neocortical circuits should probably be understood in terms of their function in the fully developed organism.

As the target article points out, the new isocortical network evolves between the olfactory cortex, which remains paleocortical in mammals, and the medial cortex, which evolves into the mammalian hippocampus, but without acquiring isocortical layers. The isocortical network promotes the expansion of the three main topographic sensory systems, visual, auditory, and somatosensory, into forebrain territory that had earlier been dominated by the nontopographic olfactory system. This suggests that the evolutionary advantage afforded by isocortical layers should be common to sensory processing that is topographic in nature (i.e., implemented through cortical maps isomorphic to the array of sensory receptors) and it should not pertain to nontopographic processing. Accounts that rely exclusively on an analysis of visual processing, on the other hand, may offer helpful indications about the role of individual layers (see Grossberg 1999; Kayser & Miller 2002), but are unlikely to offer a satisfactory explanation until they are generalized to other sensory modalities.

An evolutionary advantage that is common to vision, audition, and somatic sensation is also likely to be *quantitative* rather than *qualitative* in nature. It seems improbable that at the abstract and rarefied level at which the three modalities may be described within a common conceptual network, it would be possible to identify a qualitatively new function that the isocortex can carry out but the paleocortex cannot. It seems more reasonable to think of a quantitative improvement in carrying out functions that remain qualitatively the same.

In recent years I have explored the hypothesis that there are two key functions to consider, both of which can be expressed mathematically using a suitably defined formal model (Treves 2003). One is the cortical relay of positional information about a stimulus – that is, the transmission (with minimal information loss) of where a stimulus activates the array of sensory receptors. The second is the memory-based retrieval of identity information – the cortical analysis of all the perceptual aspects of a stimulus (some of which may be occluded or missing, and have to be reconstructed from memory) that are not mapped explicitly in terms of position on the array of receptors. Topographic maps in fact imply a generic distinction between "where" information, explicitly mapped on the cortical sheet, and "what" information, represented in a distributed fashion as a distinct firing pattern across neurons. These patterns can be stored on recurrent collaterals in the cortex, and such memory can help substantially in the analysis of current sensory input.

In analyzing how a neural network can carry out these two functions, quantitatively, it is important to control for the trivial effect of an increase in the number of network components, which is expected to be beneficial in itself. I have therefore simulated two simplified network models with the same number of components, one of which corresponds to an undifferentiated "paleocortical" patch of cortex, and the second to an "isocortical" patch, in which the main layers are differentiated. A quantitative, information theoretical analysis of these simulations demonstrates that a nonlaminated patch of cortex must compromise between transmitting "where" information and retrieving "what" information. Parameters can be chosen to optimize one or the other function, but not both at the same time. The differentiation of a granular layer affords a quantitative advantage, that is a (limited) improvement in the joint transmission of both information types, over the nongranular model. The further connectivity differentiation between infragranular and supragranular pyramidal layers is shown to match the mix of "what" and "where" information optimal for their respective target structures. The computational analysis therefore indicates that the isocortical patch may serve as an optimized component for combined topographic and memory-based information processing. One computational issue to address next is why it was so useful to use more of such components in the evolutionary process of multiplication of distinct cortical maps, known as arealization (Montagnini & Treves 2003).

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Authors' Response

An interdisciplinary approach to brain evolution: A long due debate

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Abstract: A dorsalization mechanism is a good candidate for the evolutionary origin of the isocortex, producing a radial and tangential expansion of the dorsal pallium (and perhaps other structures that acquired a cortical phenotype). Evidence suggests that a large part of the dorsal ventricular ridge (DVR) of reptiles and birds derives from the embryonic ventral pallium, whereas the isocortex possibly derives mostly from the dorsal pallium. In early mammals, the development of olfactory-hippocampal associative networks may have been pivotal in facilitating the selection of a larger and more complex dorsal pallium which received both collothalamic and lemnothalamic sensory information. Finally, although it is not clear exactly when mammalian brain expansion began, fossil evidence indicates that this was a late event in mammaliaform evolution.

