

PROJECTIONS OF THE OPTIC TECTUM IN THE LONGNOSE GAR, *LEPISOSTEUS OSSEUS*

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SUMMARY

Efferent projections of the optic tectum were studied with the anterograde degeneration method in the longnose gar. Ascending projections were found bilaterally to 3 pretectal nuclei — the superficial pretectal nucleus, nucleus pretectalis centralis and nucleus pretectalis profundus — and to a number of targets which lie further rostrally — the central posterior nucleus, dorsal posterior nucleus, accessory optic nucleus, nucleus ventralis lateralis, nucleus of the ventral optic tract, rostral part of the preglomerular complex, suprachiasmatic nucleus, anterior thalamic nucleus, nucleus ventralis medialis, nucleus intermedius, nucleus prethalamicus and rostral entopeduncular nucleus. Projections of the tectum reach the contralateral side via the supraoptic decussation and are less dense contralaterally than ipsilaterally. Descending projections resulting from tectal lesions include: (1) a tectal commissural pathway to the core of the torus longitudinalis bilaterally and the contralateral tectum and torus semicircularis; and (2) a pathway leaving the tectum laterally from which fibers terminate in the ipsilateral torus semicircularis, an area lateral to the nucleus of the medial longitudinal fasciculus, lateral tegmental nucleus, nucleus lateralis valvulae, nucleus isthmi and the reticular formation. A component of this bundle decussates at the level of the lateral tegmental nucleus to project to the contralateral reticular formation.

On the basis of comparisons of these findings with the pattern of retinal projections in gars and other data, it is argued that the nuclei previously called the lateral geniculate and rotundus in fish are not the homologues of the nuclei of those names in land vertebrates but are rather pretectal cell groups. The overall organization of both retinal and tectal projections in gars is strikingly similar to that in land vertebrates; at present, the best candidate for a rotundal homologue is the dorsal posterior nucleus.

INTRODUCTION

The actinopterygian radiation is mainly represented by teleosts, of which there are a great number of species and an extremely broad adaptive zone. Chondrosteans and holosteans are represented by only a few extant species, and are of interest in that their brain organization is more simple than that in teleosts and may serve as a model of the primitive actinopterygian stock. A better understanding of brain organization in these forms will thus provide a basis for study of evolutionary trends and adaptations within the actinopterygian radiation and of how this radiation differs from land vertebrates.

A few studies of tectal projections have been carried out in teleosts^{4,12,20,21}, but, as will be discussed below, the complexities of the tectal targets, particularly in the pretectum and thalamus, are such that a clear concept of the tectofugal system in actinopterygian fish has not resulted. The retinal projections were previously studied in the gar, a holostean, in order to compare this system with teleosts and land vertebrates¹⁷. As the retinorecipient targets were thus already defined, and as additional work has since been done on thalamic and pretectal organization in gars¹, a study of tectal projections was undertaken in this species in an attempt to clarify the organization of this system in bony fish.

MATERIALS AND METHODS

Sixteen juvenile specimens of *Lepisosteus osseus* (= *Lepidosteus osseus*) underwent unilateral aspiration lesions of portions of the optic tectum under MS222 (tricaine) anesthesia. After survival times of 4–14 days at 26–30 °C, the animals were sacrificed by transcardial perfusion with normal saline followed by 10% formalin. After further fixation in 10% formalin, the brains were embedded in 25% gelatin. Frozen sections were cut at 30 μm in either the transverse (12 cases) or horizontal (4 cases) plane. Sections were stored in 2% formalin at 5 °C and were processed by the Fink–Heimer⁷, Eager³ and Wiitanen²³ procedures for silver impregnation of degenerated axoplasm.

Additional series of sections processed with Bodian, Nissl, Golgi–Cox, and Kluver-Barrera methods and cut in the 3 standard anatomical planes were available for study of nuclear groups and fiber tracts in *Lepisosteus* and in a number of teleost species.

The term homology, as used in this paper, is defined as two or more structures, on two or more populations of organisms, that are believed to have arisen from a single structure or condition in the common ancestral population. Such homologous structures are inherited, with modification, from the common ancestor; thus the criteria for recognizing such structures are the multitude and degree of similarities between suspected homologous structures.

