put (Hellmann & Güntürkün 2001). These cells are only driven by visual stimuli (Schmidt & Bischof 2001) and some have wide dendritic trees with "bottlebrush" endings on which retinal fibers synapse (Luksch et al. 1998). Their receptive fields are 20–40° in diameter with suppressive surrounds, they are best driven by small (<1°) moving stimuli, and they are inhibited by wholefield motion (Frost et al. 1990; Jassik-Gerschenfeld et al. 1970).

In mammals the bilateral collicular projection to the LP-pulvinar is composed of at least two cell types in the lower stratum griseum superficiale/stratum opticum (Major et al. 2000) that receive monosynaptic retinal input (Michael 1972), are only driven by visual stimuli (Mooney et al. 1985), and are characterized by wide dendritic trees with bottlebrush endings on which retinal fibers synapse (Major et al. 2000). The receptive fields of these cells are 10–30° in diameter with suppressive surrounds. The neurons are best driven by small moving stimuli (<1°) and are inhibited by wholefield motion (Graham et al. 1981; Hoffmann 1973).

In birds, the different tectorotundal celltypes project into distinct rotundal domains (Hellmann & Güntürkün 2001) that can be discerned functionally (Wang et al. 1993). In mammals, different colliculofugal celltypes also project to LP-pulvinar subdivisions (Abramson & Chalupa 1988) where they probably establish distinct functional domains (Soares et al. 2001). Additionally, a side path of tectorotundal axons synapses on GABAergic pretectal nuclei that project back both onto rotundus and LP-pulvinar (Major et al. 2000; Theiss et al. 2003).

In birds (Wang et al. 1993) and mammals (Merabet et al. 1998), rotundus and LP-pulvinar process image motion, velocity, and relative motion between object and background (Casanova et al. 2001). Both in birds and in mammals, these properties arise in part from local computations (Dumbrava et al. 2001; Sun & Frost 1998). In birds (Laverghetta & Shimizu 2003) and mammals (Adams et al. 2000) the thalamotelencephalic projections target specific areas without bifurcations to the basal ganglia and are then disseminated to further forebrain regions where they partly intermingle with the thalamofugal/geniculocortical system (Husband & Shimizu 1999; Weller et al. 1984).

Thus, the similarities between avian tectofugal and mammalian extrageniculocortical pathways are impressive. Therefore, Major et al. (2000) coined the term "cellular homology" to describe the notion that for bottlebrush neurons homology can be traced back to cellular subtypes.

Is the nucleus rotundus a part of the posterior complex/intralaminar nuclei? Based on Bruce and Neary (1995), several authors (Dávila et al. 2000; 2002; Guirado et al. 2000; Redies et al. 2000) have argued that the rotundus is part of the posterior/intralaminar complex and might be equivalent to the suprageniculate nucleus. Aboitiz and colleagues support this position. So what is the evidence?

One argument is based on the position of the tectal projection neurons: In birds (and reptiles) they are located in the deep stratum griseum centrale, whereas in mammals their position is more superficial in the stratum griseum superficiale/stratum opticum. However, this argument is based on a simplified transposition of the collicular condition onto the avian/reptilian tectum. In mammals, the distinction between superficial and deep is determined by the position of the stratum opticum. In birds and reptiles, with the stratum opticum being most superficial, a similar clear-cut division is not possible. If however, monosynaptic retinal input is used to group cells into superficial (retinorecipient) and deep (nonretinorecipient), then tectorotundal cells are clearly as superficial as mammalian colliculopulvinar cells.

The second argument focuses on cellular birth dates. Based on Dávila et al. (2000), Aboitiz et al. argue that the LP-pulvinar receives axons from late-born cells in superficial colliculus, whereas rotundus receives afferents from early-born deep tectal neurons. If this were the case, early-born deep collicular cells projecting to the posterior complex would be comparable to the early-born avian tectorotundal projection. This argument is easy to contradict. Dávila et al. (2000) cited Altman and Bayer (1981) to argue that LP-pulvinar projecting neurons are born at E15–16 and the earliest rat collicular neurons are born at E13 and belong to those that project to posterior/intralaminar nuclei. In fact, Altman and Bayer reported nothing like that. They observed that E13 is only the birth date of neurons in the intermediate magnocellular zone of the stratum album intermediale. They specifically reported no difference for birth times of cells in stratum griseum superficiale (superficial) and stratum griseum intermediale (deep), with both peaking at E16. Thus, the two laminae projecting to LP-pulvinar and to posterior/intralaminar (Katoh & Benedek 1995) have indistinguishable birth times! This argument is supported by Wu et al. (2000) who showed that the birth date of the chick tectorotundal pathway is similar to that of the colliculopulvinar system in monkeys, if the relatively longer developmental times in primates are taken into account.