After all the process of open peer commentary, we feel quite satisfied with the heated – but in our view, healthy – debate our target article provoked. Overall, we consider that the main points raised in the target article remain valid. There are, however, many interesting suggestions made by the commentators that can be significant additions to our theory. We will divide our response into different sections relating to the different topics addressed by the commentators. As in the target article, we would like to emphasize that each section of this discussion should be considered largely separate from the others, because alternatives in each section may be compatible with more than one alternative in other sections. We have dedicated more space to those points that in our view required clarification. Therefore, if some commentators appear to receive less attention than others, it is basically because we agree with their points of view rather than because we have neglected them.

R1. Homology issues and the dorsalization process

Perhaps the most basic conceptual issues were addressed by **Northcutt**, who questioned the concept of similarity as the sole criterion for homology, and underlined the concept of phylogenetic continuity. At the end of the target article (sect. 8) we mentioned that the DVR and the isocortex likely had separate evolutionary origins, and that embryonic

homology does not imply adult homology (see also Aboitiz 1988; 1995). In agreement with Northcutt, we would now like to emphasize these issues more.

Northcutt argues that the most important point regarding homology between DVR and the lateral isocortex (LICx) is not so much whether or not they have a common embryological origin, but whether or not in evolution they were separately acquired via independent developmental transformations. Thus, a common embryonic origin of the DVR and the LICx could be consistent with the outgroup hypothesis (OGH), if the two structures differentiated independently after the point of phylogenetic divergence, and with the recapitulation hypothesis (RECH), if a differentiated DVR was present in a common ancestor. Conversely, a situation of different embryonic origins of DVR and LICx fits the OGH well, but some exponents of the RECH might consider that this could be explained by a change of embryonic identity of an originally common anlage (see **Butler** and **Reiner**, however, this alternative may be very difficult to prove). As Northcutt says, perhaps what matters most to the latter researchers is not the historical process of divergence between mammals and sauropsids, but whether the isocortex has a single evolutionary origin (the dorsal pallium) or a dual origin (the dorsal and the ventral pallium). In our view this is a valid question. Even if there may not be adult homology, it should be determined whether or not there is *embryonic* homology between the precursors of the DVR and the LICx. If so, there would be phyletic continuity of the embryonic primordia of the two structures, although each has followed a separate developmental course.

Northcutt is also right in that a fine-grained cladistic developmental analysis of telencephalic development is required to shed light on the origins of these structures. Unfortunately, we feel that at this time there are not enough data to perform such a study. In the target article, we placed emphasis on embryological aspects mainly because at this point they may provide the best criterion to reconstruct the phylogenetic history. In this case, development seems to be more reliable than connectional similarity in reconstructing the historical process (see Aboitiz 1995; target article), and at this point suggests different developmental histories for the DVR and the LICx.

According to the comments received, we may distinguish two versions of the RECH. One is the original version, as proposed by Karten (1968; 1969) and restated here by **Salas, Broglio, & Rodriguez** (**Salas et al.**), which implies equivalency of sensory circuits between mammals and birds, and hence, an adult ancestral circuit whose gross morphology evolved in two different directions. This version is based mostly on similarity in connectivity patterns (see **Northcutt**). The original RECH faces some problems (some of these outlined by **Butler**, **Reiner**, and in the target article), not the least of which is that it is difficult to imagine a mechanism transforming the different components of the sauropsidian DVR into specific laminae in the isocortex. Furthermore, a likely possibility at this point is that the DVR and the LICx derive from different pallial sectors. If this were so, a massive tangential migration of excitatory elements from the ventral pallium to the dorsal pallium would be required for these circuits to be considered homologues. As discussed in the T.A., there is good evidence for tangential, ventro-dorsal migration of inhibitory cells from the subpallial ganglionic eminences, but not yet from the ventral pallium. Nevertheless, to be fair, perhaps not all the tangentially migrating cells in the telencephalon are GABAergic (Bellion et al. 2003; Polleux et al. 2002), leaving open the possibility of a contribution of ventral pallial excitatory cells to the LICx. In this context, the origin of the excitatory spiny granule cells of layer IV should be addressed in future studies. Cell tracing experiments are urgently needed to determine if, and to what extent, the LICx derives from the ventral pallium, or if part of the DVR derives from the dorsal pallium. As discussed in the target article such a tangential migration, if it exists, might be a consequence of a dorsalizing influence over the ventral pallium.

