

Amphibian basal ganglia control of tectal function: a complex matter

In his article about neural correlates of key stimulus and releasing mechanisms in the tectum of anuran amphibians, Ewert¹ highlighted some aspects of the role of the telencephalon in the release of visual behavior. On the basis of lesion and anatomical studies^{2,3}, the author states that the caudal striatum exerts its influence on response gating solely via an inhibitory striato-pretectal connection. Because the pretecto-tectal connection appears to have an inhibitory effect on tectal neurons, Ewert suggests that stimulation of the striatum results in the release of pre-catching behavior by means of double inhibition. Moreover, the role of the striatum in the modulation of tectal activity would be generated by the influence of visual information of tectal origin (via the anterior division of the lateral thalamic nucleus) and internal forebrain inputs. Hence striatal influence on tectal neurons is regarded as having a single modulatory effect. Although we do not wish to question the importance of this basal ganglia pathway to the tectum, we feel that, in the light of recent findings on basal ganglia organization in frogs and salamanders, the organization of the basal ganglia-tectal connections is far more complex than that considered by Ewert. Research in recent years has revealed that the organization of the basal ganglia in extant amphibians is largely comparable to that of modern reptiles, birds and mammals⁴⁻⁸. As in birds and some reptiles, the basal ganglia of anurans have several indirect routes by which they can influence tectal activity⁹. In particular, the anuran striatum strongly projects to the mesencephalic tegmentum in a region thought to be homologous to the amniotic substantia nigra pars reticulata^{3,6}, which in turn projects to the tectum⁹. The striato-nigro-tectal pathway provides the amphibian basal ganglia with a more prominent access to central motor pathways than the striato-pretecto-tectal route^{6,9}. Moreover, the basal ganglia of anurans also project directly to the tectum, which so far seems to be a unique feature of amphibians^{6,9}. In summary, the basal ganglia in frogs might modulate tectal activity through several pathways, and not only via the pretectal region. Therefore, tectal responses obtained after striatal lesions should not be explained simply by pretecto-tectal inhibition¹, as striatal deficit would also modify several other basal ganglia pathways to the tectum.

It is certainly true that disinhibition might be a basic process in the expression of

striatal functions in amphibians, as has been proposed for the amniotes^{10,11}. It is likely that the pretectal cells are not the only inhibitory source to the frog tectum and, therefore, this raises questions about the different roles these multiple sources of putative inhibitory input might play in determining the response properties of tectal neurons. Considering the new neuroanatomical data on basal forebrain organization in amphibians, it is conceivable that the basal ganglia might play a more prominent role than suggested by Ewert in the control of movement triggering. Moreover, the idea that the striatum of amphibians receives inputs of several sensory modalities⁵, and not only visual, underscores its key position in the regulation of orienting movements through the tectum, as it occurs in amniotes^{10,11}. Future physiological studies on the role of basal ganglia-tectal projections on visually elicited tectal responses in amphibians should, therefore, take these recent anatomical findings into consideration.

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Reply

First of all, Dr Marín and his colleagues are to be congratulated on the impressive series of 1997 papers which clarifies the anatomical organization of basal ganglia in amphibians. The new neuroanatomical data – published after I prepared the *Viewpoint* article – bring additional perspectives regarding modulatory loops in the macronetwork. An earlier paper¹ from this group reported considerable differences in the mesencephalic dopaminergic innervation of the basal forebrain in anurans and urodeles, that is strong innervation of the nucleus accumbens in *Rana* and of the striatum in *Pleurodeles*, indicating that the mesostriatal system is particularly well developed in the newt, whereas the mesolimbic system prevails in the frog. Wilczynski and Northcutt² stated that it is difficult to assign point-to-point homologies of substantia nigra in amniotes and amphibians. The new neuroanatomical results provide better support.

However, hodological data realize their full potential only when complemented

with pharmaco-physiological results and behavioral correlates. Therefore, I doubt that the new anatomical data³, in particular the data⁴ explicitly referred to by Dr Marín, allow a comparison of the physiological significance of the striato-nigro-tectal connections with the striato-pretecto-tectal connections in anurans. With respect to the latter, I also think that some points in Dr Marín's comments need to be clarified. Pretecto-tectal inhibitory connections do not 'appear' to exist; rather, there is clear evidence for this from physiological experiments. One connection is mediated by neuropeptide Y with affinity for the Y₂ receptor; others may be dopaminergic^{1,5-7}. Visual smallfield and widefield pretectal TH3 and TH4 cells project to the tectum, as shown by backfiring techniques. Pretectal cells receive a substantial monosynaptic inhibitory input from the striatum, as evidenced by electrostimulation, intracellular recording, and labelling (see the original *Viewpoint* article for references).

I agree that striatal influences reach the amphibian tectum through many different pathways, and when I suggest that the