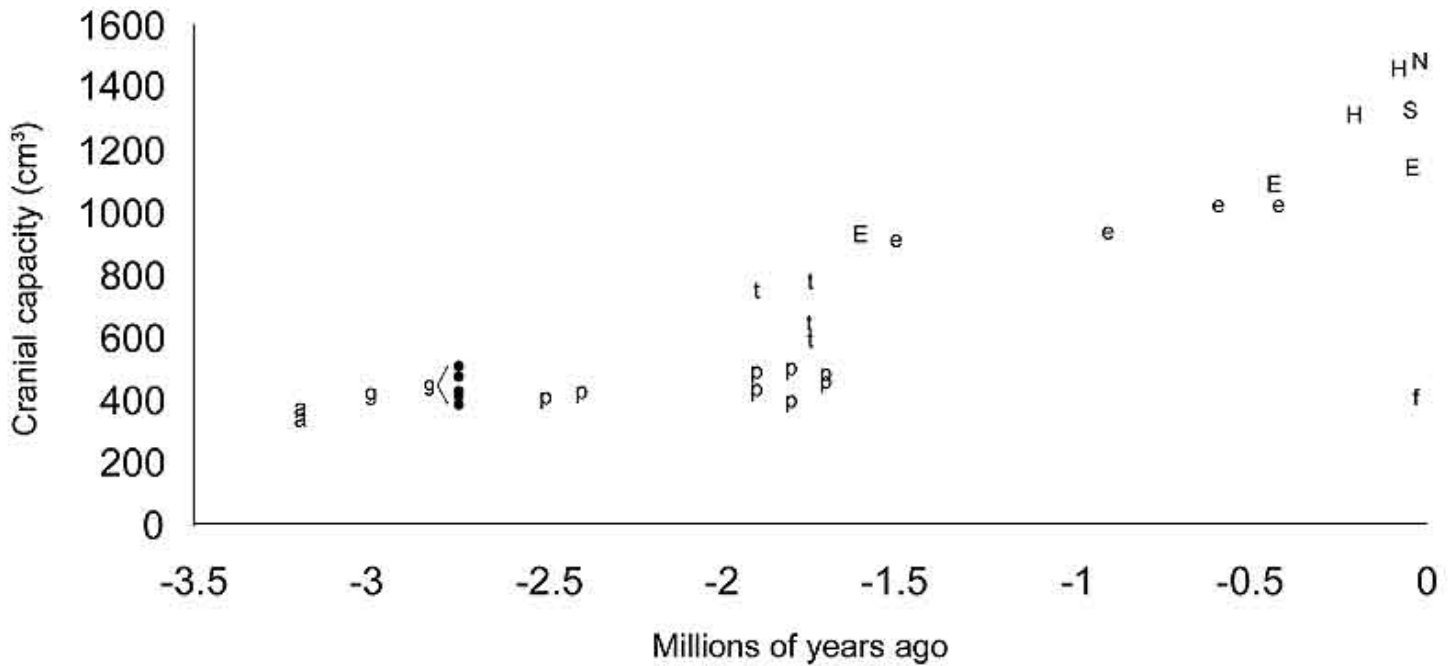
### (12.) 2. 1 Evolution of brain size in hominins

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 cm <sup>3</sup>	Cm <sup>3</sup> Reference
<b><i>Australopithecus</i></b>				
<i>A. afarensis</i>	~3.2	AL 333-105	343	Falk 1987b
-	~3.2	AL 162-28	375	Falk 1985
<i>A. africanus</i>	~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
<b><i>Paranthropus</i></b>				
<i>P. aethiopicus</i>	~2.5	KNM-WT 17000	410	Walker et al. 1986
<i>P. boisei</i>	~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 et al. 2000
-	~1.9	KNM-ER 407	438	Falk et al. 2000
-	~1.7	KNM-ER 732	466	Falk et al. 2000

<b><u>Australopithecus/Homo?</u></b>				
-	~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
<b><u>Homo erectus</u></b>				
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
<b><u>Homo</u></b>				
European	~0.2	-	Mean=1314	Hofman 1983
Neandertals	~0.07	-	Mean=1487	Hofman 1983
European	~0.04	-	Mean=1460	Hofman 1983
<i>H. sapiens</i>	~0.01	-	Mean=1330	Holloway et al. 2004
<b><u>Homo floresiensis</u></b>	~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	<i>Australopithecus afarensis</i>	g	<i>Australopithecus africanus</i>
p	<i>Paranthropus</i>	t	<i>Australopithecus/Homo?</i>
e	<i>Homo erectus</i>	E	<i>Homo erectus</i> (mean)
H	<i>Homo</i> (mean)	N	Neandertal (mean)
f	<i>Homo floresiensis</i> (LB1)	S	<i>Homo sapiens</i> (mean)

