Evolutionary Anthropology 14:238–239 (2005)

BOOK REVIEW

What Are Four Trillion Neurons Really Good For?

The Evolution of Thought. Evolutionary Origins of Great Ape Intelligence
Edited by Anne E. Russon and David R. Begun (2004) New York: Cambridge University Press. ix + 384 p. $110.00 (cloth). ISBN 0-521-78335-6

The Human Fossil Record, Volume 3: Brain Endocasts—The Paleoneurological Evidence
By Ralph L. Holloway, Douglas C. Broadfield, and Michael S. Yuan (2004) Hoboken, NJ: Wiley-Liss. xxi + 315 p. $195.00 (cloth). ISBN 0-471-41823-4

Comparative Vertebrate Cognition: Are Primates Superior to Non-Primates?
Edited by Lesley J. Rogers and Gisela Kaplan (2003) New York: Kluwer Academic/Plenum Publishers. xv + 386 p. $140.00 (cloth). ISBN 0-306-47727-0

In the Mind's Eye: Multidisciplinary Approaches to the Evolution of Human Cognition
Edited by April Nowell (2001) Ann Arbor, MI: International Monographs in Prehistory, Archaeological Series 13. xiii + 200 p. $75.00 (cloth). ISBN 1-879621-31-2

Animal Bodies, Human Minds: Ape, Dolphin, and Parrot Language Skills
By William A. Hillix and Duane Rumbaugh (2004) New York: Kluwer Academic/Plenum Publishers. xii + 310 p. $135.00 (cloth). ISBN 0-306-47739-4

The eminent neuroscientist Vilayanur Ramachandran has written that we are poised to foment the greatest scientific revolution, understanding the human brain.[1] This is certainly possible; the avalanche of insight from neuroscience conducted just in the last 30 years almost defies description. Many readers of *Evolutionary Anthropology* would agree that an integral component to understanding how the brain functions is an understanding of the forces that shaped its evolution. Anthropology is uniquely positioned to address the evolution of the human brain and intelligence because it deals most intimately with relevant sources of data that are beyond lab-bench neuroscience: hominid fossils and primate behavior and ecology, as well as a wealth of comparative cognitive data on non-human primates. Nevertheless, decades of speculation on the ecological and behavioral causes of human brain and cognitive evolution have yielded few true revelations. In fact, the best research has merely functioned to tear down preconceived and misconceived ideas that were generated within anthropology. The probable cause of this is that anthropology was waiting for comparative and cognitive neuroscience to mature, which can reasonably be said to be happening now. Given this, it seems natural to survey how advances in neuroscience are currently penetrating contemporary anthropology by affecting the assumptions made and directing the questions that are being asked by those interested in human and non-human primate brain evolution.

Humans have among the largest relative and absolute brain sizes known among vertebrates. The only evidence for the timing and pace of the increase in brain size during hominid evolution is endocasts, artificial or fossilized casts of the impressions along the inside of the braincase left by the brain, meninges, and blood vessels. Hominid endocasts are the focus of Holloway, Broadfield, and Yuan's *The Human Fossil Record, Volume 3: Brain Endocasts—The Paleoneurological Evidence,* a stunningly solid work of scholarship on the topic of the fossil evidence for human brain evolution. This monograph deserves to be read by both those interested in paleoneurology as well as the hominid paleontologists to which the entire *Human Fossil Record* series is geared. It is a valuable reference on many of the important hominid endocasts known, including qualitative, morphometric, and phylogenetic data. These data are relevant to disputed topics in hominid paleoneurology, such as the presence of Broca's Area and vocal language evolution, and the position of the lunate sulcus and the reorganization of the human visual system. The true strength of this book, however, is the discussion of the limitations that endocasts pose for addressing the question that is truly of interest in brain evolution: cognitive power. The implicit or explicit assumption when it comes to human brain evolution is that human intelligence, informally defined, evolved lockstep with brain size: Bigger brains mean smarter hominids. But this is only true in the very broadest sense. Bigger brains may have more neurons, but they also have many more axons to connect cortical areas, more myelination in those axons to maintain signal speed and integrity, more glia to supply those neurons, and so on.[2,3] The point is that much of the increase in brain size is not simply due to more neurons and therefore is not wholly dedicated to computation. In theory at least, taxa can either reorganize functional areas or evolve new brain modules without any necessary or dramatic increase in size. As such, interpreting brain sizes in comparative or evolutionary contexts is speculative and problematic in the extreme. Holloway and his co-authors place their discussion of the principles of brain construction before the data, presumably in the hope that researchers will digest these cautionary notes before cribbing all of the data that follow.

