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Preface:
From Basic Uniformity to Diversity in Cortical Organization

Todd M. Preuss

University of Louisiana at Lafayette, New Iberia, La., USA

On the eve of a new millennium, the Eleventh Annual Karger Workshop convened to consider the evolutionary diversification of mammalian cerebral cortex. The workshop was held on October 22, 1999 at the annual meeting of the J.B. Johnston Club, along the tropical shores of Miami Beach, Florida.

Why a symposium on the diversity of mammalian cerebral cortex? The answer is that there is a certain mismatch between perception and reality: exactly the sort of cognitive challenge one might expect to engage the cerebral cortex.

The perception – widely shared among scientists who study the cerebral cortex – is that there are few if any qualitative differences in cortical organization among mammalian species. The notion that there is a 'basic uniformity' of cortical organization seems to be especially strongly held among those who study the local circuitry of the cortex, the laminar and columnar distribution of cortical neurons, and the chemistry and physiology of cortical neurons. As a result, it is considered acceptable practice among cortical neuroscientists to speak of 'the cortex' without reference to a particular species, as though there were only one cortex. Contemporary textbooks and reviews are replete with species-free accounts of cortical organization that, in fact, rely heavily on the study of a very few 'model' animals (mainly rats, cats, and macaque monkeys).

Notwithstanding the widespread acceptance of basic uniformity, there is growing evidence that cortex varies at virtually every level of organization [reviewed by Preuss, 1995, 2001]. The contributions to the present volume add to this body of evidence. More importantly, however, the present set of papers represent a departure from traditional approaches to the study of mammalian cerebral cortex, taking as their starting point an appreciation that evolutionary history is tree-like, rather than scale-like.

Since the 'modern synthesis' of evolutionary theory in the 1930s and 1940s, evolutionary biologists have fully assimilated Darwin's conception of evolution as resembling a branching tree. Under this view, evolution is regarded as a process of diversification, with each species representing the outcome of a separate evolutionary experiment. Gone is the view that evolution is a steady, progressive march toward Man. Gone is the phylogenetic scale – at least from evolutionary biology.

Thirty years ago, the classic paper of Hodos and Campbell [1969] clearly articulated this new view of evolution for neuroscientists and psychologists. Yet the tree has been very slow to supplant the scale among neuroscientists who study mammalian cortex, and the contemporary literature of cortical neuroscience is filled with implicit and explicit references to the phylogenetic scale. This is really not surprising, for if one takes it as given that the internal organization of the cortex is basically uniform, there's little for evolution to do but change the size of the cortical mantle. Cortical evolution becomes a matter of change along a single scale of encephalization.

One other factor that has inhibited the development of a modern evolutionary biology of cerebral cortex has been the lack of a detailed account of the branching pattern of mammalian evolution. Unraveling the relationships among

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Todd M. Preuss, PhD
University of Louisiana at Lafayette
Institute of Cognitive Science, Cognitive Evolution Group
4401 W. Admiral Doyle Drive, New Iberia, LA 70560 (USA)
Tel. +1 337-482-0261, Fax: +1 337-373-0057, E-Mail tmpreuss@louisiana.edu

the different mammalian orders has proven a very difficult problem for evolutionary biologists. With the development of new, cladistic methods for reconstructing phyletic relationships, however, and the rapid accumulation of data about the morphological and molecular similarities and differences among taxa, the shape of the mammalian family tree is gradually coming into view (fig. 1).

Although still very much a work in progress, the modern view of mammalian phylogeny offers much for cortical neuroscientists to ponder. One point is that there are no obvious candidates among living mammals to serve as models of basal or prototypical mammals. The oldest independent branches of the tree correspond to the monotremes, marsupials, and edentates, all of which include a number of highly specialized forms. Moreover, the idea that the Insectivora provide serviceable models of ancestral cortical organization [the 'basal insectivore' concept; see Hodos and Campbell, 1969; Stephan and Andy, 1969; Sanides, 1970; Glezer et al., 1988], must now be considered problematic, as the insectivore clade is embedded within the radiation of eutherian mammals. Furthermore, like every other modern mammalian group that has been examined, insectivores exhibit a mosaic of derived traits unique to them and ancestral features shared with related groups. To reconstruct the ancestral organization of mammalian cortex, it will be necessary to compare an array of living forms that includes monotremes, marsupials, and a variety of eutherians, rather than focus on a few putatively basal or prototypical taxa.

