Kohler 1986). Damage to the orbital cortex impairs animals in the odor version of the delayed nonmatch to sample (DNMS) task when the memory delay is minimal, which suggests that this region is important in perceptual processing or learning of rules (Eichenbaum 2000a).

Neurons in the rat orbital cortex recorded during an eight-odor discrimination task correlate their activity with recent past information and anticipate future events (Schoenbaum & Eichenbaum 1995). Physiological studies of orbital neurons in the rat showed that these fire either for single events or associations of events such as initiation of trials, sampling of odors, and reward consumption of odor-guided DNMS tasks (Ramus & Eichenbaum 2000). Rodent, monkey, and human experimental data show that the orbital cortex is the place where inputs from sensory and emotional and motivational information converge and it may be involved in representation of goals (Rolls 2000; Schultz et al. 2000). The orbital cortices can be considered to be part of the partially overlapping networks that are involved in the visual and nonvisual representations of space where sensory information is associated with reward and motivational-related information for rules formation.

The survival of animals depends on the creation and storage of complex representations of space. These are not only collections of places associated with visual or nonvisual cues or associations of stimuli, but also sets of rules for navigation and associations between stimuli and rewards. The orbital cortex appears to be a place involved both in the creation of the rules needed to construct and use spatial representations in lower mammalian species such as rodents, and for encoding more abstract rules in monkeys and humans. Therefore, the successful survival of animals also depends on the orbital cortices. The existence of the orbital cortex and the connections with olfactory regions in insectivore species (Radke-Schuller & Kunzle 2000) may be an indication that this region was present in the earliest mammals, and it may have similar functions across mammalian species.

The experimental findings presented above suggest that the olfactory cortex–hippocampal formation axis can be extended to a triangle of structures involved in olfactory representations of the environment, the "olfactory cortex–hippocampal formation–orbital cortex," and it may appear early in the mammalian speciation. Nonmammalian vertebrate species present homologous structures of the olfactory cortex and the hippocampal formation, but the orbital cortex appears to be characteristic only to mammals.

One can therefore hypothesize that the network of cortical regions made of the olfactory regions, hippocampal formation, and orbital cortices is that circuit which allowed early mammals to construct complex representations of space, first olfactory-based but which, following the hypothesis of Aboitiz et al., became more visual when diurnal mammalian species emerged.

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The third alternative: Duplication of collopallium in isocortical evolution

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Abstract: One hypothesis of isocortical evolution requires tangential migration of glutaminergic neurons. A second requires invasion of collothalamic afferents into the dorsal pallium, a territory that in sauropsids is solely lemnopallial. A third alternative is noted here – duplication of the original collopallial territory. The duplicated region would be formed by radial migration of excitatory neurons and would maintain its collothalamic innervation.

The central point of this target article – the "hippocampal-olfactory hypothesis" for isocortical evolution and its adaptive advantage – is sound and has precedent in the literature. For example, Butler (1994a) noted that

> Selection pressures strongly favored those amniotes in which this pallial expansion . . . occurred. The relay of information from both divisions [collothalamic and lemnothalamic pallia] . . . to the medial pallium for memory-related functions . . . would have conferred a significant competitive advantage.

The idea of an adaptive advantage gained by increased sensory inputs to the limbic system is compatible with each of several current hypotheses for the gain and expansion of the isocortex.

Two possible scenarios for isocortical expansion are considered in the target article. Did the isocortex evolve as an expansion of the dorsal pallium, as defined by Puelles et al. (2000), and thus have a unitary origin? Alternatively, did the isocortex have a dual origin, such that its developmentally medial part evolved as an expanded dorsal pallium and its lateral part evolved due to tangential migration of glutaminergic neuronal elements from a more ventrolateral part of the pallial mantle? The latter idea can be discarded for lack of evidence. The former, single-origin scenario would have involved a substantial change in connectivity. Because the dorsal pallium is in receipt of only lemnothalamic projections in sauropsids (Butler 1994a), its expansion and gain of collothalamic afferents would require substantial changes in the molecular cues expressed in the subplate and perhaps elsewhere. As in all cases of proposed neural homology, both developmental and hodological data must be weighed and accounted for, particularly because connections are the result of molecular cues expressed and utilized during development.