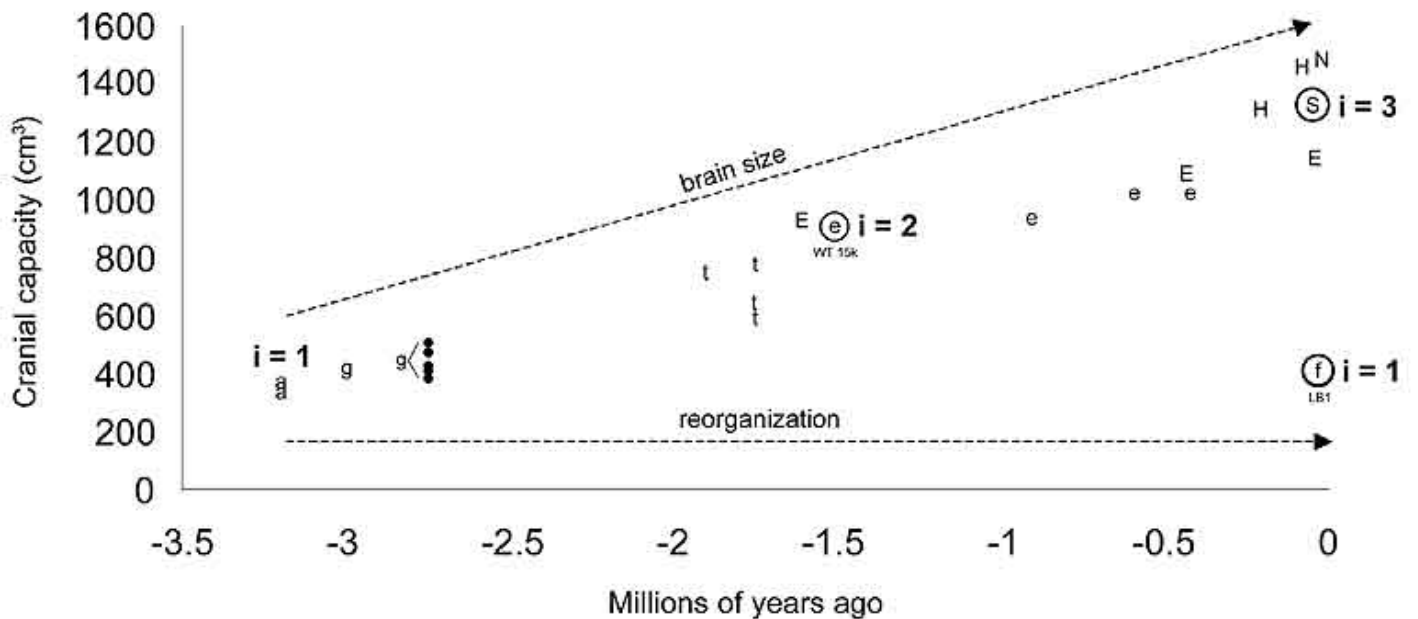


Fig (12.)3 Cranial capacities of select hominins plotted against time; data from Table 1. Above, plot includes capacities for robust australopithecines (*Paranthropus*). The trend for brain size increase appears flat until around 2.0 ma, and then begins to increase in *Homo*. Below, the same plot, but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



**men 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 et 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<sup>3</sup> 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<sup>3</sup> (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<sup>3</sup> for gorillas, 375 cm<sup>3</sup> for common chimpanzees and for orangutans [Falk 2000b:312]). It is also 2/3 of 1364 cm<sup>3</sup>, which is very close to the oft-cited world mean for contemporary *Homo sapiens* of 1350 cm<sup>3</sup>. 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

Hofman 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<sup>3</sup>, 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 tarsiiiform 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

prominent thalamic structure, the medial pulvinar, which has no obvious counterpart in other mammals. The latter suggests, “not only do primates possess primate-specific higher-order cortical territories, but these territories form a distinctive connective 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

al. 1997). For this reason, I remain respectfully skeptical about the suggestion (based on controversial redefinitions 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

and humans as well as linguistic communication in the latter (Falk 2007, 2009). 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).