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., Ebbesson 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.'"

Table 1. (Stout). *Principle components of brain-size variation in primates*

| | Component | |
|---|---|---|
| Structure | Whole Brain (83.2% of variance) | Olfactory/Visual (9.5% of variance) |
| Non-Visual Cortex (neocortex-striate cortex) | 0.974 | −0.116 |
| Cerebellum | 0.975 | 0.011 |
| Medulla | 0.969 | 0.161 |
| Mesencephalon | 0.989 | −0.062 |
| Striatum | 0.986 | −0.066 |
| Schizocortex | 0.921 | 0.346 |
| Hippocampus | 0.918 | 0.312 |
| Thalamus | 0.982 | −0.081 |
| Hypothalamus | 0.981 | 0.025 |
| Pallidum | 0.959 | −0.094 |
| Striate Cortex | 0.850 | −0.466 |
| Optic Tract | 0.840 | −0.436 |
| Lateral Geniculate | 0.892 | −0.378 |
| Olfactory Bulb | 0.344 | 0.866 |
| Septum | 0.942 | 0.273 |
| Epithalamus | 0.930 | 0.242 |
| Internal Capsule | 0.846 | 0.003 |
| Vestibular Nuclei | 0.923 | −0.077 |

Observation of such a covarying system here provides support for the widespread notion (e.g., Allman 1987; Barton 1999) that visual specialization has played an important role in primate brain evolution. The apparent "trade-off" between olfactory and visual structures seen in the second factor is further suggestive of adaptation.

The fact remains, however, that the vast majority of total variation (83%) is accounted for by the first, "whole-brain," factor. Correlated overall expansion appears to have been the dominant, if not the only, mode of primate brain evolution. As Finlay et al. have also shown, conserved developmental timing probably accounts for much of this overall regularity. Once again, this is corroborated by my own analyses: a multiple regression using the slopes and intercepts of 11 structures regressed on medulla predicts relative developmental timing (event scores from Darlington et al. 1999) with $r^2 = 0.72$ and $p = 0.006$.

What room, if any, does this leave for adaptive specialization? We have already seen that a large proportion of the variation left unexplained by the "whole-brain" factor *is* explained by an "olfactory/visual" factor. Variation in this functionally specific factor most likely reflects adaptive specialization. But what of the variation (7%) that remains even after the second factor is taken into account? Although 7% may not seem like much to be worried about, the extreme range in scale among primates means that even relatively small residuals can equate to striking amounts of absolute variation (Deacon 1990; Finlay & Darlington 1995). Because we do not really understand the relationship between size and function in neural tissue, we cannot say what the functional/adaptive significance of such absolute variation might be.

Of course much of the residual variation may simply reflect measurement error and individual variation. Brain imaging studies of modern primates (e.g., Rilling & Insel 1999; Semendeferi & Damasio 2000) are beginning to reveal just how substantial individual variation can be. In a sample of six chimpanzees, for example, Semendeferi and Damasio (2000) report frontal lobe volumes ranging from 74.1 to 133.4 $cm^3$ (a difference of 59.3 or 44%). In order to confidently attribute adaptive significance to residual variation, it will probably be necessary to demonstrate strong correlation with some socio-ecological variable such as group size or percent of fruit in the diet.

Adaptive specialization may also be sought in smaller-scale variation not captured by the analysis of large structural divisions (Finlay & Darlington 1995). Adaptive reallocation or reorganization *within* regions may often have been important, as, for example, in the evolution of human neocortex (Deacon 1997; Falk et al. 2000; Holloway 1983; Passingham 1998). In addition, many important adaptations are certain to have occurred at the microstructural level, as is now being documented by researchers including Preuss et al. (2000) and Nimchinsky et al. (1999).

Finally, global brain size change itself can also reflect adaptation. Finlay et al. argue that increased total brain size is one likely response to selection on almost any specific functional capacity, and that this tendency toward "adjunct" growth should foster widespread exaptation of neural tissue. Similar logic applies when brain size is considered in a broader, organismal, context. In any viable organism, the development and expression of such diverse traits as brain size, body size, encephalization, lifespan, range size, diet, reproduction, and social organization are thoroughly integrated. This is reflected in the multiple evolutionary "grades" recognized within the primate order (Dunbar 1998; Kaplan et al. 2000). Each such grade (e.g.,prosimian, anthropoid, hominoid) represents a stable suite of integrated adaptations allowing for pursuit of a similar lifestyle (Brace 1995, p. 70).

In addition to focusing on particular traits like dietary or social complexity, it may prove useful to consider general adaptive complexes or strategies. Whereas some variation is obviously accommodated within any grade, pressures leading to certain particular changes might precipitate a "shift" with widespread and profound implications. It may ultimately be impossible to discern primary causes in such multifaceted and recursive lifestyle shifts, but exploration of the dynamics themselves should prove to be at least as interesting.

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## Brain evolution: How constrained is it?

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**Abstract:** Allometric analyses suggest that there are some developmental constraints on brain evolution. However, when one compares animals of similar body size, these constraints do not appear to be very tight. Moreover, the constraints often differ between taxonomic groups. Therefore, one may ask not only what causes developmental constraints but also how (and why) these constraints might be altered (or circumvented) during the course of evolution.

Traditionally, biologists have been quick to conclude that an owl's large eyes are an adaptation for vision at night and that a hare's large ears are adapted for the detection and localization of sounds. More generally, biologists tend to interpret the hypertrophy of a particular organ as the result of natural selection for the principal function(s) subserved by that organ. They also tend to assume that the size of individual organs can be changed without simultane-