

# Anatomical Substrate of Amphibian Basal Ganglia Involvement in Visuomotor Behaviour

Oscar Marín<sup>1,2</sup>, Agustín González<sup>1</sup> and Wilhelmus J.A.J. Smeets<sup>3</sup>

<sup>1</sup>Departamento de Biología Celular, Facultad de Biología, Universidad Complutense, Madrid, Spain, <sup>2</sup>Departamento de Ciencias Morfológicas y Fisiología, Universidad Europea, Madrid, Spain, and <sup>3</sup>Graduate School of Neurosciences of Amsterdam, Research Institute of Neurosciences and Department of Anatomy and Embryology, Vrije Universiteit, Amsterdam, The Netherlands

**Keywords:** evolution, mesencephalic tegmentum, pretectum, *Rana perezi*, striatum

## Abstract

The optic tectum of amphibians is known to play a major role in the control of visually elicited orienting movements, such as prey-catching and avoidance behaviours. The recent finding of a direct striato-tectal connection in the frog *Rana perezi* prompted us to study in detail the anatomical substrate by which the basal ganglia of amphibians may modulate visuomotor behaviour. Injections of anterograde tracers into the striatum were combined with applications of retrograde tracers in the mid-brain tectum. Apart from a direct striato-tectal connection, at least three indirect pathways were observed, viz. a striato-anterior entopeduncular-tectal pathway, a striato-pretectal-tectal pathway and a striato-tegmento-tectal pathway. The basal ganglia-tectal connections of anurans largely resemble those described for amniotes, but appear to be more extensive. However, a pallio-tectal connection comparable to the cortico-tectal pathways of mammals was not observed in *Rana perezi*. Therefore, the striatum of anurans, which receives multimodal sensory information, seems to be the sole telencephalic structure that influences the mesencephalic tectum via a direct pathway.

## Introduction

In amphibians, it is well established that the optic tectum plays a major role in the control of visually elicited orienting movements, such as prey-catching and avoidance behaviours (for review, see Ewert, 1987). Ablation of the optic tectum, for example, abolishes all visually guided prey-catching and avoidance movements (Ingle, 1973a; Kiclíter, 1973; Comer and Grobstein, 1981), whereas electrical stimulation of the same structure elicits normal orienting responses (Ewert, 1970, 1984). Tectal efferent projections reach several mid-brain and medullary centres, as well as the spinal cord (Lázár *et al.*, 1983; Masino and Grobstein, 1990), providing the routes by which the mid-brain tectum may affect motor behaviour.

Both the pretectum and the telencephalon have been shown to modulate in different ways the responses of tectal neurons to visually elicited orienting movements (for review, see Grüsser-Cornehls, 1984). Lesion experiments have demonstrated that prey-catching behaviour is enhanced when the pretectal region is damaged (Ewert, 1970; Ingle, 1973a,b; Finkenstädt, 1980). Electric stimulation of the latter region, on the other hand, evokes escape responses (Grüsser-Cornehls, 1984). Therefore, whereas visual information transmitted directly to the tectum elicits prey-catching movements, the pathways through the pretectum activate avoidance behaviour (Ewert, 1970). Further, pretectal fatigue following long-term stimulation results in prey-catching toward normally avoided stimuli, suggesting an inhibitory nature of the pretecto-tectal pathway (Ewert, 1970).

Telencephalic lesions also impair prey-catching behaviour (Ewert,

1970, 1984). Unilateral telencephalic lesions produce a complete depression of the orienting activity via the contralateral eye, although some effect is seen via the ipsilateral eye as well, suggesting a predominantly, but not entirely, ipsilateral telencephalic influence on tectal activity. Within the telencephalon, the medial pallium and the striatum are considered to be involved in the modulation of prey-catching and avoidance responses to visual stimuli (Ewert, 1970, 1984). The medial pallium of anurans may exert its influence on the optic tectum via two disynaptic routes, viz. one via the septal nuclei and the other via the pretectal region (Northcutt and Ronan, 1992). The medial pallium has been related to the modulation of the attentional state of the animal rather than to a direct role in prey-catching and avoidance responses (Finkenstädt *et al.*, 1986; Finkenstädt and Ewert, 1988).

Although some evidence has been presented that the basal telencephalon of amphibians projects to the anterior entopeduncular nucleus, the pretectum and the brainstem tegmentum and thus may influence the mid-brain tectum indirectly, our knowledge of the anatomical substrate of basal ganglia tectal connections is still limited. This lack of information is mainly due to the shortage of tracers that are not only very sensitive but can also be applied to restricted brain regions. Recent studies of basal ganglia organization in amphibians (Marín *et al.*, 1997a,b,c) have demonstrated that the use of dextran amines as anterograde and retrograde tracers largely may overcome this problem. The main goal of the present study was, therefore, to

TABLE 1. Summary of experiments

Case	Tracer in striatum	Tracer in tectum	Survival time (days)
9666	TRDA 10kDa	–	10
9667	–	BDA 10kDa	9
9670	–	BDA 3kDa	7
9672	TRDA 10kDa	–	10
9680	–	FDA 3kDa	6
9681	–	BDA 20kDa	10
9682	TRDA 10kDa	FDA 10kDa	10
9683	TRDA 3kDa	FDA 3kDa	6
9684	–	FDA 10kDa	10
9685	TRDA 3kDa	–	7
9691	TRDA 3kDa	–	8
9692	TRDA 10kDa	FDA 10kDa	10
9693	TRDA 10kDa	FDA 10kDa	10
9694	TRDA 10kDa	FDA 3kDa	10
9696	TRDA 3kDa	FDA 3kDa	7
9697	TRDA 3kDa	FDA 10kDa	9
9698	TRDA 3kDa	FDA 10kDa	9
9699	TRDA 10kDa	FDA 3kDa	8

determine in detail the anatomical substrate by which the basal ganglia of amphibians may influence visuomotor behaviour elicited by the mid-brain tectum.

## Materials and methods

In the present study, 18 adult green frogs (*Rana perezi*), obtained from the laboratory stock of the Department of Cell Biology, University Complutense of Madrid, were used. The animals were deeply anaesthetized before surgery by immersion in a 0.3% solution of tricaine methanesulphonate (MS222, Sandoz, Basel, SW) in distilled water, pH 7.4.

