

constraint on relative brain size and that residual values of individual species relative to a best-fit line between brain size and body size values are not independent of body size itself (Fig. 3). This result is important when considering the encephalization level of small New World monkeys.

As a final word, the comparison between the behavioral capabilities of the hummingbird (brain size of less than a gram) and the baleen whale (brain size in excess of 5,000 grams) reminds us of the paradox raised by Barlow in H. J. Jerison (1985). In a heavy brain a high encephalization index might correspond to the addition of many grams of brain tissue, whereas in a light brain the same increase of the index would correspond to the addition of a comparatively small amount of brain tissue. If encephalization is related to intelligence, why does the heavy brain require many times more brain tissue than the light brain to confer the same increase in intelligence?

Clearly, spandrels – by products of structural constraints – requires more attention from evolutionary biologists. The work of Finlay et al. is most welcome.

#### ACKNOWLEDGMENT

This work was supported by the URC, University of the Witwatersrand, and by the MRC of South Africa. The authors thank J. C. Allen for helpful comments.

## Does allometry mask important brain structure residuals relevant to species-specific behavioral evolution?

Ralph L. Holloway

Department of Anthropology, Columbia University, New York, NY 10027.  
rlh2@columbia.edu www.columbia.edu/~rlh2/

**Abstract:** Despite the ontogenetic allometric size effects that explain much of phyletic variation in brain components, the residuals of some structures indicates that mosaic brain evolution was an important factor in hominid evolution, and that reorganization of the hominid brain may have occurred as early as 3+ MY. Finlay et al.'s allometric technique masks residual variation around allometric trends, and the *patterns* of residuals relevant to species-specific departures from strict allometric trends.

It has been some 25 years since I reviewed Jerison's 1973 book in *Science*. I admire the tenacity with which the allometrists continue to regard brain size as the most salient explanation for behavioral differences among species, whether extant or fossiliferous. In that review (Holloway 1974) I suggested that there was a tendency to reify numbers into a fictional realm, such as "extra cortical neurons" or the fitting of the 0.66 slope to the data without first checking the actual regression figures, something that awaited Martin's (1983) paper, demonstrating an empirical slope of 0.75. At the time of writing that review, I was concerned by Jerison's (p. 81) dismissal of the concept of "reorganization" of brain components as a trivial explanation for even more trivial behavioral phenomena, namely, species-specific behavior. How our symbolic capacities could be regarded as "trivial" surprised me. Plotting numerous graphs of log-log brain-body weight (and brain part volumes, e.g., the hippocampus) relationships completely validate, as does this article by Finlay et al., that there are indeed allometric constraints to brain development operating at ontogenetic levels, and thus having occurred in the phylogenies of most animal groups, hominids included. For this investigator, however, it is the allometric constraints which might be deemed "trivial" (*sensu* Jerison), and the residuals, or departures from the constraints that are most provocative and nontrivial in analyzing species-specific behavioral repertoires and in particular the paleoneurological evidence for hominid evolution. That was my essential message in the reference that Finlay et al. cites (Holloway 1979), and I tried at that time to make a rapprochement with Jerison which would be

holistic regarding both allometric constraints and species-specific departures from those constraints, and I did try factor analysis as one method to demonstrate this. The recent paper in *Nature* by Barton and Harvey (2000) offers a critique of the Finlay et al. study, and demonstrates correctly, I believe, that mosaic evolution did occur among brain components.

I ended my 1979 paper as follows:

By cathecting on size alone, all evolutionary paradigms become reduced to natural or genetic selection operating on incremental size increases and behavioral efficiency, which always has the underlying implicit structural argument that "intelligence" equals "brain size." Thus, for example, all of hominid evolution becomes "scaling," "allometry," or quantitative increases, whereas these are only *distal* manifestations of something more complex and important. In other words, all of individual variation, the very stuff that evolution works on, is reduced to a single dimension of either small or large. In fact, it is likely that the selection events in any animal's life depend more on the timing of maturational events, epigenesis within the central nervous system (CNS), and everyday events – that is, the "nitty-gritty" life-death "selection walks" – are matters of hierarchical organization, differentiation, and development, of which the outcomes through time can only be measured (thus far) as size increments. We should and can demand richer explanations. (Holloway 1979, p. 85)

I had (and continue to do so at present) used the visual system to illustrate my position regarding *reorganization* as being an important element of human brain evolution. There are at least two good reasons for doing so: (1) the comparative primate volumetric data (e.g., Stephan et al. 1981) shows that the primary visual striate cortex (PVC) in *Homo* is 121% less in volume than expected for a primate of its brain size (the lateral geniculate nucleus is –144% less than expected). These residuals of over 100% should command some attention, despite the small sample sizes within species, and log-log regression lines with very large errors at the extremes. (2) The paleoneurological evidence from brain endocasts occasionally shows details in the posterior cerebral region suggesting that the reduction had occurred at least 3 million years ago. We will never know about the australopithecine hippocampus, basal ganglia, septal, and amygdaloid nuclei, and so on, but we do have a chance to identify and quantify some of the external morphology of the cerebral cortex, as I have tried to show with regard to the lunate sulcus as an anterior boundary of PVC, and cerebral asymmetries in particular (see Holloway 1995 for a theoretical synthesis and Holloway 1996 for a full review).

I am also very skeptical of "spandrel" theories of brain/behavioral evolution as championed here by Finlay et al. That all of our species-specific behavioral attributes such as developing language where arbitrary symbol systems underlie most of our cognition, our emotions, our predispositions toward xenophobia and violence within and against species, our behavioral diversity with regard to intelligence(s), our musicality, and so much more, should simply be epiphenomena of an evolutionary passage (that cannot be tested without time machines) beyond some size rubicon strikes me as implausible. Spandrel theories cannot explain genius, sexual dimorphism of behavior, and brain structures such as the corpus callosum. Neither spandrel or allometric analyses can explain the difference in maternal behavior, between mountain and prairie voles when pups are taken from the nest. Spandrel theories cannot explain the recently demonstrated differences between Australian Aborigines and Caucasians with regard to PVC volumes and perceptual tasks (Klempf et al. 1994). Take any log-log regression line of mammalian brain-body weights and see which animal's behavior you can predict when they are closely adjacent, for example, whales and cetaceans, or chimpanzee and orangutan, or even various species of *Macaca*, which display differences in temperament and personality. Dog breeds would be yet another example of the failure of allometry to do more than provide an ontogenetic constraint, which while useful, begs the more difficult issues of brain structural variation and behavioral differences. For these, we can only hope that MRI, fMRI, and

PET scans will get us beyond our cathecting on size alone. I am not opposed to allometry at all; it must be a necessary component part of any future holistic theory (or theories) of brain evolution, but I am worried about dismissing evidence which suggests that quantitative shifts in neural systems through time might help us to better understand the conjoint evolution of brain and behavior.