

Although the analysis of Aboitiz and colleagues suffers from many of the same problems that have plagued other studies that depended on establishing homologies, it is quite possible that they have, indeed, correctly recognized the reptilian homologue of mammalian isocortex. In any case, their analysis differs from all previous ones in providing an explanation that is not only highly innovative but also testable by examining the correlations that should exist if their scenario is correct.

Cranial factors in neocortical evolution

Geoffrey O'Shea

Department of Psychology, Colorado State University, Fort Collins, CO 80523. goshea@lamar.colostate.edu

Abstract: Our understanding of paleoneurology can benefit through considerations of how ontogenetic patterns of skull suture ossification can limit the phylogenetic expansion of underlying brain tissue to specific regions. Additionally, the influence of biochemical, rather than biomechanical, mechanisms on skull suture morphogenesis enable a reconceptualization of the skull as an independent evolutionary system from the brain.

The field of paleoneurology is constrained by the lack of fossilized remains of the cerebral cortex. As a result, our verifiable knowledge of neocortical evolution is limited to what we can deduce from endocranial casts of fossilized skulls, or through phylogenetic comparisons of the brain structures of modern species. As Aboitiz, Morales, and Montiel (Aboitiz et al.) have demonstrated in the target article, modern paleoneurology relies on a theoretical system that attempts to integrate our verifiable knowledge of neocortical evolution with inferences from paleontological, biological, molecular, and genetic lines of inquiry. However, our present theoretical system is constrained by a lack of attention to how mammalian neocortical evolution is intertwined with and limited by cranial factors. In contrast to the constraints on our knowledge of paleoneurology, we have a more detailed fossil record of the evolution of the skull than of the brain. As a result, it might be beneficial to integrate into our present theoretical system a line of paleoneurological inquiry based on our knowledge of the evolution of the skull.

Ontogenetically, the mammalian skull is not a unitary structure, but represents an integration of four skeletal components of independent origin: the cartilaginous neurocranium, the cartilaginous viscerocranium, the dermal skull roof, and the sclerotomal occipital region (Morriss-Kay 2001). Together, these four skeletal elements suture or fuse together to form the intact skull or skull vault. However, because these skeletal elements are comprised of different types of embryonic tissue, the suturing process is affected by the rate at which these skeletal elements ossify or fuse into bone. For example, the most rostral part of the dermal skull roof, overlaying the frontal poles of the brain, ossifies at the age of 6 years, whereas the more caudal part of the dermal skull roof, overlaying the fronto-parietal and temporal brain regions ossifies late in development, if at all. These different ontological patterns of suture ossification have implications in terms of limiting the phylogenetic growth of the brain to specific regions such as the posterior cortex.

Historically, views of cranial evolution have considered skull growth to be driven by the biomechanical tension exerted by the underlying expansion of the brain on skull sutures (Wagermans et al. 1988; Weidenreich 1941). Specifically, proponents of the biomechanical model have suggested that the tension exerted by the growth of the brain regulates skull suture morphogenesis by specifying the location of sutures as well as inhibiting the early ossification of sutures (Moss 1960; Smith & Tondury 1978). More recently, the biomechanical model has been challenged by research demonstrating that biochemical interactions between the tissue comprising cranial sutures and the underlying dura mater, rather than the expanding brain, inhibit suture ossification (Opperman

et al. 1993; 1995). Interestingly, research using endocranial casts has demonstrated that over the course of evolution, a more complex dura mater venous sinus system has developed for regulating the drainage of cerebral blood (Saban 1995). It, therefore, remains to be determined how the increasing complexity of the dura mater venous sinus system has interacted with the cranial suturing process over evolutionary history. The work of Opperman and her colleagues is, therefore, important in that it has provided some evidence for the theoretical dissociation of the evolutionary systems of the skull and the brain through a biochemical rather than a biomechanical model. Moreover, Opperman's work implies that the phylogenetic growth of the skull may be independent from the phylogenetic growth of the brain.

To more fully understand how cranial factors may have influenced mammalian neocortical evolution, it might also be important to examine one of the evolutionary paradoxes of human neuroanatomy. In the human brain, the anterior tip of the hippocampus lies in close proximity to the hypothalamus. However, despite being only a few centimeters away, the efferent fibers of the hippocampus project to the hypothalamus via the fornix, curving up and, initially, away from the hypothalamus in a 270° arc that proceeds under the parietal lobes, around the anterior portion of the thalamus, and, finally, down into the hypothalamus (Carpenter 1991). Although this route of communication between the hippocampus and the hypothalamus might seem extremely roundabout, its existence can be explained by the way in which cranial factors limited the expansion of the dorsal cortex during evolution. Specifically, the early ontogenetic ossification of the cranial sutures overlaying the frontal lobe would not have been able to accommodate the anterior expansion of the dorsal cortex. As a result, it may be possible that the direction of growth of the dorsal cortex in the anterior direction was shifted to the opposite direction toward the late ossifying fronto-parietal and temporal sutures that could accommodate the expansion of the dorsal cortex. Accordingly, such a transfer in the direction of growth of the dorsal cortex would have pushed the posterior cortex down and underneath the rest of the brain so that it would begin migrating forward in the skull.

This pattern of cortical expansion, based on growth beneath nonossified cranial sutures, would enable the folding forward of the posterior portion of the cortex that would eventually lead to the formation of the temporal lobes. Furthermore, this forward migration, of what was previously the posterior cortex, served to carry the hippocampus into the temporal lobe. Thus, although prior to expansion of the neocortex the fornix originally took the shortest, most direct route to the hypothalamus, it now changed position relative to the hypothalamus, due to the forward migration of the hippocampus during neocortical evolution, so that its current route is quite circuitous. Additionally, this forward migration, which produced the temporal lobe, may also be responsible for the characteristic C-shaped curve formed by the striatum and the lateral ventricles.

ACKNOWLEDGMENTS

Thanks to Deanna Davalos and Carol Seger for their comments and suggestions on an earlier expanded version of this commentary.

Relevance of medial and dorsal cortex function to the dorsalization hypothesis

Alice Schade Powers

Department of Psychology, St. John's University, Jamaica, NY 11439. powersa@stjohns.edu

Abstract: The overall dorsalizing effect proposed by the authors may be consistent with behavioral evidence showing that the dorsal cortex of reptiles functions like the hippocampal formation of mammals. It is suggested that the dorsal cortex of reptiles expanded in this dorsalizing process to become both entorhinal/subicular cortex and sensory neocortex.