As shown in Table 1, in a first series of experiments (five cases), the retrograde tracers 10 kDa biotinylated dextran amine (BDA; D-1956; Molecular Probes, Eugene, OR), 3 kDa BDA (D-7135; Molecular Probes), 10 kDa fluorescein-conjugated dextran amine (FDA; D-1820; Molecular Probes) and 3 kDa FDA (D-3306; Molecular Probes) were applied unilaterally within different subregions of the mesencephalic tectum. In another four animals, the anterograde tracers 10 kDa Texas Red-conjugated dextran amine (TRDA; D-1863; Molecular Probes) and 3 kDa TRDA (D-3328; Molecular Probes) were injected into the striatum at intermediate rostrocaudal levels of the telencephalic hemisphere, following a ventral approach through the roof of the mouth. In a third series of experiments, nine frogs received an application of both TRDA into the striatum and FDA into the ipsilateral mid-brain tectum (Fig. 1).

In all cases, the tracers were applied by impaling the selected brain regions with a very sharp tungsten needle, on the tip of which the tracer was recrystallized from a saturated solution in distilled water. After survival times of 5–10 days, the animals were perfused transcardially, under deep MS222 anaesthesia, with 50 ml of saline followed by 200 ml of 4% paraformaldehyde in 0.1 M phosphate buffer, pH 7.4. The brains and spinal cords were removed, blocked in gelatine and cut on a freezing microtome at 25–40  $\mu$ m thickness in the frontal or sagittal plane (see Marín *et al.*, 1997a for details). For visualization of BDA, an avidin–biotin complex (Vectastain, ABC Standard kit, Vector Labs., Burlingame, CA) was used.

In the BDA experiments, the sections were mounted on glass slides (mounting medium: 0.2% gelatine in Tris buffer, pH 7.6) and dried overnight. After ethanol dehydration and xylene cleaning, they were

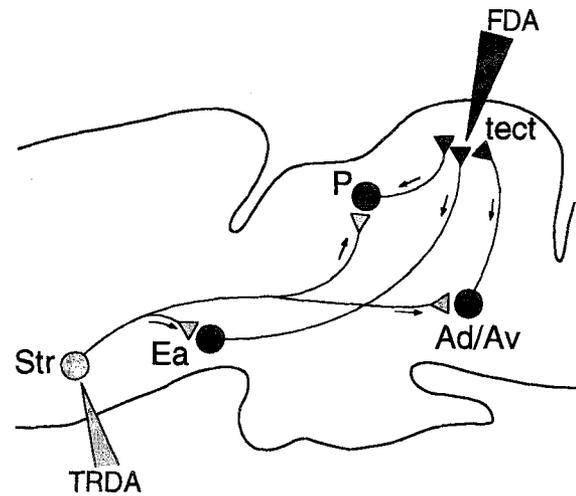


FIG. 1. Schematic drawing depicting the tracers applied into the striatum and the tectum in double labelling experiments. The sites of interaction between anterogradely labelled fibres from the striatum (TRDA, Texas Red-conjugated dextran amine) and retrogradely labelled cells from the tectum (FDA, fluorescein-conjugated dextran amine) are indicated. Str, striatum, Ea, anterior entopeduncular nucleus, P, posterior thalamic nucleus, Ad, nucleus anterodorsalis tegmenti, Av, nucleus anteroventralis tegmenti, tect, tectum mesencephali.

coverslipped with Entellan (Merck, Darmstadt, Germany). Some sections were counterstained with cresyl violet. Sections obtained from TRDA and FDA experiments were mounted immediately after sectioning (mounting medium as above), coverslipped with Vectashield (Vector) and viewed with a light microscope equipped with filter sets and barrier filters (Carl Zeiss Inc., Oberkochen, Germany) that enabled differentiation of TRDA (filter no. 487900, wavelength range 530–585 nm) and FDA (filter no. 487910, wavelength range 450–490 nm) fluorescence.

The distribution of retrogradely labelled cells and anterogradely labelled fibres in the brain of *Rana perezi* was analysed with a Zeiss fluorescence microscope with appropriate filter combinations and charted in representative transverse sections by means of a camera lucida or using a computer-aided X–Y plotting system (Minnesota Datametrics, MD-2 digitizer and software, Minnesota, USA). The nomenclature is the same as that used in our previous studies of amphibians (Marín *et al.*, 1997a,b,c).

## Results

In the following description, first the results of the experiments with single anterograde or retrograde tracing are presented demonstrating the existence of a direct pathway from the striatum to the mesencephalic tectum. Subsequently, indirect basal ganglia–tectal pathways, as revealed by the double labelling techniques, are considered.

### Direct striato–tectal pathways

After restricted tracer applications into the striatum of *Rana* (e.g. case 9666; Table 1), anterogradely labelled fibres were found in all major divisions of the brain, as described previously (Marín *et al.*, 1997c). Fibres were also found throughout the rostro–caudal extent of the mid-brain tectum, being more abundant in its rostral half (Fig. 2). Striatal fibres reach the mesencephalic tectum following two different pathways. The highest number of fibres arrives into the tectum coursing through the pretectal grey. Other fibres reach the

