mains notably well conserved in amniotes. For example, the hippocampal pallium of birds and reptiles share with the mammalian hippocampus the pattern of connectivity, histochemistry, topology, significant electrophysiological properties, and synaptic plasticity mechanisms. Thus, the profile of electrophysiological activity of the neurons in the avian hippocampus is notably similar to the unit types described in the mammalian hippocampus (Siegel et al. 2002). An electrophysiological theta rhythm can be recorded in the avian hippocampus that parallels the hippocampal theta of mammals (Siegel et al. 2000). Both NMDA-receptor dependent and non-NMDA dependent long-term potentiation have been found in the hippocampus of birds and in the medial cortex of turtles (Muñoz et al. 1998; Shapiro & Wieraszko 1996). In addition, presynaptic, CaMKII dependent, long-term depression and a variety of neurotransmission regulatory mechanisms have been recently described in the avian hippocampus which closely parallel those described in mammals (Margrie et al. 2000). All these impressive similarities suggest that mammals, birds, and reptiles share the basic mechanisms for information processing and learning and memory.

Strong evidence indicates also that the hippocampal pallium of reptiles and birds, like the mammalian hippocampus, play an essential and selective role in spatial cognition. The hippocampal pallium of pigeons and turtles is involved in the generation and use of maplike spatial allocentric or relational representations of the environment, but is not necessary for nonrelational, egocentric-based representations (Gagliardo et al. 1999; Rodríguez et al. 2002b). Furthermore, recent evidence indicates that the pallial homologue of the hippocampus in ray-finned fishes, one outgroup of amniotes, is similarly involved in allocentric spatial cognition (Rodríguez et al. 2002a; 2002b; Salas et al. 2003; Vargas et al. 2000), suggesting that these traits were present in the ancestral stock of amniotes that gave rise to mammals, birds, and reptiles. In this context, the shift in hippocampal function from olfactory to visual-spatial processing proposed by Aboitiz et al. is not likely. Moreover, considerable evidence indicates that the basic organization of the olfactory system is well conserved in vertebrates and no major innovation is present in mammals (Eisthen 1997).

In the dorsal pallium of amniotes, the degree of similarities at multiple functional levels is also notable. For example, at single cell level, the neurons of the avian visual Wulst closely parallel those of the mammalian striate cortex with respect to electrophysiological profiles and response properties, and organization of the receptive fields or binocularity (Pettigrew 1979). As in mammals, visual motion induces synchronous transient oscillations in the turtle visual cortex, based in cortico-cortical connections and cortico-thalamic loops (Prechtl 1994). Also mismatch negativity and oddball evoked potentials can be obtained in the turtle's visual cortex that closely resemble those observed in humans, cats, or rats, reflecting fundamental cognitive processes (Prechtl & Bullock 1994). The dorsal pallium of amniotes appears organized in multiple, separate sensorial and motor areas that parallel in relative topology, topographical organization, and connectivity (Medina & Reiner 2000), and display closely similar activity-dependent plasticity and reorganization characteristics (Manger et al. 2002). In addition, the dorsal pallium of reptiles, birds, and mammals is similarly involved in learning and remembering sensory discriminations (Macphail 2001; Powers 1990).

Besides the impressive multilevel, connectional, and functional similarities in the hippocampal and dorsal pallium of amniotes, some conspicuous divergences appear in the cytoarchitectural organization (e.g., the six-layered lamination, or an inside-out neurogenetic gradient of the mammalian isocortex). These differences have impelled the recurrent suggestion that the functional similarities of the hippocampal and dorsal pallium in amniotes are examples of convergent evolution. One possible way to reconcile this apparent contradiction comes from Karten's (1991) proposal that cortical circuits and lamination evolved independently in the phylogenetic history of the mammalian lineage. The basic constituent forebrain neuron populations and their interconnections could have evolved early in vertebrate phylogenesis and, being present in every amniote group, could support the observed common functional characteristics. In fact, despite an enormous range of morphological variation, equivalent telencephalic cell populations and their interconnections and highly conserved developmental patterns have been recognized not only in amniotes, but also in nonamniote vertebrates such as amphibians, ray-finned fishes, or cartilaginous fishes (Butler 1994a; Northcutt 1995; Puelles & Medina 2002).