Considering this evidence, a new version of the RECH (**Butler**, **Furtado**, **Reiner**, and **Shimizu**) states that there is a common region that may have been independently transformed into the reptilian DVR and into the mammalian LICx. This version does not imply phyletic continuity between LICx and the DVR and therefore there may be no homology in **Northcutt**'s terms. Proponents of the new RECH may agree with a situation of separate embryonic origins: a ventricular zone originally destined to the ventral pallium might have been transformed into a cortical ventricular zone during mammalian evolution. The dorsalization process that we propose could provide the embryological mechanism required for this transformation. For example, a scenario of de-repression of Pax-6 expression as proposed by Furtado (among other changes) would be quite consistent with our proposal (see Stenman et al. 2003). As we mentioned in the target article, one difficulty with the new version of the RECH is the different topographic position of the DVR and the LICx with respect to the lateral cortex (see also Northcutt), which would imply a rearrangement of topographic boundaries in the adult. In addition, if separate embryonic origins were demonstrated for the DVR and the LICx in all reptiles and mammals, it would be practically impossible to prove that, phylogenetically, the LICx originally arose from an ancestral ventral pallial region.

Another point raised by **Butler** and **Reiner** is that the intermediate territory does express some Emx-1 in mammals, which is not fundamental for our proposal (in fact, this finding was made by defendants of the OGH; Gorski et al. 2002). The main point, for us, is that much of the DVR probably derives from a ventral pallial sector and that there is yet no evidence that the LICx derives from that sector. Reiner concludes that since "only the ventralmost part of the ventral claustrum is entirely Emx-1 negative," this renders "problematic the claims of homology for ventral DVR of birds and specific claustro-amygdaloid nuclei in mammals," which is exactly what we argued in the target article: we discussed the possibility that there may not be specific mammalian counterparts of the ADVR (see sect. 4.3). The fact that there may not be a structure homologous to the DVR in the ventral pallium does not imply that it should be sought in the dorsal pallium. Reiner also raises the issue that monotremes seem to lack a claustrum, which in our view is not indicative of any alternative of homology for DVR, even less for the RECH. Monotremes may have secondarily lost a claustrum; or if the claustrum is a late acquisition of mammals, there may be other structures, or simply no structures that correspond to the DVR.

Shimizu makes some interesting points in relation to the expansion of the dorsal pallium in birds, and a possible parallelism between mammals and birds in the development of

hippocampal-dorsal pallial networks. He also points out that the ADVR of birds is a highly complex structure and only a few components have been sufficiently studied. We completely agree on this, but the claims for homology between ADVR and LICx have been based on these few, well-studied regions. In this context, there are two intriguing components in the reptilian/avian DVR: (1) the hyperstriatum ventrale of birds (Emx-1 positive), which has been proposed to correspond to the reptilian dorsolateral ADVR and to the mammalian dorsolateral claustrum, dorsal endopiriform nucleus, and the basomedial amygdala, all Emx-1 positive (Guirado et al. 2000; Puelles et al. 2000); and (2) the avian archistriatum or posterior DVR of reptiles, whose homologies have been proposed to be many mammalian structures, including the (pallial) laterobasal amygdala (Lanuza et al. 1999), the (subpallial) centromedial amygdala (Smith-Fernández et al. 1998), and others (see Aboitiz et al. 2002). Certainly, further studies are needed to correctly determine the possible mammalian homologies to these structures, if they exist.