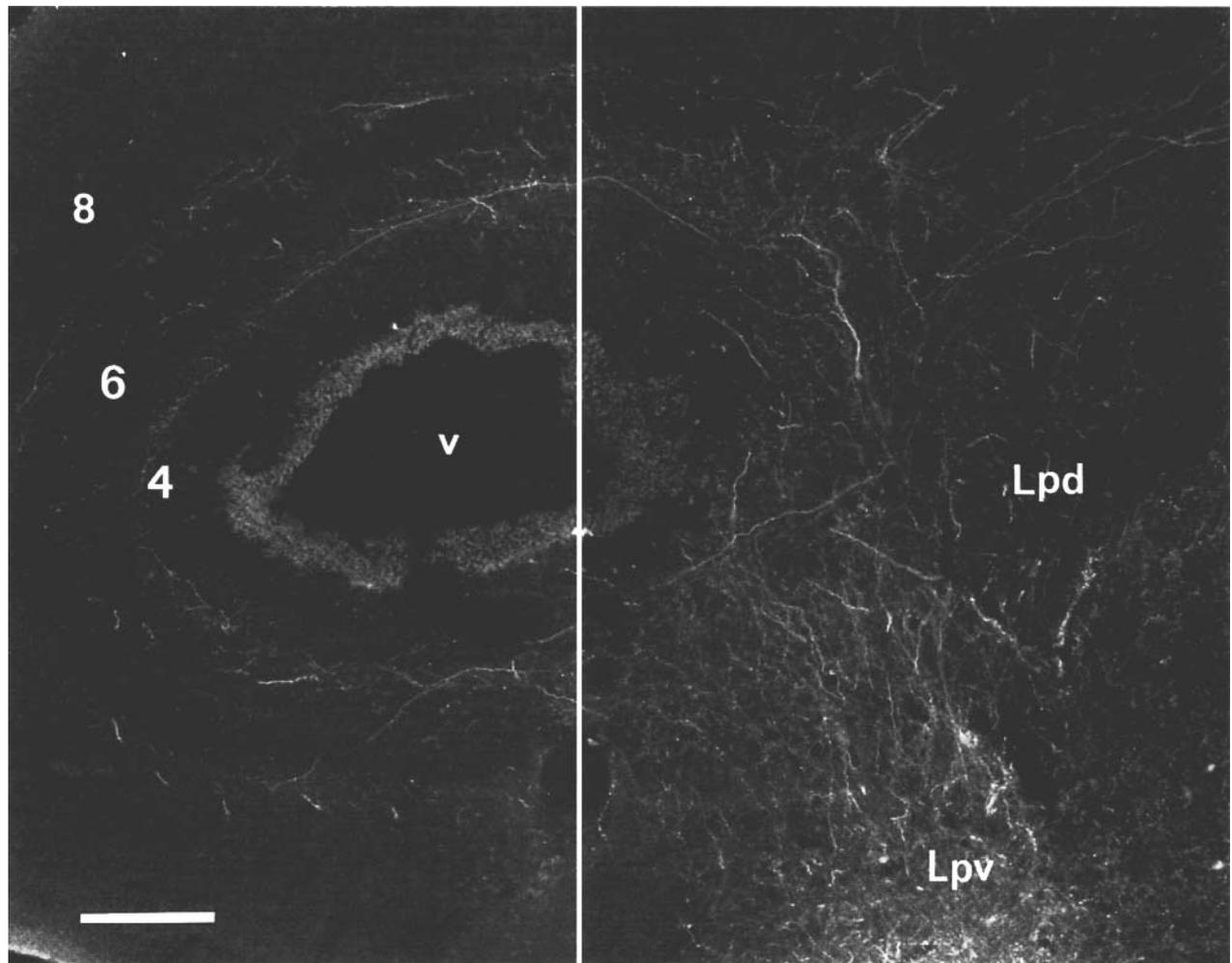


FIG. 2. Photomicrograph of a transverse section through the rostral mesencephalic tectum showing anterogradely labelled fibres from the striatum. Scale bar, 200  $\mu\text{m}$ . v, ventricle, Lpd, lateral thalamic nucleus, posterodorsal division, Lpv, lateral thalamic nucleus, posteroventral division.

mid-brain tectum via the posteroventral division of the lateral thalamic nucleus and, more caudally, via the laminar nucleus of the torus semicircularis. In the optic tectum, fine varicose fibres were observed primarily within layers 4–8. A few fibres project to the contralateral optic tectum, crossing the mid-line in the posterior and tectal commissures.

Tracer applications to the mid-brain tectum (e.g. case 9667; Table 1) retrogradely labelled cells in the striatum at intermediate and caudal levels (Fig. 3). Most of the labelled neurons were restricted to the ventral division of the striatum, which is caudally continuous with retrogradely labelled cells in the anterior entopeduncular nucleus.

#### *Indirect striato–tectal pathways*

From the results of the single labelling experiments, it became clear that at least at three places in the brain substantial overlap may occur between terminal fields of striatal efferent fibres and cells projecting to the tectum. Experiments in which applications of TRDA in the striatum were combined with FDA in the ipsilateral mesencephalic tectum have confirmed such overlap in the ventral striatum–anterior entopeduncular nucleus continuum, the pretectum and the mesencephalic and isthmic reticular formation (e.g. case 9693; Table 1; Fig. 4). In the ventral striatum–anterior entopeduncular nucleus continuum,

cells retrogradely labelled after tectal applications were completely embedded in striatal descending fibres within the lateral forebrain bundle (Fig. 4C, D). In addition, striatal projections terminate within the contralateral anterior entopeduncular nucleus, where numerous fine varicose fibres were found.

In the caudal diencephalon, striatal fibres terminate predominantly in several pretectal structures. Thus, striatal fibres reach the posterodorsal division of the lateral thalamic nucleus, the nucleus of the posterior commissure and the periventricular pretectal region (*posterior thalamic nucleus* after Neary and Northcutt, 1983). The latter structure has been recently interpreted as a tripartite pretectal structure, including precommissural, juxtacommissural and commissural regions (Puelles *et al.*, 1996). Although striatal fibres reach all three pretectal regions, the most prominent innervation is found in the lateral half of the juxtacommissural and precommissural nuclei, which contain cell bodies retrogradely labelled after tracer applications to the tectum (Figs. 4E–H, 5A, B). Since apical dendrites of periventricular pretectal cells traverse the adjacent superficial cell populations extending into the optic neuropil of the nucleus lentiformis (Fig. 5A), striatal fibres also overlap with the proximal part of the dendrites of juxtacommissural and precommissural cells projecting to the tectum. Striatal efferent fibres were also found in the caudal

