

fectively summarizes the point convincingly driven home by the thorough statistical analysis of Finlay et al. What is truly remarkable when we examine regressions of brain structures on each other (at least for mammals) is the strength of the resulting correlations; the consistently large proportion of the variance that is accounted for.

But if the third colleague had stayed a little longer, I would have told him about the grade shift and why I was excited by it. I would have said that the departure from allometry revealed something about primate brain evolution that a strictly linear relationship could not, namely that hominoid evolution likely involved focused selection for expansion of a specific brain structure; the cerebellum. Furthermore, if we had a clear idea of the functions supported by the cerebellum, we might be able to make some inferences about the type of capacities that were selected for in apes. On the other hand, as the authors emphasize, if growth in all brain structures is perfectly correlated, and structure volumes do not vary independently of each other, then we cannot say anything about the anatomical locus of selection. We do not know which brain structures selection acted on and which were dragged along for the ride; we don't know what is an "arch" and what is a "spandrel." Researchers studying primate brain allometry often focus more on departures from allometry than the allometric trends themselves because the former provide clues with respect to what brain regions and mental operations were selected for. In so doing, however, we often lose sight of the forest for the trees.

Considering this, it is fortunate for our knowledge of hominid brain evolution that the human brain is not simply an allometrically scaled-up version of a nonhuman primate brain. The human cerebellum is smaller than predicted for a nonhuman anthropoid primate with a human-sized brain (Rilling & Insel 1998; Semendeferi & Damasio 2000). Consequently, some other brain region must be larger than predicted by nonhuman primate allometry. Analysis of both post-mortem and in vivo MRI brain data reveal that the human cerebral cortex is larger than predicted by nonhuman primate allometry (Deacon 1988; Rilling & Insel 1999). The human frontal lobe, when defined by cortical surface landmarks, is not disproportionately large for an ape brain of human size (Semendeferi & Damasio 2000). However, although still debated, there are data (Brodmann 1912) showing that when the prefrontal cortex is defined cytoarchitectonically, the volume of the human prefrontal cortex is twice the size predicted for a nonhuman primate of the same neocortical surface area (Passingham 1973). Evidence is also accumulating that the human temporal lobes are disproportionately large for our brain size (Rilling & Seligman 2000; Semendeferi & Damasio 2000), and the latter observation may be related to the expansion of language cortex and associated connections. In this case, the enlarged temporal lobes and the capacity for language are unlikely to be spandrels resulting from selection for some other ability or brain structure. Instead, the adaptive value of language may have driven human brain evolution.

Another criticism of this otherwise superb article is the discussion of human brain evolution, in particular the statement, "Only with the appearance of anatomically modern humans did brain size become somewhat disproportionate." The fact that there is a fairly regular pattern of change in brain size with changes in body size among the sample of hominid taxa considered does not mean that increases in brain size were merely passive responses to selection on body size (Armstrong 1985; Martin & Harvey 1985; Stephan et al. 1988). Artificial selection experiments with mice produce correlations between brain and body size, regardless of which trait is the focus of selection (Lande 1979). The difference is in the steepness of the resulting slopes, with selection on brain size producing slopes of around 0.8, and selection on body size producing much shallower slopes of around 0.4. I calculated an allometric slope of 1.50 for the logarithmic regression of brain size on body size for the sample of hominids referenced by Finlay et al. (Wood & Collard 1999), and Pilbeam and Gould (1974) calculated a brain:body slope of 1.73 for a smaller sample of hominid

taxa. As Pilbeam and Gould emphasized, the steepness of this slope almost certainly implies selection on brain size and a correlated, perhaps more passive, increase in body size. Brain:body slopes for non-human anthropoids and mammals are 0.70 and 0.77, respectively (Martin 1996; Stephan et al. 1988). If the hominid data points were compared to one of these two reference lines, then scaling along the hominid curve (with its slope of 1.5) would produce marked increases in encephalization (the distance of the points with respect to the reference line would get larger with increasing body size). What appears to have been altered in hominid evolution is the slope of the scaling relationship between brain and body size, and this in itself is likely an adaptation.

Brain scaling, behavioral ability, and human evolution

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Abstract: The existence of linked regularities in size among brain components across species is, by itself, not a strong argument against the importance of behavioral selection in brain evolution. A careful consideration of hominid brain evolution suggests that brain components can change their scaling relationships over time, and that behavioral selection was likely crucial. The best neuroanatomical index of a given behavioral ability can only be determined empirically, not through comparative analysis of brain anatomy alone.

Finlay et al. make a strong case for linked regularities in size changes among at least some brain components in primates, insectivores, and bats over their evolutionary histories. Their argument that these regularities are a reflection of some basic features of neurogenesis is quite reasonable. However, as they point out, this account is essentially a mechanistic one. The interpretation of these patterns, with respect to what they imply about developmental constraints as well as structure/function relationships, is not particularly clear-cut.