The OGH implies that there has been a re-routing of thalamic axons from the ventral pallium to the dorsal pallium (see target article, sects. 6.3, 6.4, and 8). **Butler** contends that the invasion of new territory by axons may be a too complex phenomenon, but in mammalian brain evolution this has occurred more than once (e.g., interhemispheric fibers and the corticospinal tract). In this context, transient embryonic structures like the subplate or cells in the pallial-subpallial or the telencephalic-diencephalic boundaries (Molnár et al. 2003) may have played key roles attracting both lemnothalamic and collothalamic axons into the developing cortical plate. Favoring the OGH, **Medina** and **Guirado** propose an enlargement of the dorsal pallium concomitant with expansion of the dorsal thalamus, which could be consistent with our dorsalization hypothesis. However, we are not sure yet whether this was an automatic consequence of increased thalamic axon growth. In mammals, thalamic expansion has been much more limited than cortical expansion, suggesting that thalamic influence may not account for all cortical growth. Furthermore, the concept of an expansion of dorsal tier thalamic nuclei as proposed by these authors largely relies on the presumed absence of homology between the mammalian pulvinar nucleus and the avian nucleus rotundus: the pulvinar would be a new nucleus which expanded greatly in the dorsal tier of the mammalian dorsal thalamus. On the other hand, **Güntürkün**, **Reiner**, and **Salas et al.** make an argument for homology between the rotundus and the pulvinar, and Güntürkün and Reiner, especially, strongly criticize the proposal of homology between the rotundus and the mammalian intralaminar nuclei. Although in a previous article (Aboitiz et al. 2002) we somehow favored the intralaminar-rotundus homology interpretation, at this point our intention was mainly to expose the two different viewpoints. We admit that this issue is not settled yet and further evidence may be needed to accept the intralaminar/rotundus homology hypothesis. As we stated in the target article, this issue is not germane to the OGH/RECH debate. In fact, the OGH appeared long before the pulvinar/rotundus homology was under question.

In addition, **Guirado** seems not to be convinced of adaptive explanations for macroevolutionary phenomena. Briefly, we consider that if an adaptive explanation is sound and consistent with the evidence, it should be taken as seriously as any other scientific proposal, and not be a priori rejected (Aboitiz 1990). Of course it is the entire postnatal structure that is presented to nature, but development makes up this structure, and changes in function imply structural changes mediated by development. Furthermore, purely developmental explanations are usually not sufficient to explain the origin of a structure: an obvious requisite for any evolutionary novelty is to work well (consider the evolution of the eye; see also comment by **Treves**). Guirado also thinks we are trying to compare the isocortex with all of the reptilian cortex, and that we claim that every component of the mammalian pallium must have a homologue in reptiles, which is not exactly what we argued in the target article.

Medina proposes several candidate genes for the dorsalization process, which need to be evaluated by future studies. In this context, it will be interesting to investigate the possible participation of the *sonic hedgehog/Gli* signaling pathway, which may promote cortical expansion (Ruiz i Atalba et al. 2002). We are not so sure that a single or a few mutations may have produced a fully working mammalian brain. It is perhaps more likely that changes in gene expression patterns involved several genes and occurred gradually, rather than all of a sudden. For example, there may be many genes that cooperate in the establishment of the pallial-subpallial boundary and in regulating cortical expansion (Bishop et al. 2003; Stenman et al. 2003). Probably many or all of these genes were involved in the origin of the isocortex. In this context, **Miu & Olteanu** propose a research program in which the costs and benefits of distinct developmental transformations should be weighed to evaluate the different alternatives. This could be a promising endeavor that may lead future research.

Martínez-García and **Guirado** claim that the argument for homology between the reptilian dorsal cortex and mammalian somatosensory and primary visual cortices is not correct; a cladistic analysis implies that the stem amniote had a multimodal pallium that underwent independent parcellation in the sauropsidian and in the synapsid lineages. **Powers** makes a similar argument when comparing the reptilian dorsal cortex with the mammalian entorhinal/subicular cortices. We believe that this is a very interesting possibility that deserves further study. In a way, this can be conceived of as a more radical form of the OGH that in our view would be consistent with the main hypotheses presented in the target article, especially with the claim that the mammalian and reptilian brains diverged very early in evolution. **Powers**'s suggestion for the role of dorsalization in the expansion of the dorsal cortex is also welcome. In this way, the dorsal pallium would have accommodated the lemnothalamic and collothalamic sensory input that began participating in associative networks.