Current evidence also suggests that primates are rather distantly related to rodents and carnivores (which provide the nonhuman species most commonly used as models of the human brain), and are perhaps even more distantly related to carnivores than to rodents. The closest relatives of primates appear to be bats, flying lemurs, and tree shrews. These other 'archontan' mammals deserve particular attention in efforts to identify the specializations of primate cortex.

Finally, modern phylogenetic investigations have yielded interesting results regarding the relationships of cetaceans. There is now very strong evidence from comparative molecular biology and paleoanatomy that the closest relatives of whales and dolphins are the even-toed ungulates (artiodactyls). In fact, it has recently been suggested that the cetacean clade is actually embedded within the artiodactyl radiation, their closest relatives being hippopotamuses [Nikaido et al., 1999]. These results are important for evaluating the cortical histology of cetaceans, which has a very distinctive appearance. Cetacean cortical histology has sometimes been interpreted as primitive [Glezer et al., 1988]. However, with the knowledge that cetaceans are closely related to artiodactyls, we should expect to find some specific resemblances in the cortical histology of these two groups, and such resemblances are now being identified (see below).

The papers in this symposium volume represent several approaches to investigating mammalian cortical organization within a modern evolutionary framework. The first three papers deal with the diversity of adult cortical organization. Todd Preuss considers the implications of cortical diversity for scientists who are not primarily interested in evolution, but who want to use animal studies to uncover general organizational principles of mammalian organization or to understand human cortex. Patrick Hof and colleagues examine the expression of calcium-binding and neurofilament proteins in the cortical neurons of a wide array of mammals. They reveal a wealth of phyletic variation in the morphology and laminar distribution of neurons expressing these proteins, and note similarities in the cortical histology of cetaceans and artiodactyls, similarities consonant with the close evolutionary relationship of these taxa. Kenneth Catania was invited to review his recent comparative studies of sensory cortex in the Insectivora. Catania's detailed analysis documents some remarkable differences among extant insectivore species in the topography and internal compartmentation of homologous somatosensory areas, which in turn reflect their striking specializations of peripheral sensory systems and behavior.

How did evolution generate the diversity of cortical organization we see among extant mammalian forms? We can gain insight into this problem by considering how modifications of developmental processes could yield differences in adult organization. Leah Krubitzer and Kelly Huffman take such an 'evo-devo' approach to the regionalization of the cortex, considering genetic and epigenetic factors that could modify the amount and location of cortex devoted to a particular sensory system, and that could lead to the formation of new cortical modules and areas. Their approach is informed by comparative cortical mapping studies, experimental manipulations of brain morphogenesis, and studies of molecular expression in ontogeny. David Kornack addresses a traditional concern of brain evolution studies, the enlargement of the cerebral cortex, from the standpoint of our current understanding of neurogenesis. He shows how evolutionary changes in the number of symmetrical cell divisions in the ventricular zone could change the size of the cortical mantle, and how changes in the length and duration of the cell cycle during asymmetrical division could modify the numbers and phenotypes of neurons deployed in cortical columns.