A key issue regarding isocortical evolution is whether a ventral pallial division can be separately distinguished on gene-expression criteria. A ventral pallium was identified by lack of Emx-1 expression (Puelles et al. 2000; Smith-Fernandez et al. 1998), and at least some of its derivatives are collothalamic targets in both mammals and sauropsids. However, Gorski et al. (2002) have demonstrated that all pallial regions contain neurons that express Emx-1 at some time during development. All parts of the pallium – medial, dorsal, lateral, and ventral – express Pax-6, Tbr-1, and Emx-1. Although the ventral pallial territory may be distinguished by some other markers, such as differences in the degree of expression of cadherins (Redies et al. 2001), it may vary only as a matter of degree from other pallial areas due to gene-expression gradients rather than as a sovereignly discrete entity.

A third alternative exists that involves dual evolutionary origin of the isocortex but does not require either changes in molecular guidance cues or tangential migration of glutaminergic neurons. Although differing to some extent in details and rationales, dual-origin hypotheses for the isocortex have been previously proposed (e.g., Abbie 1940; Butler 1994a; Karten 1969; Reiner 1993; 2000; Sanides 1970). The "dual expansion hypothesis" (Butler 1994a) was based to a large extent on the recognition that two separate divisions of the dorsal thalamus – the lemnothalamus and collothalamus – exist, have different patterns of telencephalic projections, and were differentially expanded in the mammalian and sauropsid lineages (Butler 1994b; 1995). Recently, the separate identities of these two dorsal thalamic divisions have received strong support from molecular data, including calcium-binding protein immunoreactivity, Gbx2 expression, and Math4a expression (Dávila et al. 2000; González et al. 2002; Martínez-de-la-Torre et al. 2002). If there are two such separate divisions of the dorsal thalamus, two comparably separate divisions of the isocortex – lemnocortex and collocortex – might likewise exist in mammals and be under separate selective pressures.

The third alternative requires only a feature of collocortex that is already firmly established: the marked propensity of collocortical areas to duplicate themselves, as has occurred independently within several mammalian lineages (Allman 1977; Kaas 1982; 1995; Krubitzer 2000). The recently proposed field homology

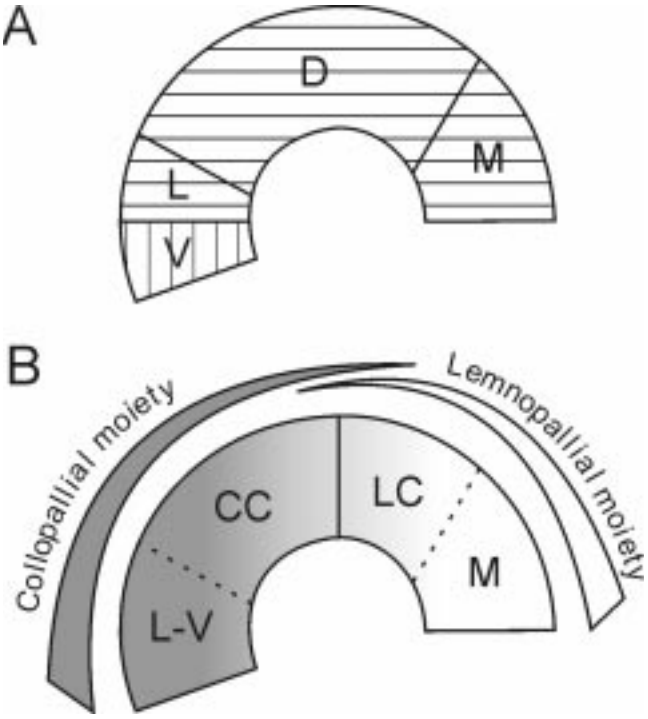

Figure 1 (Butler). **A:** Pallial divisions as originally proposed by Puelles et al. (2000) with Emx-1-positive medial (M), dorsal (D), and lateral (L) pallia and an Emx-1-negative ventral (V) pallium. Subsequent work (Gorsky et al. 2002) has demonstrated Emx-1-positivity in the ventral pallium as well. This model requires an invasion of collothalamic projections into the lateral part of the dorsal pallium. **B:** Collopallial and lemnopallial moieties proposed on the basis of lateromedial and mediolateral gradients (represented by curved narrowing slivers above the pallial hemisphere) of gene expression patterns. (The lateral and medial pallia are included here in this broader, developmental concept of the collo- and lemnopallial territories, even though in most cases they are not in direct receipt of the ascending thalamic projections.) This model retains collothalamic projections to collopallial territory. The collocortex (CC) arose by duplication of the original lateroventral (L-V) part of the pallium; only the lemnocortex (LC) is the derivative of the original dorsal pallium and is homologous to the Wulst of birds and the dorsal cortex of reptiles.