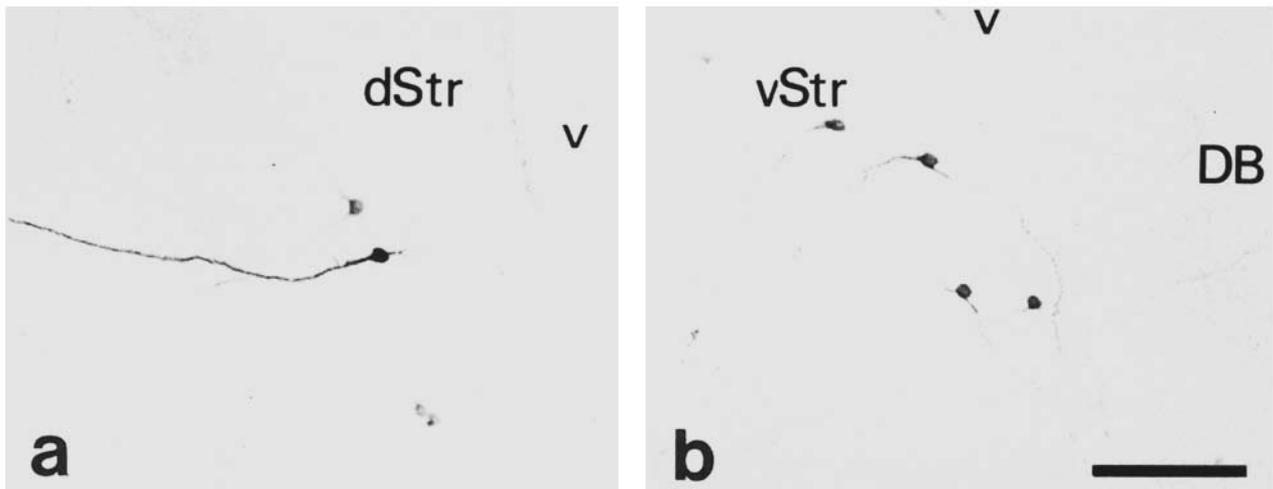
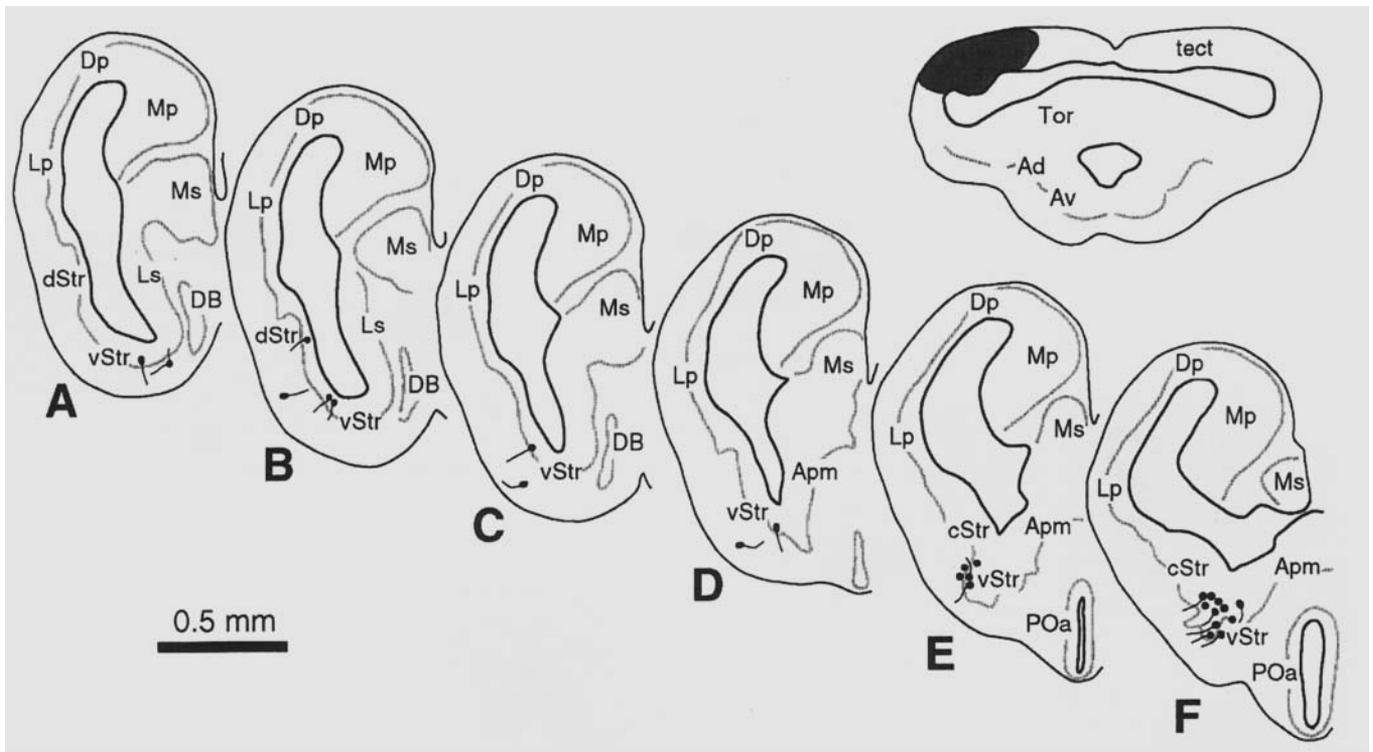


FIG. 3. Schematic drawings of transverse sections through the telencephalon of *Rana perezi* illustrating the distribution of retrogradely labelled cells after tracer application to the optic tectum (section in the upper right). Photomicrographs in the lower part illustrate two examples of retrogradely labelled cells in the dorsal (a) and the ventral (b) divisions of the striatum. Scale bar, 100  $\mu$ m. Dp, Dorsal pallium, Lp, lateral pallium, dStr, dorsal striatum, vStr, ventral striatum, DB, nucleus of the diagonal band, Ls, lateral septum, Ms, medial septum, Mp, medial pallium, Apm, Amygdala, pars medialis, POa, anterior preoptic area.

pole of the central thalamic nucleus, where they overlap with a group of cells that were retrogradely labelled after tectal applications (Figs. 4G, 5C, D). However, since striatal projections to the pretectal region pass across the caudal pole of the central thalamic nucleus, it is difficult to establish whether these fibres actually terminate within the latter nucleus.