RESULTS

Following tectal lesions, the optimal survival time for silver impregnation of

degenerated axonal fibers and terminals was 6–8 days. The levels and plane of section of the case selected for illustration are shown in Fig. 1. Terminology of nuclei and fiber tracts (Figs. 2–7) is after Northcutt and Butler¹⁷ and Braford and Northcutt¹.

Ascending projections

The ascending projections are charted in Figs. 2–4A. Ascending fibers course out of the optic tectum primarily in layer 9, part of the superficial white and gray zone¹⁷, although there may also be a contribution from fibers in layer 6, which lies in the central zone¹⁷.

Ipsilateral to the lesion, there are dense projections to the 3 pretectal nuclei. Degenerated terminals in the superficial pretectal nucleus are mainly confined to its magnocellular portion (MSPN, Fig. 3A), and while the dorsal part of the deep pretectal nucleus (PPd) receives a tectal projection, a terminal field is not seen over the ventral part of this nucleus (PPv, Figs. 3B and 4A); the possibility remains, however, that apical dendrites of PPv neurons may extend into the terminal field of PPd. Degeneration is present throughout the central pretectal nucleus (NPC, Fig. 3B). Fibers which exit the tectum from layer 6 at a more caudal level may turn rostrally and contribute to the pretectal projection (arrow in Fig. 4B), but continuity of the specific fibers could not be traced.

Ipsilaterally, the tectum projects to 3 caudal thalamic nuclear groups — the central posterior (CP, Figs. 3B and 4A), the dorsal posterior (DP, Fig. 3B) and the accessory optic (AON, Fig. 3B). As is the case throughout most of the diencephalic tectal targets, terminal degeneration is confined to the lateral parts of the dorsal thalamic nuclei, leaving their periventricular regions clear.

To reach more rostral diencephalic levels, fibers exit the tectum in two groups (Fig. 3A), a medially positioned bundle which lies in the region of the medial optic tract¹⁷ and a more centrally positioned bundle in the region of the dorsal optic tract¹⁷.

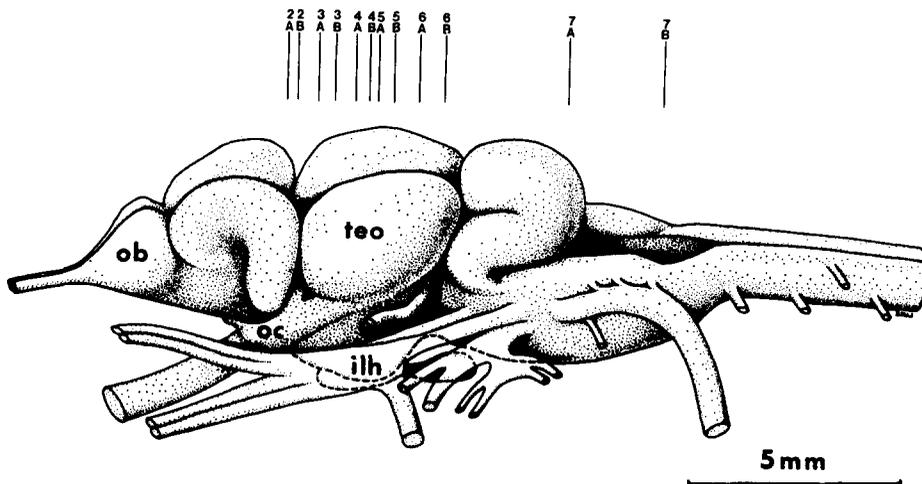


Fig. 1. Dorsolateral view of the brain of *Lepisosteus osseus*. Numbered lines indicate the levels of the transverse sections in Figs. 2–7.