First, it is important to recognize that the existence of scaling regularities among brain components (and between brain and body) is a completely orthogonal question of whether or not the driving force behind brain evolution is behavioral adaptation. Selection on specific behaviors could still logically have been the ultimate cause of any species differences in brain anatomy no matter how closely linked brain components appear to be over evolutionary time.

Second, the lessons of hominid brain evolution make it unclear just how tightly brain components must be connected. There appear to be quite clear differences in the relative proportions of various functional regions of the cerebral cortex between humans and all other primates (e.g., Armstrong 1991; Brodmann 1912). For example, Brodmann's data suggest that humans have about twice the prefrontal cortical surface area that we would predict for primates, based on the overall surface area of their cortex (Deacon 1988; 1997). Holloway (1992) and others have shown (using Stephan et al.'s 1981 data) that the primary visual (striate) cortex in humans is only ~60% as large as predicted from primate brain size scaling relationships. Clearly, some species can significantly change the relative proportions of some components compared to others, and this raises the distinct possibility that natural selection, as opposed to strong developmental constraints, is the explanation for these patterns across species.

The authors' claim that most of hominid brain evolution can be explained as a simple "straightforward function of body mass" is actually very misleading. Their conclusion is based on a regression of brain volume on body mass for hominid estimates (extracted from the literature by Wood & Collard 1999). From this they cal-

culate that greater than 90% of the variability in hominid estimated brain volume can be explained by variation in estimated body mass (if modern humans are excluded). This conclusion, however, completely misrepresents the context (and therefore the significance) of hominid brain evolution, which actually shows clear and consistent trends away from the primate (and mammalian) brain/body relationship. Finlay et al.'s calculation is based solely on estimates from hominid fossil species, and ignores entirely this phylogenetic context. Figure 1 shows the hominid fossil data the authors used in their calculations, along with the primate best fit regression (calculated from Stephan et al.'s 1981 data). One can see that *Australopithecus africanus* estimates are already significantly above primate expectations for their body size (by 199 cc). If further increases in brains size among later hominids were to occur solely in accordance with the empirically derived primate scaling relationship, we would never expect brain sizes to be larger than ~657 cc (i.e., for Neanderthals, the heaviest hominids). In fact, Neanderthal brain sizes are less than 19% as large as one would predict on this basis (actual change from *A. africanus* sized brain was 1,055 cc, predicted change should only have been 200 cc), and modern human brain sizes are less than 10% what we should expect (actual increase: 898 cc, predicted: 89 cc). Thus, in point of fact, only a small proportion of hominid brain size increase can be explained by body size if we take the proper context into account. Finlay et al.'s treatment of the hominid data is completely at odds with their own central focus on broad cross-species comparisons. It also, ironically, is an example of what they specifically caution against: separating human evolutionary processes and patterns from those used to explain other species. To

separate hominids from primates the way they do is to suggest that each evolutionary lineage can set its own rules regarding brain/body size relationships, yet this completely undermines the thesis that brain scaling is strongly constrained across broad groups of species.

The discussion of Neanderthal and anatomically modern *Homo sapiens* is also problematic. It is true that these species (assuming they really are different species) do not show obvious behavioral differences for ~40,000 years of temporal and geographic overlap – at least judging from their tool assemblages – and that they also differ in encephalization quotient (EQ). The authors point out that this is consistent with their idea that “big isocortices may be spandrels – byproducts of structural constraints for which some use is found later” (sect. 5). However, Neanderthal appear to have had very large brain sizes in absolute terms (toward the high end of populational variation in modern humans, see Fig. 1 and Holloway 1985). Thus, the authors' explanation first requires us to assume that behavioral capacity is a function of the extent to which a species departs from brain/body scaling relationships (i.e., their EQ). While it is commonly assumed that behavior can only be properly indexed in this way (e.g., Wood & Collard 1999), it does not follow that because brains scale with body size, all relevant behavioral capacities must therefore be a function of deviations from brain/body scaling relationships. Exactly what brain measurement is the best index of any given behavioral attribute is an independent empirical question, not one that can be decided a priori. In fact, there are several studies suggesting that absolute brain size, independent of body size, has important behavioral implications (Beran et al. 1999; Rensch 1956; Riddell & Corl 1977; Rumbaugh