Striatal efferent fibres constitute a rather continuous terminal field within the mesencephalic and isthmic reticular formation, including the nucleus profundus mesencephali, the anterodorsal, anteroventral, posterodorsal and posteroventral tegmental nuclei, and the superficial isthmal reticular nucleus (Fig. 4I–K). Applications of retrograde tracer

into the mid-brain tectum resulted in a large number of labelled cells in the mesencephalic tegmentum, which were mainly confined to the dorsal tegmental tier (Fig. 4I–K). Moreover, tegmental projections to the tectum appears to be topographically organized, since applications to different regions within the mesencephalic tegmentum resulted in distinct sets of retrogradely labelled neurons. Thus, the sites of overlap between striatal terminal fields and cells retrogradely labelled from the tectum in the dorsal tegmentum slightly differ between the various cases (Figs 4I–K, 5E, F). It is worth mentioning that, in all cases, in addition to the regions of overlap, there are areas in the dorsal tegmentum with labelled cells or fibres only (see e.g. Fig. 5E,

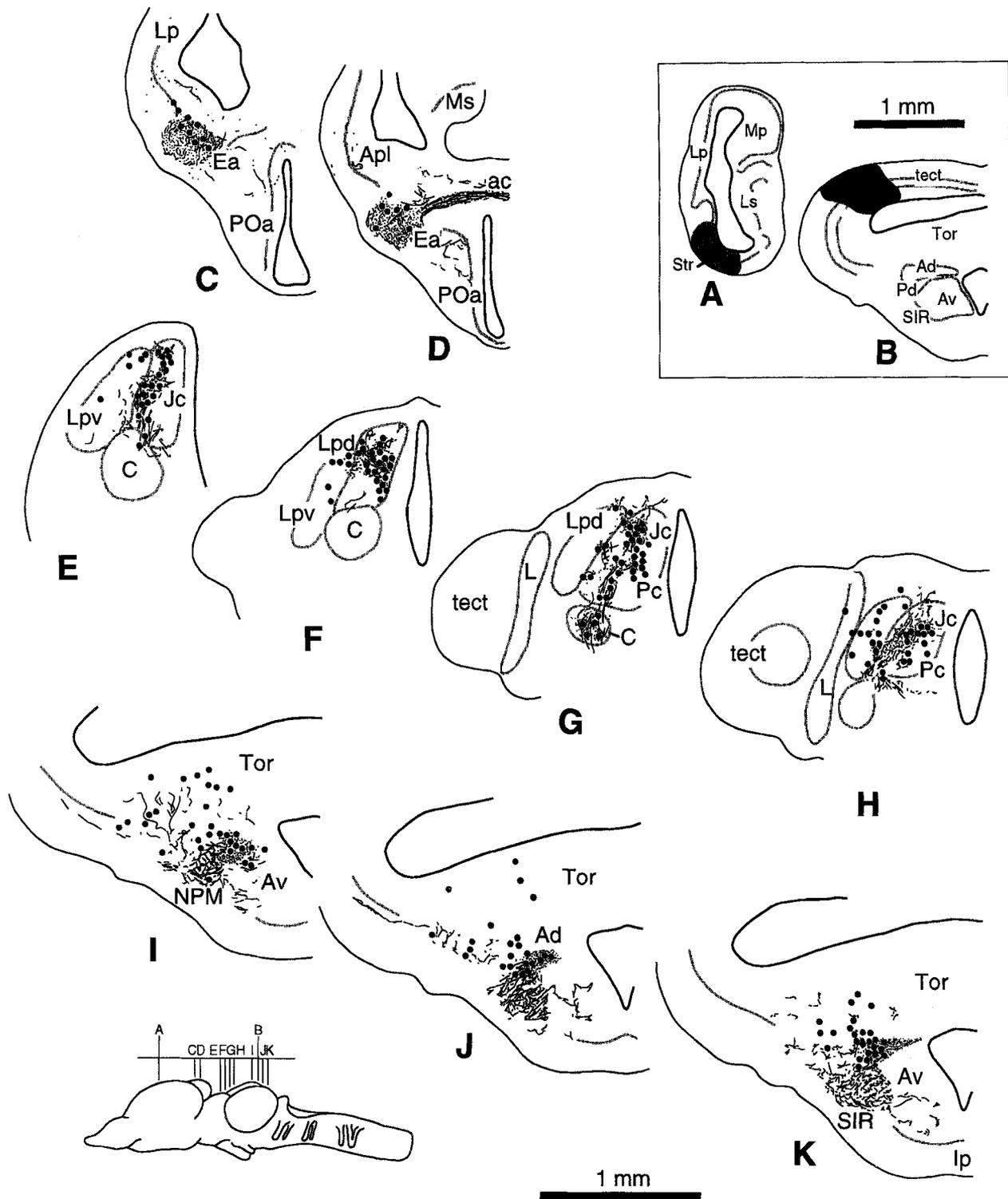


FIG. 4. Diagrams of transverse sections through the brain of *Rana perezi* illustrating the localization of retrogradely labelled cells from the optic tectum (large dots) and anterogradely labelled fibres from the striatum (dashes, wavy lines). The application sites in the striatum and the tectum are indicated in sections A and B, respectively. The levels of the represented transverse sections are indicated in the schematic lateral view of the brain. Lpv, lateral thalamic nucleus, posteroventral division, C, central thalamic nucleus, Jc, juxtacommissural nucleus, Lpd, lateral thalamic nucleus, posterodorsal division, Lp, lateral pallidum, Ea, anterior entopeduncular nucleus, POa, anterior preoptic area, Apl, amygdala, pars lateralis, Ms, medial septum, ac, anterior commissure, tect, tectum mesencephali, L, lentiform nucleus, Pc, precommissural nucleus, NPM, nucleus profundus mesencephali, Av, nucleus anteroventralis tegmenti, Tor, torus semicircularis, SIR, superficial reticular isthmal nucleus, Ip, interpeduncular nucleus.