(Butler & Molnár 2002; Molnár & Butler 2002a; 2002b) of the sauropsid anterior dorsal ventricular ridge to the claustrum (where present; see Butler et al. 2002), pallial amygdala, and collocortex of mammals incorporates the idea that duplication of the ventrolateral pallium could account for the origin of the collocortex. With duplication, tangential migration of excitatory neurons is not required; within the more dorsally lying "copy" of the original collopallial field, radial migration of excitatory neurons would produce the cortex.

The specification of the collothalamic moiety (including lateral pallium, claustroamygdalar formation, and collocortex) and the lemnothalamic moiety (including medial pallium and lemnocortex) may be accomplished during development by a combination of gradients of gene expression patterns (Fig. 1). For example, Pax6, Tbr2, and Tlx are all expressed in a high-lateral to low-medial gradient across the pallium in mice (Muzio et al. 2002a; Stenman et al. 2003). This model allows for maintenance of developmental guidance cues for separate collothalamic and lemnothalamic projections and requires only radial migration of excitatory neurons in the collocortical region.

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Avian and mammalian hippocampus: No degrees of freedom in evolution of function

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Abstract: Aboitiz et al. suggest that the mammalian isocortex is derived from the dorsal cortex of reptiles and birds, and that there has been a major divergence in the connectivity patterns (and hence function) of the mammalian and reptilian/avian hippocampus. There is considerable evidence to suggest, however, that the avian hippocampus serves the exact same function as the mammalian hippocampus.

Aboitiz, Morales, and Montiel (Aboitiz et al.) are to be complemented for their fine thesis on the evolution of the mammalian isocortex. The issue I would like to raise is not with the developmental or connectional transformations that may have occurred, but rather with the purported functional transformations that accompanied the evolution of the mammalian isocortex from the dorsal pallium of reptiles and birds. (For ease of exposition, I will restrict my discussion to birds.)

In section 6.1, the authors argue that in mammals, thalamofugal and tectofugal sensory information blend together and ultimately project to the hippocampus and the amygdala. In birds, on the other hand, the majority of the thalamofugal sensory information is sent to the hippocampus but the majority of the tectofugal information is transmitted to the ADVR and the PDVR, the latter of which is comparable to the mammalian amygdala (see target article, sect. 3.2). According to the authors, these differences in connectional patterns suggest that the hippocampus of mammals receives a much heavier sensory projection than the hippocampus of birds, and that birds "may rely more on amygdalar components (PDVR/archistriatum) than on the hippocampus to process certain types of sensory and mnemonic information" (sect. 6.1, para. 1). The implication is that the avian hippocampus may process different, or perhaps a more restricted range of, information than the mammalian hippocampus.

Over the past six years we have conducted a number of studies looking at the function of the hippocampus in birds (Colombo & Broadbent 2000). Our data indicate that damage to the avian hippocampus causes the same constellation of impairments as does damage to the mammalian hippocampus. Part of the problem with the mammalian hippocampal lesion literature is that in most early studies the damage often extended well beyond the hippocampus into structures whose exact function was not known. So although early studies did show impairments on visual memory tasks after damage to the "hippocampus" (Zola-Morgan & Squire 1986), later studies in which the lesions were restricted to the hippocampus failed to find any impairments on the three standard tasks used to assay visual memory in mammals: visual delayed nonmatching-to-sample, visual concurrent discrimination, or, retention of a visual discrimination (Alvarez et al. 1995). (The small visual impairments seen at the longest delay on the visual delayed nonmatching-to-sample task in the Alvarez et al. [1995] study is likely the result of a design flaw that may have inadvertently introduced a spatial component into the task.) Just as in mammals, birds with damage to the hippocampus also show no impairments on these three visual memory tasks (Colombo et al. 1997b). In short, there is no convincing evidence to date that damage to the hippocampus in either mammals or birds impairs performance on a purely visual memory task.

In contrast to the lack of effects of hippocampal lesions on visual tasks, both mammals and birds with damage to the hippocampus show profound impairments on tasks that require the processing and retention of spatial information. Mammals with hippocampal damage, for example, are impaired on both the radial-arm maze task (Olton et al. 1979) as well as the water maze task (Morris et al. 1982). Likewise, birds with hippocampal damage are also impaired on an analogue of the radial-arm maze task