The third argument is that the position of the avian rotundus is in the intermediate tier, whereas the mammalian pulvinar is a dorsal tier nucleus. This is based on Redies et al. (2000) who mapped cadherin expressions and radial glial topology in chicks to show prosomeric divisions. Unfortunately, it is not clear how the tier divisions of this study emerged from the presented data. All cadherins used can be found in all major divisions, and especially the rotundus expresses all cadherins mapped. At present, then, the prosomeric division of the avian thalamus is more theory-based than data-based. It does not provide a major challenge to the assumption that tectorotundal and colliculopulvinar systems are homologous.

However, let us assume for a moment that the rotundus is homologous to the suprageniculatus. Then we would have to explain why the rotundus has no afferents from the spinal cord (Berkley et al. 1986), vestibular nuclei (Mickle & Ades 1954), dorsal column nuclei (Feldman & Kruger 1980), reticular formation (Hicks et al. 1986), auditory structures (Berkley 1973), and the cerebellar fastigial nucleus (Katoh et al. 2000), but receives afferents from tectal cells with retinal input. Additionally, we would have to explain why rotundal and posterior/intralaminar units differ so radically (Korzeniewska et al. 1986).

Occam's razor. The tectorotundal pathway is homologous to the colliculopulvinar system. To defend the contrary requires the incorporation of a fantastic number of assumptions. These would have to explain the rearrangement of major projection streams, neurochemically defined systems, and cellular properties at the biophysical and morphological level. Such a pursuit would run contrary to the principle formulated by William of Occam: "You should not assume plurality without necessity." There is no necessity. Several theories have beautifully outlined the ways in which the temporal cortex could be related to the DVR (Butler & Molnar 2002; Reiner 2000). I see possibilities to incorporate these ideas to develop a true grand theory on isocortical evolution that is not plagued by unsolvable contradictions. The great effort of Aboitiz and colleagues is definitely worth this extra mile.

The evolution of neural dynamics permitting isocortical-limbic-motor communication

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Abstract: The first cortically based associative circuits integrated olfactory, motivational, and motor information. Many of the neural dynamics present in these evolutionarily ancient, olfactory-motor circuits, such as the broadband frequency, phase, and amplitude modulations seen during recognition of a rewarded olfactory stimulus, are also found in isocortical circuits. These results suggest that mechanisms permitting olfactory associative processing formed the basis for evolutionarily more recent large-scale couplings involving isocortical areas.

Aboitiz et al.'s argument that the mammalian isocortex evolved from the reptilian dorsal cortex is a tour de force that elegantly integrates comparative anatomical, developmental, genetic, paleontological, and behavioral evidence. We are neurophysiologists who study associative learning and predict impending motor action in mammals by recording simultaneously from olfactory and motor areas as they execute voluntary, skilled tasks. As such, we would like to address how the neural dynamics used by circuits including the isocortex, hippocampus, olfactory cortex, and motor areas may have concurrently evolved.

At the behavioral level, animals' actions stem from an integration of sensory cues, motivational states, and motor planning. Underpinning this integration is an intricate interplay among signal transduction, gene expression, and electrical activity within and across neurons that evolved over the course of billions of years. These biochemical and biophysical mechanisms in turn permit neurons to communicate with one another such that, at times, vast neural networks transmit information to and from one another using common rhythmic states. Our research has shown that in rodents, olfactory and motor circuits interact in a distinctive, time-locked manner just prior to the execution of a learned, olfactorily guided motor task (Hermer-Vazquez et al., in press). We believe that the dynamics allowing this integration date back to the earliest chordates such as amphioxus, which acted predominantly using olfactory cues (Holland & Holland 2001; Lacalli 2001; Satoh et al. 2002). The olfactory-motor linkage was refined in the agnathans and other early vertebrates, whose entire pallium received olfactory inputs subserving the behavioral goal of predation (cf. the target article; Lacalli 2001).

Further anatomical and physiological evidence suggests that the earliest cortically based sensory-motivational-motor linkages recruited olfactomotor dynamics. The lateral pallium of reptiles is thought to be homologous to the piriform cortex of mammals (Martinez-Garcia et al. 1986), which is considered to be an evolutionarily ancient multimodal associative area facilitating simultaneous linkages among olfactory, somatosensory, autonomic, motivational, and motor information (Johnson et al. 2000). Furthermore, the piriform cortex projects heavily to the entorhinal cortex (Johnson et al. 2000), just as the lateral cortex in reptiles (along with lemnothalamic inputs) projects heavily to the hippocampus (cf. the target article). With the evolution of cellular mechanisms permitting graded, *persistent* neural activity in the entorhinal-hippocampal complex, percepts could be *maintained* in memory (Egorov et al. 2002), facilitating the formation of associations among stimuli occurring at different points in time. Later in evolution (e.g., in primates), previously olfactory memory circuits such as those involving the perirhinal cortex came to be used for nonolfactory memory such as visual object recognition (Bussey et al. 2003; Murray & Richmond 2001).