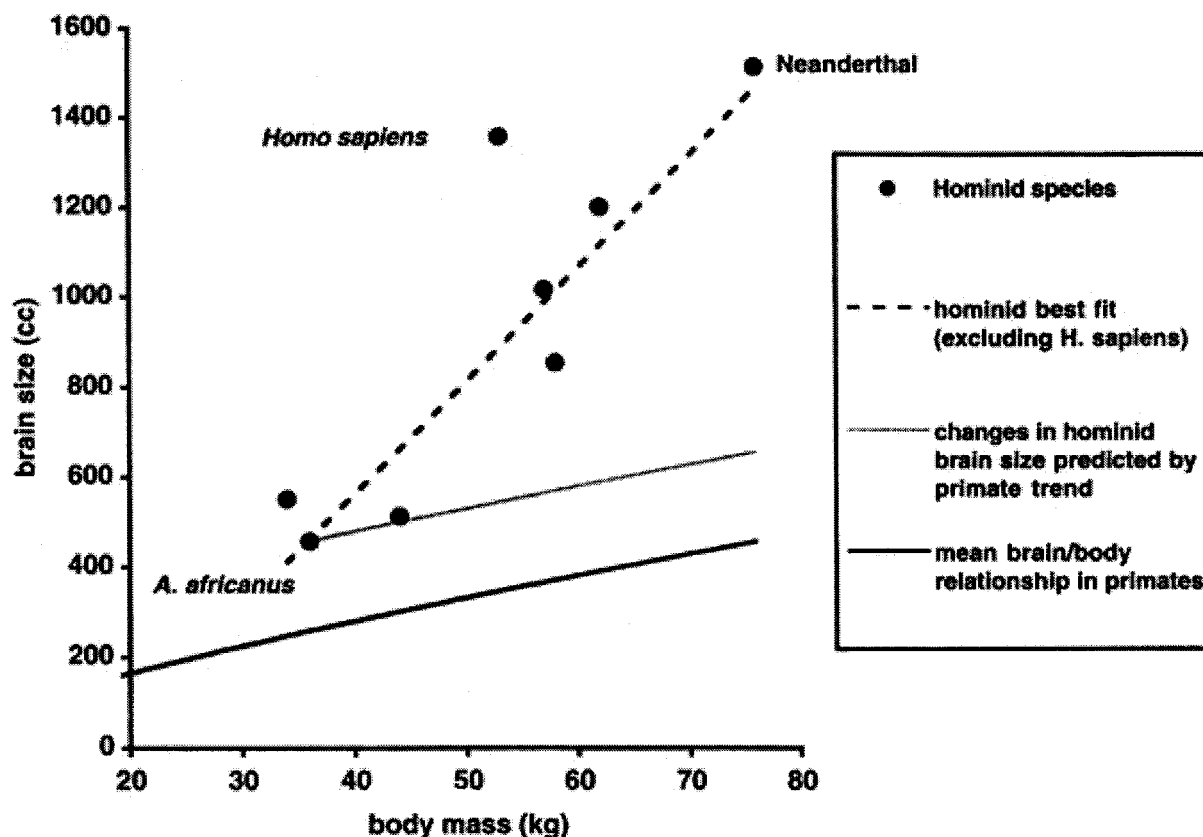


Figure 1 (Schoenemann). Brain size plotted against body mass in hominid species (data from Wood & Collard 1999). Dark solid line represents the best fit (least squares) regression for primates: $(\text{brain cc}) = .084(\text{body kg})^{.766}$ ($N = 44$, $r = .97$ using log transformed variables; data from Stephan et al. 1981). The gray solid line represents increases in brain size from *A. africanus* that would follow the primate trend. Dotted line represents the relationship reported by Finlay et al. for this data. The extent to which the gray and dotted lines diverge is a measure of how poorly body size predicts brain size evolution in hominids.

1997). While there are undeniable problems in studying relative abilities across species (Essock-Vitale & Seyfarth 1986; Macphail 1985), lack of unequivocal evidence does not license us to conclude that absolute brain size has no behavioral implications (note that Finlay et al. themselves seem perfectly willing to accept that EQ is behaviorally relevant across species). The authors' comment that "There is really no justifiable metric of behavioral complexity that would account for most of the excess poundage of the whale brain [over that of hummingbirds]." But do we really know enough about whale and hummingbird behavior to legitimately come to this conclusion? Is it really the null hypothesis that, for example, guinea pigs (*Cavia cutler*) are likely to be more behaviorally complex than elephants (*Loxodonta africana*) simply because they have higher encephalization quotients (EQs): .95 versus .63? Guinea pig brains weigh ~3.3 grams, while elephant brains weigh over 5,700 grams (data from Quiring 1950, EQs calculated using Martin's 1981 mammalian brain/body scaling relationship). Is it really likely that this extra ~5,700 grams in elephants has no behavioral implications?

One intriguing possibility is Ringo's (1991) suggestion that the increase in the number of neuronal connections (as estimated from cortical white matter volume) is not sufficient to maintain equal connectivity between all regions. This suggests that a natural by-product of increasing brain size is the increased likelihood of cortical specialization. This, in fact, appears to be the case across species (e.g., Ebesson 1984; Uylings & Van Eden 1990).