R2. Evolution of cortical lamination

We would like to acknowledge **Marín-Padilla**'s earlier theory of a dual origin of cortical laminae, with an ancestral, early-produced component and a phylogenetically new, late-produced component. We think our hypothesis of cortical lamination (which is also partly based on Reiner 1993) has several points in common with Marín-Padilla's original proposals, especially the concept that the developmental sequence in this case seems to correspond with the phylogenetic sequence. The evidence that mutations in the gene Tbr-1 cause specific defects in the early cortical compo-

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nents, and that mutations in other genes like Pax-6 cause deficits in late-produced components, supports this view. The early cortical components (especially cells in the subplate and layer VI) are reminiscent of an ancestral structure, which in mammals differentiated into a subplate and infragranular cortical layers. Note that in mammals, the ability to migrate past layers of preexisting cells developed among these early components. As said, cells in layer V may represent an intermediate stage in which cells acquired the migrating properties of the phylogenetically newer cortical neurons (cdk5/p35 dependant, glial-guided locomotion), but retain some phenotypic characteristics of ancestral cells (Aboitiz 1999a; Aboitiz et al. 2001b). As we mention in the target article, one point that deserves further study is to which extent the mammalian subplate can be considered comparable to early produced cells in the developing reptilian cortex or to cells in the adult reptilian cortex (Bernier et al. 1999; Cordery & Molnár 1999; Goffinet et al. 1999; Nacher et al. 1996; Supér et al. 1998b; Tissir et al. 2003). Another point that should be borne in mind is that the preplate has continued evolving in mammals by virtue of its role in cortical plate development. In addition, Marín-Padilla's suggestion about using the term "neocortex" rather than "isocortex," considering that it contains so many new elements, is reasonable to us. Our initial intention when using the term isocortex was to avoid implying a progressionist view of evolution, but if it were understood that this is not what is meant, we would see no problem in using the term neocortex.

Supèr contends that we do not explain "why" the dorsal cortex expands in mammals in conditions under which other structures like the hippocampus do not change their organization. He considers that the main cause for cortical expansion may have been the re-routing of thalamic axons from the superficial marginal zone to the deep subplate. As mentioned by other commentators (**Colombo**, **Martínez-García**, **Powers**, **Salas et al.**), hippocampal function and processing strategy may be somewhat more conservative than that of the isocortex, and its tangential organization is perhaps well suited for its functions (**Treves**). In addition, Supèr does not explain "why" axons were re-routed in the first place. We agree with Supèr in that the re-routing of corticothalamic axons may have released an important constraint on cortical expansion, but we are not so sure that this was the cause for all the rearrangements that occurred in isocortical origins. Rather, we prefer to think of this process as a gradual, reciprocal situation, in which small cortical expansions facilitated re-routing of some axons, which may have permitted some further expansion, then more re-routing, and so on. Still another possibility is that the true homolog of the reptilian cortex is the subplate (see comment by **Marín-Padilla**). If this was so, axonal rerouting might not have had to be so dramatic, since the cortical plate could have developed partly over the axons synapsing in the subplate/reptilian cortex (this would also be consistent with the notion of the inverted neurogenetic gradient as a strategy to maximize synaptic contacts with superficial afferents). An argument for a reciprocal relation may also be made about **Guirado**'s concern that cortical expansion drove the development of associative networks and not vice versa. These processes may have developed hand-in-hand, instead of occurring first one and then the other. Finally, Supèr argues that changes in cell number are not sufficient to increase cortical size, and gives as an example the visual cortex with a cell density double that of other cortical areas. Across species, there is a good correlation between neuronal number and cortical size (see, e.g., Haug 1987; Jerison 1973). In addition, the cortical cell numbers in mammals are probably orders of magnitude higher than in reptiles, not just double.