These facts and arguments suggest that the emerging neural dynamics underlying olfactory-motor associations could have formed the basis for multimodal associations involving isocortical areas when collothalamic inputs were routed to the hippocampus. What are the hallmarks of the interlocking biochemical, biophysical, and large-scale network processes found in olfactory-motor circuits? One example that illustrates this multiscale coordination involves the frequency-dependent modulation of piriform and motor cortical activity by projections from a third brain system, the basal forebrain. Basal forebrain glutamatergic, GABAergic, and cholinergic neurons project topographically to both the piriform and motor cortices (Donoghue & Parham 1983; Manns et al. 2003; Rosin et al. 1999; Wenk et al. 1980; Woolf et al. 1984). The coordinated release of these neurotransmitters, among others, during attentive perception and recall, sculpts the patterns of activity in task-related neural circuits in part by modifying the dynamics between inhibitory and excitatory network elements (Hagevik & McClellan 1994; Poschel et al. 2002; Steriade 1997; Whittington et al. 1995). These modifications – again, among other effects – alter the coupled, transient oscillatory states seen across large networks such as the olfactomotor circuitry. There is debate over the precise role played by subthreshold oscillations and suprathreshold oscillations, as manifested in regular interspike intervals, in neural coding. However, most researchers now agree that both rate coding and temporal coding, including modifications of the phase, amplitude, and frequency of oscillations, are involved in neural computations (Ahissar 1998; Mehta et al. 2002). It is also widely agreed that oscillatory states and precise spike timing are required for many forms of learning, as instantiated in changes in synaptic efficacy via long-term potentiation or depression (Bach et al. 1995; Tsien 2000; Tsodyks 2002).

Our recordings of local field potentials and spikes in the posterior piriform cortex, primary motor cortex, and subcortical motor areas of awake, behaving rats exemplify the importance of oscillatory states during learned behaviors. During olfactory recognition preceding the execution of a learned motor skill to attain an olfactory target, we have found a characteristic, transient, low-frequency oscillation occurring across the olfactory and motor areas (Hermer-Vazquez et al., in press). Concurrently, the amplitude and coherence across beta to gamma frequency bands in these task-related areas increase (Hermer-Vazquez et al., in press). A growing body of evidence indicates that the release of acetylcholine, glutamate, and GABA by the basal forebrain, in concert with dopamine release by the nigrostriatal and VTA systems, norepinephrine release by the locus coeruleus, and the release of other neuromodulators, causes this suite of changes in frequency, phase, and amplitude (Cassim et al. 2002; Lestienne et al. 1997; Manns et al. 2003; Taschenberger et al. 2002). In contrast, when the animal is not engaged in olfactory-related behaviors, the low-frequency rhythms are not synchronized across olfactory cortices and other brain areas and activity in other frequency bands, on average, is at background levels (Manns et al. 2003; Vanderwolf 1992).

This evolutionarily ancient, momentary broadband coherence on olfactory stimulus recognition appears to have been conserved in isocortical-motor circuits. For example, during a visual GO–NO GO paradigm run with monkeys, coherence among multiple high frequency bands increased at specific moments during each trial in task-related visual and motor areas (Bressler et al. 1993), similar to what we have found in olfactory and motor circuits in rodents. Transient coherence across multiple high-frequency bands has also been reported across task-related isocortical visual and somatosensory areas in humans during an associative learning task in which a color cue predicted a mild electric shock (Miltner et al. 1999). Also as in the piriform cortex, hippocampus, and M1 (Barkai & Hasselmo 1997; Hasselmo 1999; Hasselmo et al. 2002; Linster & Hasselmo 2001), acetylcholine (Hohmann & Berger-Sweeney 1998; Kilgard & Merzenich 1998; Schultz et al. 2000) plays a prominent role in attention, synaptic plasticity, and recall in all tested isocortical areas (e.g., Hohmann & Berger-Sweeney 1998; Kilgard & Merzenich 1998; Schultz et al. 2000). These observations support the hypothesis that the spatial and frequency modulations seen in ancient vertebrate olfactomotor circuits formed the biophysical basis for communication across isocortical, limbic, and motor circuits.

Reptilian cortex and mammalian neocortex early developmental homologies

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Abstract: I agree with the view expressed in the target article that the early structural organization of the mammalian neocortex (the primordial neocortical organization) is different from its final one and resembles the more primitive organization of reptilian cortex. During the early development of the neocortex, a distinctly mammalian multilayered pyramidal-cell plate is introduced within a more primitive reptilian-like cortex, establishing simultaneously layer I (marginal zone) above it and layer VII (subplate zone)

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