Nevertheless, the most popular and prevalent method for analyzing brain evolution from fossils involves brain size and its relationship with body size. Based on Harry Jerison's "principle of proper mass," a size residual is computed relative to a regression line describing the brain size–body size relationship; taxa with large positive residuals, or encephalization quotients (EQ), are believed to have extra neurons that are not devoted to innervating the body.[4] In other words, such taxa are believed to be more intelligent due to the presence of these "extra," or free, neurons. This idea is synthesized by Jerison in his prospectus in Nowell's *In the Mind's Eye,* on how

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archeology might tease apart cognitive advances from archeological remnants of human cultural evolution. Why brains scale with body mass has been explained by Jerison among others as driven by either somatic or metabolic demands, neither of which explain why regions of the brain not related to these demands also scale with body mass.[3] Objections such as this notwithstanding, the brain–body size scaling assumption and its relationship with intelligence underlies many of the contributions to Russon and Begun's *The Evolution of Thought: Evolutionary Origins of Great Ape Intelligence,* a uniformly thought-provoking and insightful volume on the multiple sources of data on hominoid and hominid cognitive evolution. But, the lack of a theoretical foundation to brain scaling undermines substantive conclusions. For example, in their chapter on fossil hominoid brain endocasts Begun and Kordos struggle with their interpretation of EQs and the significance of these for hominoid cognitive evolution. The result that *Proconsul* has an encephalization quotient below but vaguely in the range of papionins and hylobatids is a bit ambiguous. What does it really mean that a species, such as gorillas, has a smaller brain than expected for its body size? Do they suffer a neuronal deficit, or is this merely an artifact of computing residuals from a line where some points must by definition fall close to or below the line? The fact that the brain–body size relationship is unexplained renders deviations from an "expected" line uninterpretable at present. However, an intriguing alternative explanation for brain scaling can also be found in the Russon and Begun volume. Ward and her coauthors suggest that one reason for the strong relationship between brain and body masses is that factors believed to select for larger bodies, such as social complexity, diet, life history, and environment may have similar effects on brain sizes, at least among hominoids. This co- and multivariate approach to selectional factors on brains and bodies is an idea that needs further exploration and this paper, like most contributions to this volume, deserves to be read.

The state of brain scaling research underscores that alternative approaches and sources of data are required to address human brain evolution, and examples of these can be found from the comparative cognitive literature. Perhaps the most theoretically impressive and data-rich such example is Rogers and Kaplan's *Comparative Vertebrate Cognition,* the subtitle to which asks the question, *Are primates superior to non-primates?* Apparently not, as judged by traditional benchmarks of primate cognitive superiority: tool use and innovation, communication, planning, and even relative brain size. Chapters by Emery and Clayton on birds, and van Bergen and coauthors on fish, are especially illuminating in demonstrating the potential that other vertebrate study taxa have for comparative cognitive studies of primates. My favorite example involves guppies. These animals have brains the size of a fingernail, yet they are capable of the kind of high-order socially mediated learning that is thought to be the private domain of primates. What these authors also have is access to experimental designs that are unavailable to primatologists, who are often restricted to field studies where control and manipulation of the environment and other factors isn't possible. As such, these studies provide important sources of data on the cognitive abilities of vertebrates that are beyond primatology. A historical note on animal cognition can be found in *Animal Bodies: Human Minds,* which is a more accessible introduction for the non-specialist.

Finally, the best example of how neuroscience is being applied to this question in anthropology is Semendeferi's review from *In the Mind's Eye* on her ongoing hominoid neuroanatomy research program. Semendeferi uses MRI data on hominoid brains with reference to modern neuroscience data on function to evaluate assumptions on human brain differences. One such example is the comparative analysis of frontal lobe and cortex. Frontal cortex is known to act as an executive module involved mediating goals, planning, and decision-making among other functions. Humans have been thought to have exceptionally large and derived frontal lobes (and therefore cortex), and this has been cited as one possible factor contributing to unique human cognitive ability. This is not so when comparative samples of adequate size are used: Humans scale just as any extant hominoid of their size. However, when functional and comparative analyses are combined, human specializations, such as an especially enlarged Area 10, a part of the prefrontal cortex known to be involved in future planning, become apparent. This is an exciting example because it not only tests long-held size and function assumptions, but also lays the groundwork for comparative cognitive research on planning behavior among hominoids. Such examples also imply that evolutionary anthropology has great potential to contribute to a major synthesis of brain evolution. Let the revolution begin!

REFERENCES

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