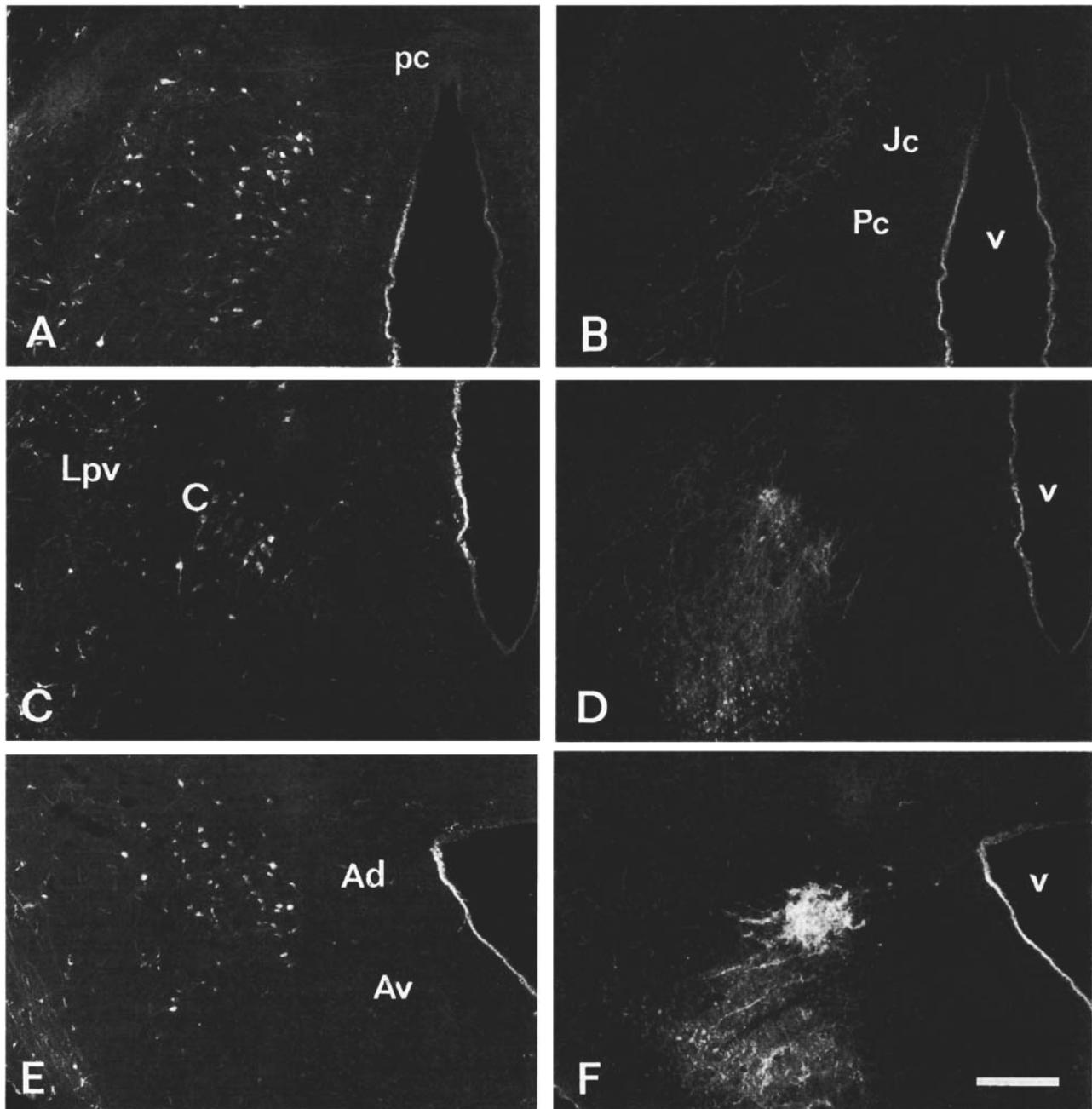


FIG. 5. Pairs of photographs of the same sections showing retrogradely labelled cells from the optic tectum (A, C, E) and anterogradely labelled fibres (B, D, F) from the striatum. The close relationship and overlap between cells and fibres is illustrated for the pretectal regions (A, B), the caudal pole of the central thalamic nucleus (C, D) and the tegmentum (E, F). Scale bar, 200  $\mu$ m. Pc, precommissural nucleus, Jc, juxtacommissural nucleus, v, ventricle, Lpv, lateral thalamic nucleus, posteroventral division, C, central thalamic nucleus, Ad, nucleus anterodorsalis tegmenti, Av, nucleus anteroventralis tegmenti.

F). In those regions, synaptic contacts seem to be highly unlikely because of the distance between retrogradely labelled cells and anterogradely labelled fibres.

#### *Cells projecting to both the striatum and the mid-brain tectum*

Depending on the way of application and the size of the injection, dextran amines can be transported retrogradely or anterogradely (Fritsch, 1993; Marín *et al.*, 1997a,b,c). Thus, although TRDA has been predominantly used as an anterograde tracer in the present study, large TRDA applications in the striatum also resulted in retrogradely

labelled cells in several brain centres. Among others, labelled neurons were found in the anterior entopeduncular nucleus, which is in agreement with previous findings (Wilczynski and Northcutt, 1983a; Marín *et al.*, 1997a).

As mentioned above, the anterior entopeduncular nucleus contains cells that project to the mesencephalic tectum. In double labelling experiments, it was observed that a small subpopulation (~10%) of cells in the anterior entopeduncular nucleus projects to both the striatum and the mesencephalic tectum suggesting a high degree of axonal collateralization.

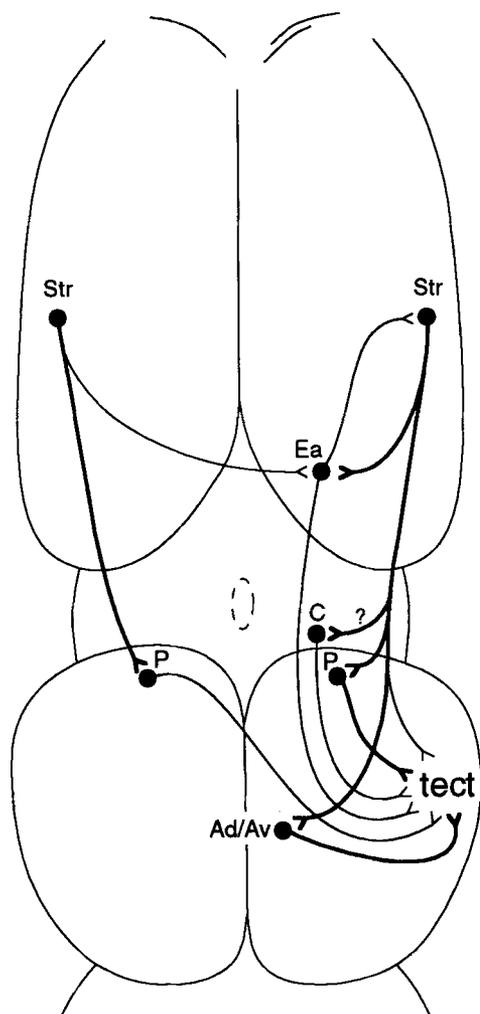


FIG. 6. Summary diagram illustrating in a dorsal view of the brain of *Rana perezi* the pathways found in the present study by which striatal information may reach the optic tectum. Str, striatum, Ea, anterior entopeduncular nucleus, P, posterior thalamic nucleus, C, central thalamic nucleus, tect, tectum mesencephali, Ad, nucleus anterodorsalis tegmenti, Av, nucleus anteroventralis tegmenti.