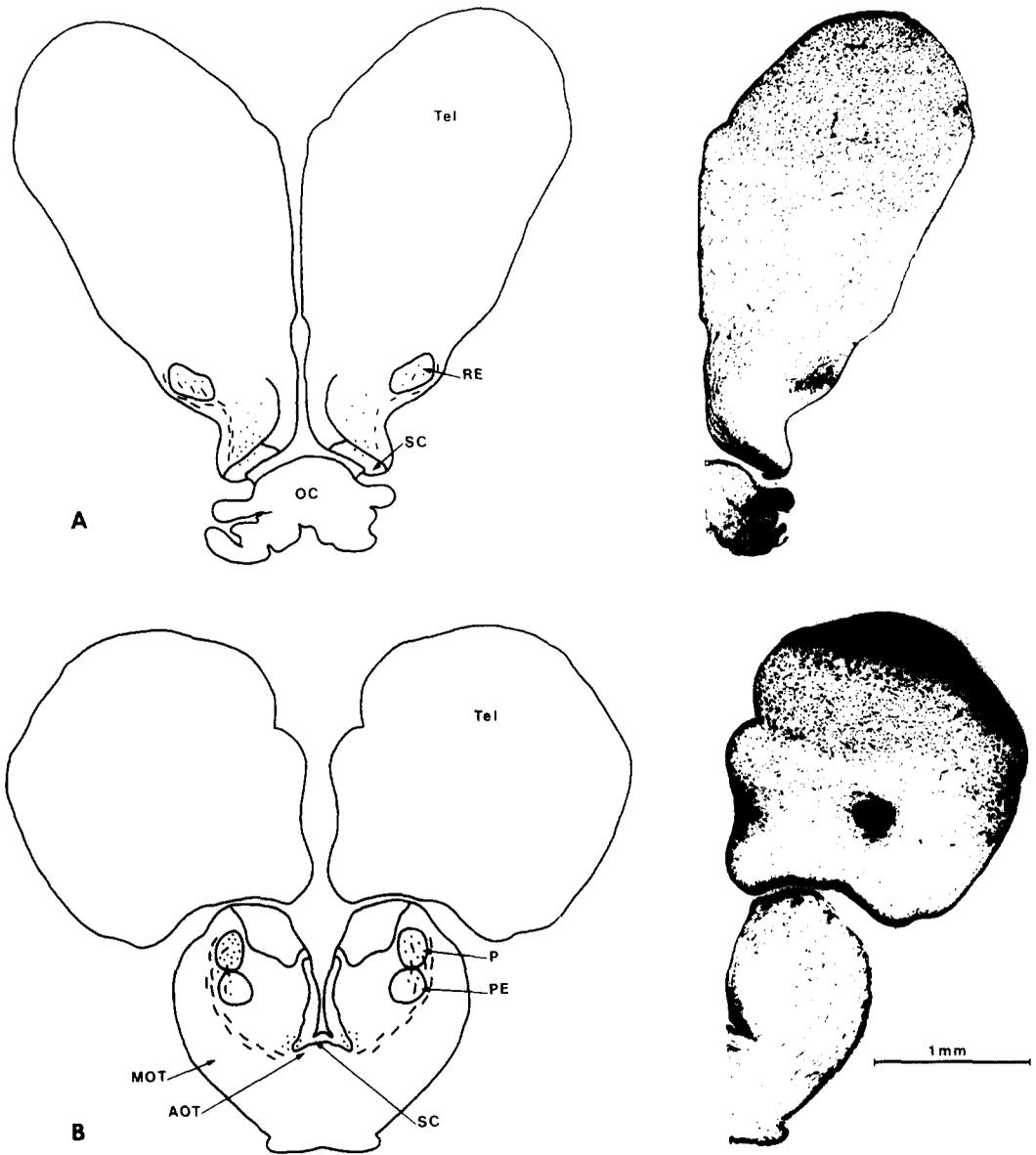


Fig. 2. A: transverse section through the level of the optic chiasm. In this and subsequent figures, a Nissl preparation is shown to the right comparable to the charting on the left. Degenerated fibers are indicated by dashed lines, terminal degeneration by stippling, and the extent of the tectal lesion by the shaded area. Magnification of Figs. 2-7 is identical. B: transverse section through the telencephalon median. *Abbreviations used in Figs. 2-7.* A, anterior thalamic nucleus; AON, accessory optic nucleus; AOT, axial optic tract; Au, auricle; CC, corpus cerebelli; CCs, cerebellar crest, CP, central posterior nucleus; DI, nucleus diffusus of inferior lobe; DN, descending nucleus of VIII; DP, dorsal posterior nucleus; FR, fasciculus retroflexus; G, secondary gustatory nucleus; H, habenula; I, nucleus intermedius; IL, inferior lobe of hypothalamus; IP, interpeduncular nucleus; LT, lateral tegmental nucleus; LV, nucleus lateralis valvulae; M, nucleus medius; MLF, medial longitudinal fasciculus; MOT, marginal optic tract; MSPN, magnocellular superficial