Interestingly, in the mutant mice reeler, the hippocampal and isocortical neurons fail to align into appropriate cell layers. Nonetheless, these neurons make appropriate synaptic connections and also the electrophysiological response properties of the reeler isocortex seem remarkably normal (Rice & Curran 1999). The hypothesis of convergent evolution concerning several functional traits in amniotes might be the most parsimonious alternative if the feature essential for isocortical processing is lamination. But if the equivalent, conserved circuits are the most relevant feature, then in accordance with a principle of parsimony these functional characters are homologous. It should also be noted that not every morphological change can be considered to be an adaptive trait or to have an exact correspondence with a functional benefit. Some of the observed morphological traits could be incidental byproducts without a functional significance or could be neutral covariations linked to other (relevant) factor not taken in consideration.

Of course, the hexa-laminated structure of the mammalian isocortex may provide additional organizational and computational advantages, as well as some disadvantages and constraints. A rigorous cladistic methodology at multiple biological levels, including the functional analysis, can contribute to identify the fundamental features of the telencephalic pallium organization and the relevant adaptive and evolutionary mechanisms among a constellation of possible biological events.

Toward the answer, but still far to go

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Abstract: The target article about the origin and evolution of the isocortex triggers questions about unresolved issues that still need to be dealt with, including: (1) the evolutionary scenario of the origin of the lateral isocortex, (2) the expansion of the dorsal pallium in nonmammals, and (3) the heterogeneity of the anterior dorsal ventricular ridge.

Many hypotheses have been proposed about the origin of the mammalian isocortex; however, not one can fully account for all of the currently available hodological and developmental information. Therefore, the controversy continues. In the target article, Aboitiz et al. extensively review previous proposals and related issues. Their review has resulted in an interesting idea about the origin and evolution of the isocortex and provides directions for future comparative studies. I will comment on three unresolved issues provoked by their article.

First, I would like to comment on the general organization. The authors have categorized previous proposals about possible evolutionary scenarios of the isocortex into two main groups: those aligned with the recapitulation hypothesis and those aligned with the outgroup hypothesis. However, this dichotomy is not as up-to-date as it could be. Although the dichotomy at first lends readability, it also brings an inevitable lack of clear distinctions to the subtle but important differences among various new proposals. This is particularly the case when one tries to digest the different scenarios of the outgroup hypothesis, many of which have been presented and revised based on the recent findings of develop-

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mental studies. In this sense, the target article would be more immediately useful as a framework for future studies if the categorization were based on interpretations of the origin of the lateral isocortex. Based on this criterion, the differences could be more manifest between the authors' proposal and other interpretations, including Karten (1969; 1991), Bruce and Neary (1995), Butler (1994a; 1994b), Butler and Molnár (2002), Fernández et al. (1998), Puelles et al. (2000), Reiner (1993), and Striedter (1997). In particular, the authors suggest that "the confluence of the lemnothalamic and the collothalamic pathways" occurred in the dorsal pallium in the origin of the mammalian brain. More details of this intriguing scenario will be needed to understand the authors' unique viewpoint on the origin of the lateral isocortex.

Second, I want to comment on the subject of the expansion of the dorsal pallium of nonmammals – birds in particular. As in mammals, birds experienced a massive expansion of the dorsal pallium Wulst, which today coexists with a developed anterior dorsal ventricular ridge. Unlike the dorsal cortex of many reptiles, the avian Wulst is a large longitudinal structure, which, in the case of pigeons, occupies more than 12% of the total telencephalon volume and is equivalent to the size of the basal ganglia (unpublished observation). Within the Wulst, the focus of investigation tends to be on only the small sensory-recipient areas (e.g., visual and somatosensory Wulst), whereas exact functions of the remaining large regions have not yet been clarified. Based on such a scarce amount of information, it has been difficult to identify the exact selective pressures that caused the expansion of the avian Wulst. In this context, it may be important and useful to compare the possible mechanisms involved in the expansion of the dorsal pallia in birds and mammals. For example, it is interesting to note that both birds and mammals are endothermic and share similarities in their lifestyles, such as the extensive care of offspring by parents (Shimizu 2001). As the authors suggest in the target article, networks involving the hippocampus and dorsal pallium might be important for developing and maintaining the lifestyles of mammals. This may be the case for birds as well. I completely agree with the authors, who suggest that further comparative studies about the hippocampus and amygdala functions are important for understanding the expansion of the dorsal pallium.