## Discussion

### *Amphibian basal ganglia–tectal connections*

As shown by the present study, the basal ganglia of anurans may possess several routes by which they could influence tectal functioning (Fig. 6). Firstly, there is a direct striatal projection to the mid-brain tectum. Furthermore, striatal efferent fibres terminate in the anterior entopeduncular nucleus, the pretectal region, the caudal pole of the central thalamic nucleus and the mesencephalic and isthmic dorsal tegmentum, where they partially overlap cell groups that project to the mid-brain tectum, thus suggesting several possible indirect routes by which the basal ganglia could influence the tectum.

Evidence for a direct striato–tectal connection in anurans was recently obtained by means of anterograde tracing techniques (Marín *et al.*, 1997c). It is now clear that the cells of origin of the striato–tectal pathway are mainly confined to the caudal half of the ventral striatum. Furthermore, the present study has revealed that the neurons projecting to the optic tectum in the ventral striatum and the adjacent anterior entopeduncular nucleus constitute a continuous field of

neurons along the rostrocaudal axis, extending from mid-telencephalic levels to the caudal pole of the anterior entopeduncular nucleus. Previous studies of tectal afferents failed to label cells in the striatum proper of anurans (Wilczynski and Northcutt, 1977; Zittlau, 1988; Masino and Grobstein, 1990; Montgomery and Fite, 1991), although sometimes the anterior entopeduncular nucleus was referred to as ventral striatum (Masino and Grobstein, 1990; their Fig. 8C, D). There is no clear boundary between the ventral striatum and the anterior entopeduncular nucleus, but, on the basis of cytoarchitectonic criteria, a subdivision between the two structures can be made (Northcutt and Kicliter, 1980). Direct striato–tectal connections may be a common feature of amphibians, since this has also been reported for urodeles (Finkenstädt *et al.*, 1983; Marín *et al.*, 1997c). The efferent fibres of both the striatum and the anterior entopeduncular nucleus terminate within tectal layers 4–8, whereas the cells of origin of the tecto–bulbar pathway are located in the superficial half of layer 6 or at the border of layers 6–7, extending their dendritic arbors throughout the superficial layers (Lázár *et al.*, 1983). Thus, basal forebrain inputs are likely in direct contact with the tecto–bulbar cells.

The present study has shown that the basal ganglia might modulate tectal activity through several indirect pathways in frogs. In anurans, at least three disynaptic striato–tectal pathways are recognized: (1) a striato–anterior entopeduncular–tectal pathway; (2) a striato–pretectal–tectal pathway; and (3) a striato–tegmento–tectal pathway. In addition, the present study provides evidence that the caudal pole of the central thalamic nucleus may also serve as a striato–tectal relay centre. Striatal projections to the anterior entopeduncular nucleus, the pretectal region, the caudal pole of the central nucleus and the mesencephalic and isthmic reticular formation have been reported previously (Wilczynski and Northcutt, 1983b; Marín *et al.*, 1997c). Only the anterior entopeduncular nucleus receives a conspicuous contralateral projection (Wilczynski and Northcutt, 1983b; Marín *et al.*, 1997c). Tectal projections originating from the anterior entopeduncular nucleus, the pretectal region and the dorsal tegmental nuclei were also observed (Wilczynski and Northcutt, 1977; Zittlau *et al.*, 1988; Masino and Grobstein, 1990; Montgomery and Fite, 1991), although in the present study the number of cells labelled after tectal injections is considerably higher. A projection from the caudal pole of the central nucleus to the tectum has never been described before. The present study has also provided more detailed information on the organization within the basal ganglia–tectal relay centres. In the anterior entopeduncular nucleus, the caudal pole of the central nucleus, and the dorsal tegmental nuclei, the cells projecting to the tectum are completely embedded within the terminal fields of striatal projection fibres. In the pretectal region, however, striatal efferent fibres are predominantly distributed in a lamellar or shell-like pattern, thus overlapping the somata and the basal aspect of their apical dendrites.

### *Comparative aspects*

In contrast to amphibians, only indirect striato–tectal pathways have been identified in reptiles, birds and mammals. Two different patterns of connections are recognized: i) in mammals, some lizards and snakes, striatal projections reach the optic tectum exclusively via the substantia nigra, pars reticulata (Faull and Mehler, 1978; Graybiel, 1978; Reiner *et al.*, 1984; Medina and Smeets, 1991); and ii) in birds, turtles, crocodiles and some lacertid lizards, basal ganglia–tectal pathways are largely relayed via the pretectal region, although a minor involvement of the mid-brain tegmentum also exists (Brauth *et al.*, 1978; Brauth and Kitt, 1980; Reiner *et al.*, 1980; Medina and Smeets, 1991). From the present account, it is clear that in modern amphibians a ventral (tegmental) route as well as a dorsal (pretectal) route are present. It is tempting to correlate these pathways in

amphibians to those found in reptiles, birds and mammals. As reviewed by Medina and Smeets (1991), the presence of both ventral and dorsal basal ganglia–tectal routes represents most likely the primitive condition. That notion is mainly based on the fact that in amphibians, some reptiles and birds, the dorsal route comprises a pretectal, enkephalinergetic cell group, which receives a projection from the basal forebrain and projects, in turn, to the mid-brain tectum. Other lizards as well as snakes and mammals seem to lack this dorsal route. On the other hand, a basal ganglia–tectal relay via the mid-brain tegmentum is a common feature of amphibians and amniotes.

A careful evaluation of the results of the present study, however, complicates a direct comparison. First, a common feature of amphibians seems to be direct projections from both the striatum and the anterior entopeduncular nucleus to the tectum. Such connections have not yet been reported for amniotes. In addition, amphibians may have a direct striato–pretectal connection, which is also lacking in amniotes. Thus, basal ganglia–tectal connections in amphibians appear to be more elaborate than in amniotes. The existence of a direct striato–tectal pathway is corroborated by the finding that lesion experiments have revealed the existence of a second, pretectal independent, inhibitory effect on prey-catching movements mediated by the telencephalon (Ewert, 1970).