pretectal nucleus; MTP, nucleus medianus tuberculi posterioris; MVII, motor nucleus of VII; MX, motor nucleus of X; NC, nucleus cerebelli; NI, nucleus isthmi; NM, nucleus of medial longitudinal fasciculus; NPC, nucleus pretectalis centralis; NPT, nucleus posterior thalami; NTL, nucleus of torus lateralis; OC, optic chiasm; P, nucleus prethalamicus; PC, posterior commissure; PE, posterior entopeduncular nucleus; PEV, plica encephali ventralis; PG, preglomerular complex; PPd, nucleus pretectalis profundus pars dorsalis; PPT, periventricular nucleus of posterior tuber; PPv, nucleus pretectalis profundus pars ventralis; PSPN, parvocellular superficial pretectal nucleus; RE, rostral entopeduncular nucleus; RI, nucleus reticularis inferior; RPG, rostral part of preglomerular complex; RS, nucleus reticularis superior; SC, suprachiasmatic nucleus; SR, superior raphe nucleus; Tec, tectum; Tel, telencephalon; TL, torus longitudinalis; TS, torus semicircularis (central nucleus); V, ventricle; Va, valvula; VL, nucleus lateralis valvulae; VM, nucleus medialis medialis; VOT, nucleus of ventral optic tract; VP, nucleus