We welcome **Treves**'s analysis of processing capabilities of the isocortex; his "why" questions are more related to functional considerations that are interesting to investigate further. However, we think that the isocortical design may not be the only one that works; birds seem to do quite well with a different, non-laminated design (see **Shimizu**). In our view, isocortical architecture evolved as a consequence of a mixture of functional and developmental factors resulting in a design that worked well under specific circumstances – the world of early mammals. Subsequently, this design proved successful in colonizing other behavioral and ecological niches. The point we are trying to make is that some evolutionary innovations may originate as adaptive/developmental transformations that take place under very specific circumstances, and then turn out to be successful in a variety of conditions. This does not mean that this design is necessarily the optimal one that could be conceived for every situation.

R3. The "olfactory-hippocampal" hypothesis

We apologize for not having referred adequately to **Butler**'s early "olfactory-hippocampal" proposal and her considerations regarding the confluence of the lemnothalamic and collothalamic pathways in mammals. Our proposal also has a long date (cf. Aboitiz 1992). **Guirado** seems to disagree with the concept of confluence of collo- and lemnothalamic pathways in mammals as an evolutionary novelty. We claim that such a degree of confluence as is observed in mammals is not observed in reptiles. The fact remains that in sauropsids the bulk of the collothalamic input (which goes to the DVR) is largely independent from the lemnothalamic input (see also comments by Butler and **Shimizu**). In mammals, the pulvinar receives quite an important part of the visual collicular projection and sends a massive projection to the extrastriate cortex, in which both processing streams converge.

Bota and **Hermer-Vásquez & Hermer-Vásquez** propose to expand the olfactory-hippocampal axis to the orbitofrontal and the motor cortices, respectively. Hermer-Vásquez & Hermer-Vásquez also suggest a role for synchronized oscillatory activity as a linking mechanism in these networks. We are certainly in agreement with these proposals, especially considering that these associative networks may have been widespread in the early mammalian dorsal pallium. The point is to define an evolutionary starting point for these networks, which we believe may have been the hippocampal-olfactory axis. The proposals by **Martínez-García**, **Guirado**, and **Powers** about an ancestral multimodal dorsal pallium, perhaps comparable to the entorhinal/subicular cortex are especially relevant in this context.

Colombo and **Salas et al.** mention good evidence for conservatism of hippocampal involvement in spatial learning across vertebrates, which, as claimed by Colombo, raises the question of how function was maintained despite the important changes in overall connectivity in the differ-

ent lineages. Anatomical evidence suggests that there are more heavy sensory (collothalamic) inputs to the hippocampus of mammals than to that of reptiles (see comments by **Butler**, **Shimizu**, **Supèr**, and Butler 1994a; 1994b). In the target article, we mention that this is an intriguing question and is clearly matter for future comparative research. For example, an interesting lesion experiment would be to evaluate the role of collothalamic and lemnothalamic projections in spatial memory in mammals and reptiles. In addition, perhaps more subtle analyses will unveil processing differences in the hippocampi of mammals and reptiles, and many of the differences may be quantitative rather than qualitative. As we argue in the target article, a more detailed sensory input might not be necessary for the elaboration of crude maps of space but rather for complex forms of episodic memory and other memory functions (Eichenbaum 2000b).

Just to clarify issues, our main claim is that olfactory-hippocampal-dorsal cortex networks, present in ancestral reptiles and involved in spatial learning, were especially important in early mammals. The development of visual-olfactory associative networks involving the hippocampus may have a favored selection of an expanded dorsal pallium. In this way, despite an overall conservatism in function, perhaps more subtle forms of spatial or episodic memory and other functions may have developed in the hippocampus of the early mammalian brain.