Another complicating factor is that pallidal compartments have not yet been identified in the anuran basal ganglia. However, some evidence exists in favour of the hypothesis that the ventral striatum–anterior entopeduncular nucleus continuum constitutes the amphibian counterpart of the amniote pallidum (Marín *et al.*, 1997c; present study). Moreover, it has been suggested that the pretectal relay nucleus in the pathway from the basal ganglia to the tectum in reptiles and birds is chemically characterized by the presence of enkephalin-immunoreactive neurons (Reiner *et al.*, 1984; Medina and Smeets, 1991). Accordingly, enkephalin-immunoreactive cell bodies have been described in the pretectal region and the caudal pole of the central thalamic nucleus of anurans (Merchenthaler *et al.*, 1989), which, as shown by the present study, may receive striatal and pallidal-like inputs. It should be noted, however, that other neurochemically distinct pretectal cell groups may also receive direct basal ganglia projections. Thus, striatal projections have been demonstrated to terminate also in close relation to pretectal dopaminergic cells in anurans (Marín *et al.*, 1997c).

In mammals and birds, direct striatopallidal projections to the superior colliculus have never been described, although a projection from the globus pallidus to the inferior colliculus has been reported in the rat (Yasui *et al.*, 1990). In contrast, direct striatal projections to the tectum appear to be a common feature in anuran (Marín *et al.*, 1997c; present study) and urodele amphibians (Finkenstädt *et al.*, 1983; Marín *et al.*, 1997c), whereas comparable projections have been described in holostean (Northcutt, 1982) and teleostean fishes (Ito and Kishida, 1977; Grover and Sharma, 1981; Lee and Bullock, 1990; Schlussman *et al.*, 1990). In bony fishes, they originate from the area dorsolateralis, which is proposed to be homologous to the striatum of tetrapod vertebrates (Northcutt, 1982).

In agreement with previous studies (Wilczynski and Northcutt, 1977; Masino and Grobstein, 1990), the present study failed to demonstrate a direct projection from the telencephalic pallium to the mid-brain tectum in amphibians. Direct cortico–colliculus superior connections have been reported for mammals (Huerta and Harting, 1984a,b), whereas direct Wulst–tectal projections are present in birds (Casini *et al.*, 1992). As yet, no direct cortico–tectal connections have been observed in reptiles. Remarkably, in sharks and skates, direct projections from the telencephalic pallium (roof) to the mid-brain tectum have been identified (Smeets, 1982).

Basal ganglia projections to the isthmic tegmentum of amphibians may be comparable to those found in amniotes (Medina and Reiner, 1995; Marín *et al.*, 1997c), since in both amphibians and amniotes such projections appear to terminate in close relation to the cholinergic neurons of the pedunculo-pontine nucleus (Nauta and Mehler, 1966; Karten and Dubbeldam, 1973; Rye *et al.*, 1987; Russchen and Jonker, 1988; Medina *et al.*, 1993; Medina and Reiner, 1994; Marín *et al.*, 1997c,d). The results of the present study further strengthen this notion, since the amphibian striatal projection to the isthmic tegmentum may constitute an additional route by which the basal ganglia can be modulatory, as in mammals (Parent and Hazrati, 1995).

The present study also revealed the existence of divergent collateral projections from the anterior entopeduncular nucleus to the striatum and the mid-brain tectum. Remarkably, it has been shown that nigral neurons of rats project to both the striatum and the superior colliculus (Takada *et al.*, 1988). Since the nigro–tectal pathway appears to be the only route by which the basal ganglia of mammals influence tectal activity, the presence of a population of neurons projecting simultaneously to the striatum and to the mid-brain tectum in amphibians and mammals suggests a primitive mechanism in visuo-motor behaviour control. The specific role of these projection neurons remains still unknown.

#### Functional considerations

The mid-brain tectum, a site of convergence of signals from several sensory modalities (e.g. Stein, 1984; Meredith and Stein, 1986), contains neurons that are involved in the generation of directed movements in amniotes, such as, for example, visually elicited movements. The topographic retinotectal projection provides an appropriate framework for the production of visually guided motor responses (Schiller, 1984). However, additional sets of tectal afferents appear to modulate visuomotor behaviour in amniotes. Hence, it is well established that descending pathways from the basal ganglia to the mid-brain tectum provide the route by which they can influence tectal functioning (Graybiel, 1978; Reiner *et al.*, 1980, 1982; Medina and Smeets, 1991). The nigrotectal connection appears to constitute a common pathway for the engagement of the basal ganglia in tectal mechanisms of motor control (Hopkins and Niessen, 1976; Faull and Mehler, 1978; Graybiel, 1978; Reiner *et al.*, 1980, 1982; Medina and Smeets, 1991). Moreover, a basal ganglia–pretectal–tectal route is found in birds and some reptiles, providing an additional path to influence the tectum (Reiner *et al.*, 1982; Medina and Smeets, 1991).

As in amniotes, the mid-brain tectum of amphibians plays a key role in the control of visually triggered movements, such as prey-catching and avoidance responses (for review, see Ewert, 1987). On the basis of the present results, it can be postulated that the striatum of amphibians accomplishes a modulatory effect on the tectal responses to visual stimuli resulting in orienting or avoidance behaviour. Further, the access of the striatum to multimodal sensory information (Marín *et al.*, 1997a) constitutes an adequate substrate for its key role in regulating orienting movements through the tectum. In this regard, it is worth mentioning that the lack in anurans of direct pallio–tectal connections, presumptively comparable to the cortico–tectal pathways of mammals, may be reflected in the elaborate striato–tectal connections. As mentioned before, the direct striato–tectal pathway represents a good candidate for the reported telencephalic inhibitory effect on tectal neurons (Ewert, 1970), whereas the indirect pathways most likely result in disinhibition of tectal activity, as in mammals (Chevalier and Deniau, 1990). It would be interesting to know whether the cortico–tectal pathways of mammals, like the striato–tectal pathway of amphibians, has an inhibitory effect on tectal projection cells. Recent results, however, show that the majority

of the cortical cells projecting to the superior colliculus in the rat visual cortex contains the excitatory amino acids glutamate and aspartate (Dori *et al.*, 1992).

## Acknowledgements

This research was supported by grants of the Spanish DGICYT PB96-0606 (A. G.), Spanish FPU Grant (O. M.) and NATO Collaborative Grant CRG 910970. The authors are also grateful to Mr D. de Jong for preparing the photomicrographs.

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