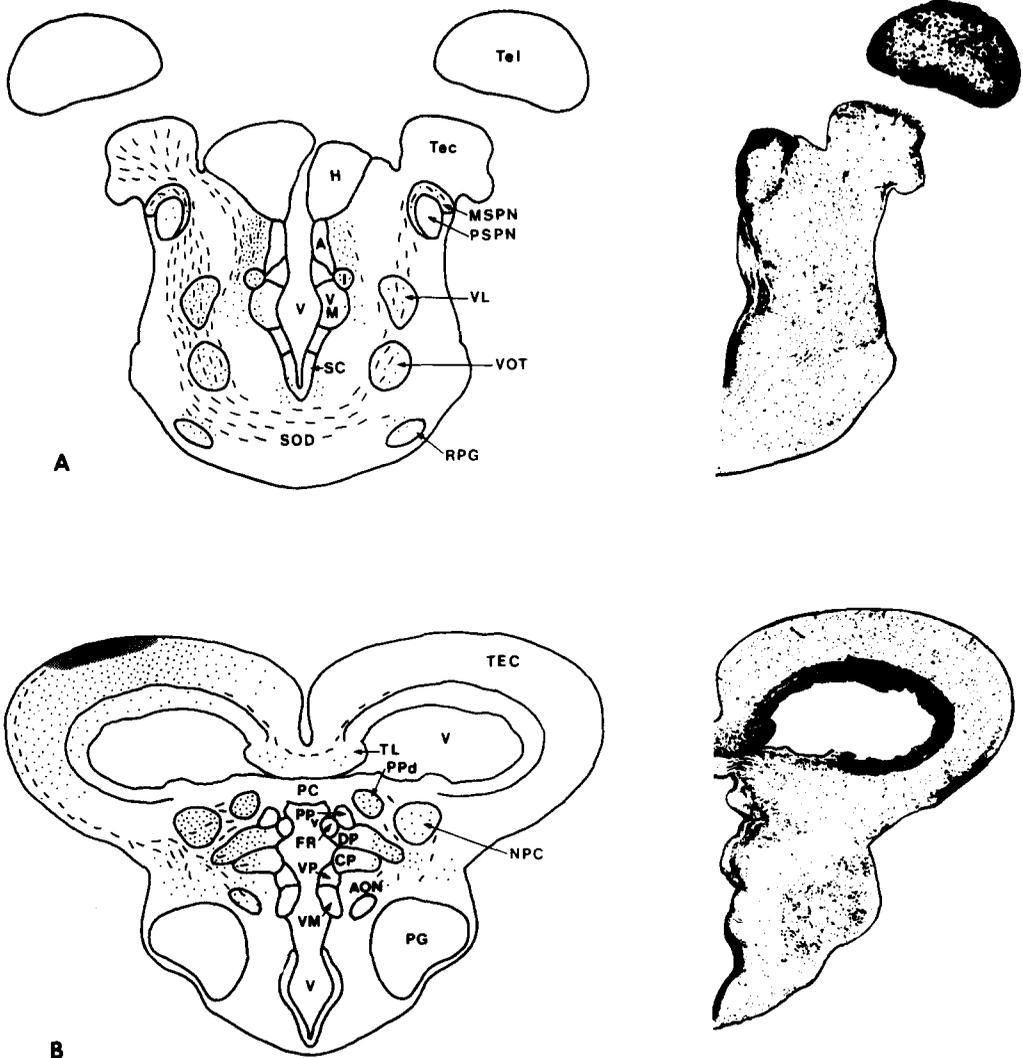


Fig. 3. A: transverse section through rostral thalamus. B: transverse section at level of posterior commissure.

The latter bundle projects (Fig. 3A) to nucleus ventralis lateralis (VL), the nucleus of the ventral optic tract (NVOT), the rostral part of the preglomerular complex (RPG), and the suprachiasmatic nucleus (SC). In the preglomerular complex, degeneration is confined to this rostral part and does not continue caudally (PG, Figs. 3B and 4A). The projection is also confined to a region of large cells in the rostral part of the complex and does not extend among smaller, more medially lying cells. The fiber bundle then continues to the contralateral side of the brain via the supraoptic decussation (SOD, Fig. 3A). The more medially positioned bundle gives rise to terminal degeneration (Fig. 3A) in the lateral portions of the anterior thalamic nucleus (A) and nucleus ventralis medialis (VM), as well as to nucleus intermedius (I) in which all of the cells have migrated away from the ventricular surface.

Further rostrally (Fig. 2), degenerated fibers course along the medial border of the marginal optic tract (MOT, Fig. 2B) and project to the suprachiasmatic nucleus (SC), nucleus prethalamicus (P), and the rostral entopeduncular nucleus (RE). Degenerated fibers also course through the posterior entopeduncular nucleus (PE, Fig. 2B), and while sparse terminal degeneration is charted in the nucleus, its presence could not be established with absolute certainty, due to the nature of the degenerated fibers.

Degenerated fibers were also observed in parts of the optic chiasm and nerve. These were not charted, however, as it could not be established whether they were tecto-retinal fibers or aberrant decussating fibers from the supraoptic pathway.