More generally, does the bias for EQs make sense from an evolutionary perspective? As the authors point out, brain tissue is very metabolically expensive (Hofman 1983). It is also highly correlated with maturation time (at least within primates; Harvey & Clutton-Brock 1985). Both of these evolutionary costs operate on absolute amounts of brain tissue – not relative amounts. In the absence of specific benefits accruing to larger brains, a smaller brained animal would necessarily have an adaptive advantage over a larger brained one (Smith 1990). The argument that such adaptive changes would be constrained by a tight linking between brain and body size – making it very difficult for a species to decrease unneeded "excess" brain tissue over time – is belied by the wide variation in brain sizes shown by mammals of the same body size, as the authors themselves point out (see also Schoenemann 1997). The hominid example is a dramatic case in point of the possible disconnect between brain and body size (contrary to the authors' suggestions). If hominid brain size could change so dramatically with respect to body size over the last 2.5 million years, significant deviations from brain/body trends clearly can happen, given the appropriate adaptive environment. The fact that brain and body show tight statistical connections across large groups of species may simply be due to larger bodies allowing for larger brains (perhaps because of metabolic resources; Armstrong 1983; Martin 1981) without strictly requiring them. Selective interactions between and within species would then tend to keep species brain sizes towards the large end. This model is just as consistent with the empirical data as one based on neurogenetic constraints.

However, even if we accept that EQ is the behaviorally relevant variable in the Neanderthal/modern human question, the authors' suggestion requires us to believe that ~2,000 generations (assuming an average time per generation of ~20 years) separate changes in brain structure from their behavioral payoffs. Why would these changes have occurred in the absence of selection? The idea that any significant change in the brain could occur independent of selection for behavioral adaptation is, though possible, just not likely. One can show that adaptive benefits can be extremely weak over evolutionary time and still explain large changes in brain evolution (Schoenemann et al. 2000). Behavioral advantages could have been very subtle (and hence not easy to detect in stone tool assemblages).

Finally, I would take issue with the authors' suggestion that the persistence of behavioral adaptationist views of human evolution are "yet another way to set humans apart from the rest of the animal kingdom" (sect. 8.2). This comment assumes something the

authors have not and cannot demonstrate with the data: that brain size differences in other animals have not also been driven by behavioral adaptations. More generally, the implication that human brain evolution is not particularly unique in the natural world is difficult to support empirically. Humans are demonstrably different at a cognitive level precisely because we have more behavioral flexibility. The evolution of the human brain has clearly not led to an increase in the number of hard-wired behavioral reflexes. Thus, it is quite clear, if one actually looks at the behavioral differences between humans and other animals, that humanity has in some nontrivial sense "authored" itself. This is a conclusion based on behavioral data – not brain anatomy data. Anatomy alone cannot determine the significance of behavior.

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Constraint and adaptation in primate brain evolution

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Abstract: Constraint has played a major role in brain evolution, but cannot tell the whole story. In primates, adaptive specialization is suggested by the existence of a covarying visual system, and may explain some residual variation in the constraint model. Adaptation may also appear at the microstructural level and in the globally integrated system of brain, body, life history and behavior.

Before asking questions about *why* brains have evolved as they have, we must understand *how* they have evolved. Finlay et al. have made a major contribution by demonstrating that large-scale covariance associated with conserved developmental timing has dominated mammalian brain-size evolution. In the process, they have successfully addressed major concerns (e.g., Barton 1999; Dunbar 1998) about their previous work (Finlay & Darlington 1995) on the subject. It is not surprising that my own limited analysis of published primate data corroborate the authors' more general findings.

I used the CAIC program of Purvis and Rambaut (1995) to calculate independent contrasts from published (Stephan et al. 1981) volume data for 19 brain structures in 48 primate species. I then assessed covariation in these contrasts by testing for correlation between each of 170 possible pairs of non-overlapping structures and running a principal components analysis of the entire set.

Overall, r^2 values from the pair-wise comparisons were quite high (21% = 0.95, 48% = 0.90). Lower values occurred primarily in comparisons involving olfactory bulb and, to a lesser extent, limbic structures. Interesting to note, visual system structures (striate cortex, lateral geniculate, and optic tract) correlated more highly with each other than with other structures. Principal components analysis of the independent contrasts revealed that two factors accounted for roughly 93% of the observed variance (Table 1). These may be characterized as (1) a "whole-brain factor" loading on all structures except olfactory bulb, and (2) an "olfactory/visual factor" loading positively on olfactory bulb and limbic structures and negatively on visual system structures. Adding body size to the analysis simply introduced a third "somatic" component of variation.

These results closely agree with the three-factor model of Finlay et al., and provide general corroboration for the constraint hypothesis. An important exception, however, is the inclusion of visual system structures in the second factor of variation. This is at odds with the contention of Finlay et al. that there is no "covarying unit, distributed across structures, that is the 'visual system.'"