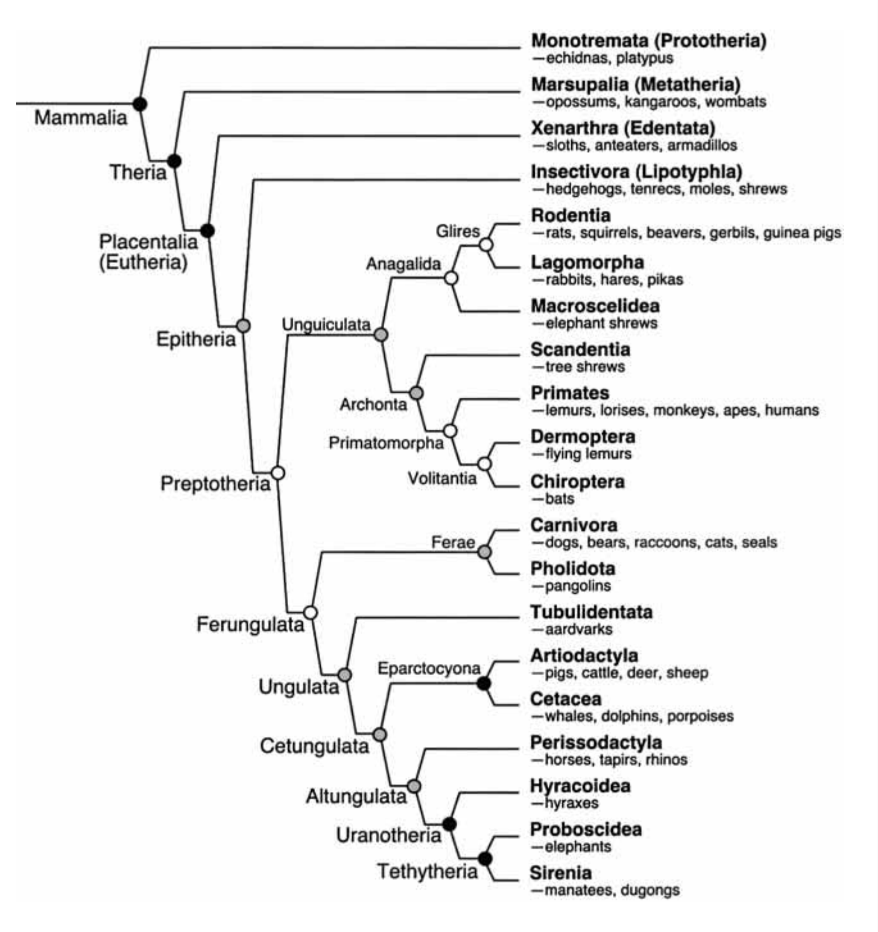

Fig. 1. A modern interpretation of the phylogenetic relationships among extant mammalian orders, modified from Shoshani and McKenna [1998]. The thrust of recent research, based on comparative studies of morphology and molecules, is to organize the orders into nested sets of higher-order groups. So, for instance, the orders Chiroptera (bats) and Dermoptera (flying lemurs) are thought to constitute a higher-order monophyletic group, termed Volitantia. Volitantia is considered to be the group most closely related to the order Primates, and Primates and Volitantia together constitute the Primatomorpha. Primatomorpha is the sister group of the order Scandentia (tree shrews), and these two groups comprise the Archonta. Similarly, cetaceans are closely related to artiodactyls, which together comprise the Eparctocyona; the Eparctocyona are in turn nested within a series of additional higher-order groupings that include mammals such as carnivores, aardvarks, horses, and elephants. In reconstructions such as these, taxa are joined at nodes that represent hypothesized sister-group relationships. The strength of such hypotheses can be evaluated in various ways. In this case, Shoshani and McKenna first reconstructed the tree from an analysis of morphological characteristics, taking as the best tree the one that required the fewest evolutionary changes to account for the pattern of similarities and differences between taxa (that is, a maximum-parsimony tree). Then they assessed the support offered by comparative molecular evidence for each of the nodes suggested by the morphological data. In this figure, nodes that are strongly supported by the molecular data currently available are indicated with black circles, nodes that have some molecular support are indicated with gray circles, and nodes that have little or no support from molecular studies are represented with white circles. A number of important issues remain to be resolved concerning mammalian relationships. For example, while the clade Archonta enjoys reasonably strong support, the current lack of molecular support for the nodes within this group suggest that these may not yet be correctly resolved. The results of this analysis by Shoshani and McKenna [1998] are similar to those presented by Novacek [1992], one important difference being that Novacek would embed the Insectivora within the Unguiculata.

It is a pleasure to acknowledge my gratitude to the many individuals who helped bring this project to fruition. Glenn Northcutt, past editor of *Brain, Behavior and Evolution*, set the ball rolling with his enthusiastic response to the initial workshop proposal. The support of Laura Bruce, Secretary of the J.B. Johnston Club, and the members of the program committee – Golda Leonard, Walt Wilczynski, and Georg Striedter – were instrumental in making the workshop a success. The workshop participants and contributors – Patrick Hof, Ken Catania, Leah Krubitzer, and Dave Kornack – did the really hard work and naturally deserve the lion's share of the credit. I'm grateful to Pat Leavitt for his outstanding keynote presentation. Rob Williams gave generously of his time to provide critical comments on early versions of the manuscripts. Walt Wilczynski and Blinda McClelland were responsible for transforming a stack of manuscripts into actual scientific papers. Finally, I want to thank Thomas and Steven Karger, whose generous financial support has made it possible to continue the workshop series.

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