necessary to give rise to an isocortex. However, some refinement should be made to their review of the thalamo-telencephalic connections and, even more important, to their conception of the evolutionary processes originating the isocortex.

A recurrent problem in analyzing thalamo-telencephalic connections from a comparative view is to describe only one target (usually the more conspicuous) for the thalamic projections. This approach does not analyze the entire set of connections and tends to underestimate other thalamic projections. It implies that thalamic projections found in mammals and not in other vertebrates must be interpreted as redirected to one specific telencephalic target, when in fact new thalamic projections can be considered as further acquisitions (and likely appeared as collateral axons) within a basic common pattern of connections shared by different vertebrates, but with their own evolutionary history.

In reptiles, dorsal thalamic nuclei localized to the middle and ventral tiers receive strong mesencephalic (collicular) inputs and project to the basal ganglia (Gonzalez et al. 1990) and then to ventral (and likely lateral) pallium derivatives (Guirado et al. 2000). Thus, basal ganglia receive a major input from the dorsal thalamus, as in amphibians. On the other hand, dorsal thalamic efferent projections from dorsal tier nuclei end mainly in the medial, dorsal, and lateral cortices of reptiles. These connections convey lemnothalamic as well as collothalamic information (the latter through the dorsolateral anterior nucleus, a multimodal nucleus in the dorsal tier receiving afferent fibers from a variety of sources including the optic tectum). Therefore, the confluence of lemnothalamic and collothalamic pathways in the dorsal pallium is not an innovation of mammalian brains, as postulated in the target article. Aboitiz et al. propose that the development of collothalamic sensory projections into the isocortex was an important factor in the expansion of the isocortex. Why not consider the possibility that the development of the isocortex was *concomitant* with the development and increasing complexity (i.e., more mantle derivatives and more superficially located nuclei) of dorsal tier nuclei in the dorsal thalamus? These nuclei convey both lemniscal and collicular information to the isocortex.

On the other hand, the visual thalamofugal projection to the cerebral cortex has been usually considered as a major shared feature between the isocortex and the reptilian dorsal cortex. It should be noted that only turtles among reptiles seem to have a visual thalamic projection to the dorsal cortex. There is not any description of such a projection in other reptilian groups. Thus, depending on what phylogenetic analysis of the relations between turtles and mammals is considered, the more parsimonious explanation for this feature is either that the thalamo-cortical visual projection is secondarily lost in nonchelonian reptiles (the case of a close relation between turtles and mammals), or the result of a convergent (nonhomologous) evolution (the case of considering turtles as a group of reptiles with no direct relation to the ancestral anapsids).

Regarding the conceptual concern I cited above, Aboitiz et al. propose a scenario where changes necessary to construct a six-layered isocortex are sequentially explained. In other words, they intend to explain how to transform gradually a reptilian dorsal cortex into a mammalian isocortex. Aboitiz et al. assume that each gradual transformation has an adaptive value, and that selective pressures drive each transformation. These transformations (which are well delineated in the target article) actually correspond to changes in embryonic development that are able to modify the final state of the organ (in this case the brain). However, conceptually there is no need for each transformation to be adaptive. For example, the inside-out neurogenetic gradient itself does not necessarily need to have an adaptive value. It is the entire postnatal/adult structure that is presented to nature, then adaptation to environment allows for the fine-tuning (brain plasticity) of the structure. Thus, in my opinion, selective pressures can account for the adaptive, small changes in the adult brain morphology, but they are neither the driving forces for major changes (especially those features characterizing a whole class of vertebrates) nor the motor of evolution.

There is a tendency throughout the target article to compare the isocortex with the entire reptilian cortex; however, the isocortex would be better compared with those parts of the reptilian cortex derived from the dorsal pallium. I agree with Aboitiz et al. that two structures being homologous does not imply that homology must be found among each of their components: The reptilian pallium is homologous as a field to the mammalian pallium, but that does not imply that every component (subdivision) of the mammalian pallium must have a reptilian homologue. The isocortex may be seen as an innovation in mammals (i.e., a new derivative of the dorsal pallium) that undergoes a surface expansion concomitant with the expansion of the dorsal tier of the dorsal thalamus. In any case, to find the homologue of the isocortex in sauropsids implies first identifying a series of developmental processes characteristic and exclusive of the isocortex (e.g., the expression pattern of some regulatory genes; in this sense it is important to find molecular markers defining exclusively the dorsal pallium), and then finding a region in the pallium of sauropsids that displays differentially the same developmental processes.

Finally, an important proposal of Aboitiz et al. is that the progressive involvement of visual information in associative networks triggered the expansion of dorsal pallium derivatives. However, this phenomenon may also be the opposite: It may be that the expansion of the dorsal pallium allowed the progressive formation of associative networks (more complex structures allow the performance of more complex tasks).

ACKNOWLEDGMENTS

Preparation of this commentary was supported by a grant from the Spanish DGI (BFI2000-1359-C02-01) and the Spanish FIS (01-0057-01). I wish to thank José Carlos Dávila and Manuel José Andreu for helpful related discussion.

Occam's razor and the collothalamic projection

Onur Güntürkün

Department of Biopsychology, Institute of Cognitive Neuroscience, Faculty of Psychology, Ruhr-Universität Bochum, D-44780 Bochum, Germany.
onur.guentuerkuen@ruhr-uni-bochum.de
www.bio.psy.ruhr-uni-bochum.de

Abstract: Aboitiz and colleagues propose that the tectorotundal pathway of birds and reptiles is homologous not to the mammalian colliculopulvinar system but to the posterior complex/intralaminar nuclei. However, as outlined below, a large amount of strong evidence points to a homology of the tectorotundal and the colliculopulvinar system. This makes it likely that DVR and isocortex might be in part homologous.

Aboitiz and colleagues present a brave attempt to integrate literature from diverse areas into a coherent theoretical frame. However, as often in grand approaches, obstacles are discussed away to preserve coherency. But the beauty of obstacles is their ability to uncover serious inconsistencies. This is exemplified in the issue of collothalamic projections.

The thalamic lateral posterior-pulvinar nucleus of mammals (LP-pulvinar) receives afferents from the superior colliculus and projects to the extrastriate cortex. If this structure is homologous to the reptilian and avian nucleus rotundus, the mammalian isocortex would probably be constituted by reptilian dorsal cortex plus parts of the DVR. Based on a review by Bruce and Neary (1995) and anatomical evidences (Dávila et al. 2000; 2002; Guirado et al. 2000; Redies et al. 2000), Aboitiz and colleagues argue that the rotundus is homologous to parts of the posterior complex/intralaminar nuclei. However, evidence to the contrary is huge.

The tectorotundal projection in birds and mammals. In birds, the rotundus receives bilateral afferents from the tectal stratum griseum centrale. At least five cell types constitute this tectorotundal pathway and four of them receive monosynaptic retinal in-

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

Hermer-Vazquez, R. and Hermer-Vazquez, L.

Department of Physiology, SUNY Health Science Center at Brooklyn, Brooklyn, NY 11203. **Linda.Hermer-Vazquez@downstate.edu**
hermvazq1@palm.com

The two authors contributed equally.

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.