Finally, I would like to point out an issue related to the heterogeneous nature of the anterior dorsal ventricular ridge (ADVR) of sauropsids. As other researchers (including myself) have done previously, Aboitiz and colleagues developed their argument by focusing on only a portion of the ADVR (or "IT/VT") as "an important part of the ADVR." This simplification is understandable because, in contrast to extensive data regarding this portion of the ADVR – in particular, the sensory-recipient areas – only limited information is available on the rest of the ADVR. However, in order to study its origin and evolution we cannot ignore its heterogeneous nature. For example, the avian ADVR includes not only the neostriatum (N), but also the hyperstriatum ventrale (HV) located dorsal to the N. Often, only limited areas in the N that receive tectofugal thalamic input are the subject of hodological and developmental studies, although the rest of the N and HV are as large as the sensory-recipient areas in terms of size. Figure 5 of the target article presents a good example of the heterogeneous nature of the ADVR. The figure shows that the expression of some marker genes in the HV is more similar to the Wulst (i.e., Emx1+ / Tbr1+ / Pax6+) than to the rest of the ADVR (i.e., Tbr1+ / Pax6+). Although the origin of the HV needs to be clarified (i.e., whether cells in the avian HV are apomorphic or plesomorphic), these data caution us that the ADVR cannot be interpreted simply as a sensory-specific, homogeneous entity receiving input from the tectofugal pathways.

Cortical evolution: No expansion without organization

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Abstract: Aboitiz et al. describe a hypothesis on the origin of the isocortex. They propose the reptilian dorsal cortex to be the ancestral brain structure to the mammalian isocortex. But why did the dorsal cortex expand in mammals and not in reptiles? A change in development may have provided the mammalian cortex with the ability to organize and therefore the potential to expand.

The exclusive presence of a six-layered cortex in the dorsal pallium of mammals and its enormous expansion during evolution has long intrigued many scientists. In the target article, Aboitiz et al. describe a hypothesis on the origin of the isocortex in mammals that is based on the molecular and connectivity similarities between reptilian and mammalian brain structures. According to the authors, the dorsal cortex in reptiles is the main ancestral structure to the isocortex in mammals. The authors propose that a dorsalizing effect during early pallial development in mammalian-like reptiles was the trigger for the expansion of the dorsal cortex in mammals. The dorsalizing effect comprises an increase in the expression of genes in the dorsal pallium, an increase in the number of cells migrating from adjacent brain compartments into the isocortex, and an increased pool of progenitor cells in the dorsal ventricular zone. The expansion of the mammalian dorsal pallium is associated with the development of interconnected networks between the olfactory system and the hippocampus, where the dorsal cortex became progressively incorporated in order to develop complex behavior. The paper concludes that the addition of more neurons and the entrance of more projections in the dorsal cortex produced an enormous lateral expansion of the cortical plate.

Although these factors are important in cortical evolution, it does not explain why a simple pallium, like the dorsal cortex in reptiles, could transform into a highly complex pallium – the mammalian isocortex. For example, in the hippocampus, which according to my view resembles the cortical organization of the reptilian dorsal pallium (Supèr et al. 1998b), the number of projections into the marginal zone increased during mammalian evolution (Stephan & Manolescu 1980). These extra projections toward the hippocampus did not result, however, in a lateral expansion of the hippocampal cortical plate (Frahm & Zilles 1994). Similarly, more neurons are required but are not sufficient to produce lateral expansion of the cortical plate. In the primary visual cortex of primates, about twice the number of neurons are produced than are produced in any other cortical area (Rockel et al. 1980). The increase in neural production in this area does not produce a lateral expansion of the cortical plate but results in a higher density of neurons. Therefore, the existence of more connections or more neurons is not a sufficient explanation for the lateral expansion of the cortical plate and therefore of cortical evolution. It might be necessary to know the mechanism that allowed the dorsal cortex in mammals to expand in order to understand cortical evolution. The question is: What are the possible mechanisms for the transformation of the dorsal pallium into an isocortex?

Evolutionary expansion of the dorsal cortex is paralleled by an increase in the differentiation of the cortical plate (Northcutt & Kaas 1995). In the reptilian dorsal cortex, the cortical plate remained as one cell-dense layer that is subdivided into few, poorly segregated cortical areas. The evolution of the cortical plate in the mammalian dorsal cortex, in contrast, shows a progressive differentiation into numerous cortical (sub)layers and a segregation into many functional discrete regions (areas, columns). Unlike the reptilian cortex, the cortical plate in mammals evolved into a highly

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