R4. Fossil brains

Gilissen & Smith make an important contribution to our work by describing the multiple trends in brain expansion in early mammals, and the lack of detachment of ear ossicles in *Morganucodon,* implying that non-mechanical factors may have been important in early mammalian brain growth. In the target article, we admit that the interpretation of posterior brain expansion in *Morganucodon* may be questionable. Nevertheless, Gilissen & Smith point out that *Therioherpeton* (a Cynodont, see Figure 7 in the target article) might show signs of dorsal cortex expansion even earlier than *Morganucodon,* which would put the beginning of cortical expansion before what we originally proposed. However, the alternative that true brain expansion began much later, with the eumesencephalic type of brain (such as the eutherian *Barunlestes;* see Figure in Gilissen & Smith), is also possible. **O'Shea** proposes that there must have been interplay between patterns of braincase ossification, controlled by inhibitory signals from the dura mater, and evolutionary brain expansion in mammals. We believe that it could not be otherwise. Skull volume puts an obvious limit to brain expansion, and there must have been a coordinated evolution between these two parameters. This is a very interesting area for further research. Finally, we commend **Furtado** for his proposal of a scenario for early tetrapod evolution.

R5. Final comments

In the end, we feel that our main hypotheses are still in good standing after the commentary process. This has demonstrated that our proposal is a good basis for interdisciplinary research and discussion on the embryologic and evolutionary aspects of isocortical origins. Our intention at this point has been basically to outline a developmental and adaptive evolutionary scenario for isocortical origins, which needs to be evaluated by future research. The main idea is that a dorsalizing influence in telencephalic development triggered the origin of the isocortex, expanding the dorsal pallium both tangentially and radially. Generally speaking, a dorsalization process based on increased activity of dorsal-inducing factors may not help discriminate between the different hypotheses of homology of the isocortex. However, different homology hypotheses may imply specific mechanisms of dorsalization (tangential migration, change of identity of ventral pallial cells, or expansion of the dorsal pallium). We prefer the interpretation that the isocortex evolved its own circuitry and therefore its sensory circuits may not be homologous to those in the DVR of reptiles and birds. Furthermore, current developmental evidence suggests that the isocortex originated mostly from an ancestral dorsal pallium. Whether, in addition, some components of the ventral pallium became transformed into cortical phenotypes remains to be investigated, but, as stated, they would not be inconsistent with a dorsalization process. In this context, the controversy between the concepts of *field homology* and *embryonic homology* will probably remain for some time (Butler & Saidel 2000; Northcutt 1999; Puelles 2001b; Puelles & Medina 2002).

Except for some details, our views on the evolution of cortical lamination do not strictly contradict those of **Marín-Padilla** and **Supèr**, and we believe that they have both contributed importantly to this issue. Functional comparative studies may also be quite helpful in understanding the early evolution of cortical processing.

As an adaptive complement to this developmental process, we have proposed the "olfactory-hippocampal" hypothesis, which, even if it is not strictly new (Jerison 1973; Lynch 1986; Sagan 1977; see also commentary by **Butler**), contains new elements like the collothalamic/lemnothalamic confluence and the role of the olfactory-hippocampal axis in episodic memory (Eichenbaum 2000b). There is strong evidence of a conserved role of the hippocampus in spatial memory, but in mammalian evolution it may have incorporated additional or more complex forms of memory, partly because of the increased confluence of sensory inputs to this structure. In addition, we agree that in mammals these hippocampal-olfactory networks may correspond to widespread ensembles of activity in the lateral, dorsal, and ventral pallium, including elements like the orbitofrontal and motor cortices. The point is whether one can speak of an orbitofrontal and a motor cortex in the early evolution of the isocortex.

Finally, it has become clear that endocast information and the study of cranial anatomy may provide important clues to the origin of the mammalian brain. Open questions like when brain expansion began, and whether it was in Cynodonts or in crown mammals, will probably need to wait for further evidence.

We want to acknowledge all the reviewers and commentators for taking their time to participate in this exciting project. We feel that an open, interdisciplinary debate of this topic was long due, and expect that from this discussion new experiments will be made, oriented to address many of the questions that were raised.

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Letters "a" and "r" appearing before authors' initials refer to target article and response respectively.

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