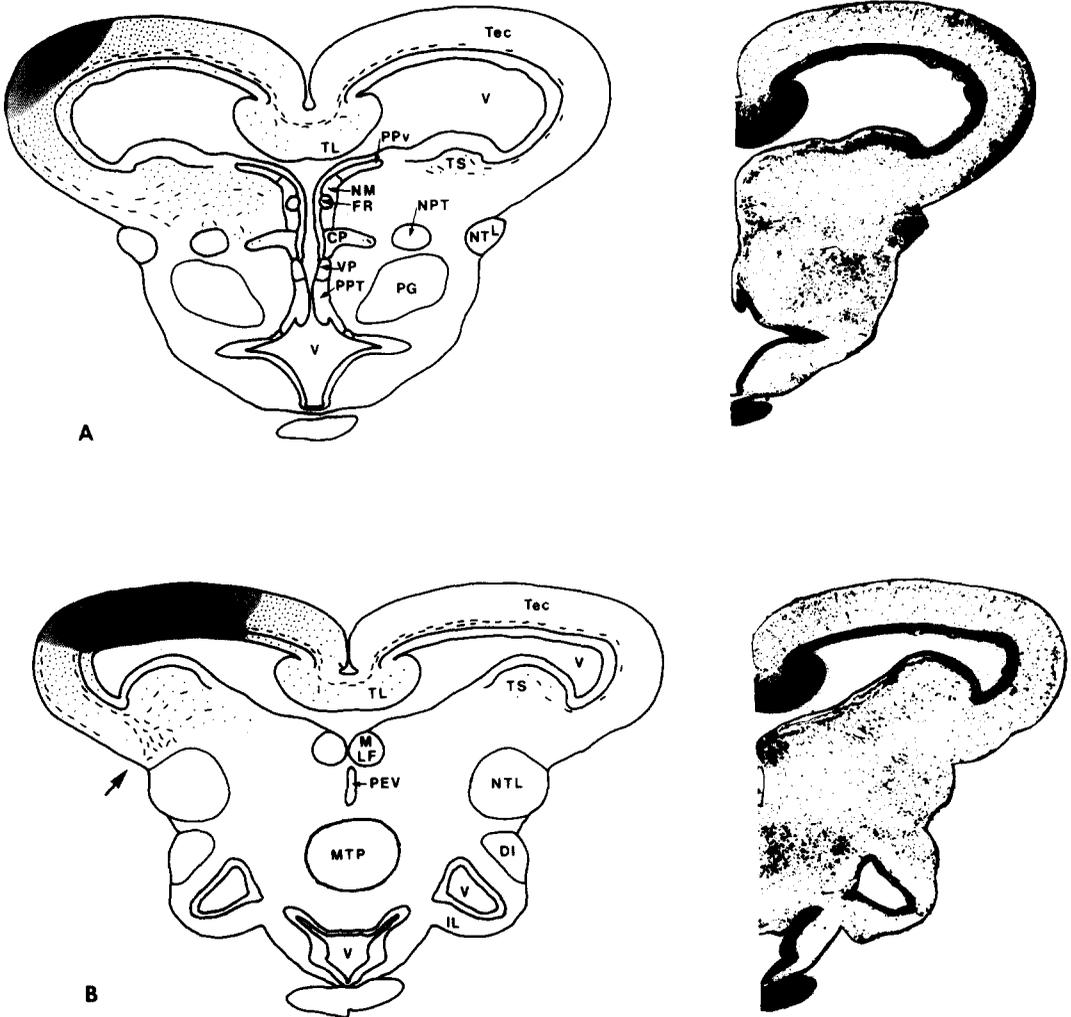


Fig. 4. A: transverse section at level of posterior thalamus dorsally. B: transverse section at level of maximal extent of posterior tuberal area.

Degenerated fibers reach the contralateral side of the brain by coursing through the supraoptic decussation (SOD, Fig. 3 A). While the density of degeneration is less on the contralateral side than on the ipsilateral side, it is by no means sparse. The tectum projects contralaterally to all of the targets which receive ipsilateral ascending projections (Figs. 2-4A).

Descending projections

The descending projections course out of the tectum laterally from layer 6 (Figs. 4-6A) and medially via the tectal commissure (Figs. 3B-6A). The commissural bundle gives rise to terminal degeneration in the torus longitudinalis (TL) bilaterally (Figs. 3B-6A). The small cells of the periventricular gray tectal zone¹⁷ continue medially to form the periventricular portion of the torus longitudinalis, and terminal degeneration within the torus is restricted to its core, being absent over all regions where the periventricular cell bodies are tightly packed or clumped together. The projection to the torus longitudinalis appeared to be homotopic to the rostral-caudal extent of the tectal lesion.



Fig. 5. A: transverse section at level of midbrain tegmentum. B: transverse section at level of rostral pole of cerebellar valvula.



Fig. 6. A: transverse section at level of isthmus. B: transverse section through caudal pole of optic tectum.

Commissural fibers continue laterally through the deep white zone¹⁷ of the contralateral tectum. While terminal degeneration is sparse, the number of degenerated fibers progressively decreases, indicating termination of a portion of them. A sparse number of fibers could be traced leaving the contralateral tectum in layer 6. These fibers project to the contralateral central nucleus of the torus semicircularis (TS, Figs. 4 and 5), approximately homotopic to the extent of the lesion.

Degenerated fibers which leave the tectum in layer 6 ipsilateral to the lesion constitute the major portion of the descending projections. At the level of the rostral part of the plica encephali ventralis (PEV, Fig. 4B), an area of extracerebral space caused by folding of the brain, degenerated fibers course out of the tectum in layer 6 to form the descending tectobulbar bundle. While degenerated fibers also lie in layer 9 at and caudal to this level, they do not contribute to the descending projections.

Some of the fibers course medially and caudally, innervating the central nucleus of the torus semicircularis (TS, Figs. 4–6A) and an area lateral to the nucleus of the medial longitudinal fasciculus (NM, Fig. 4A). The majority of fibers continue caudally

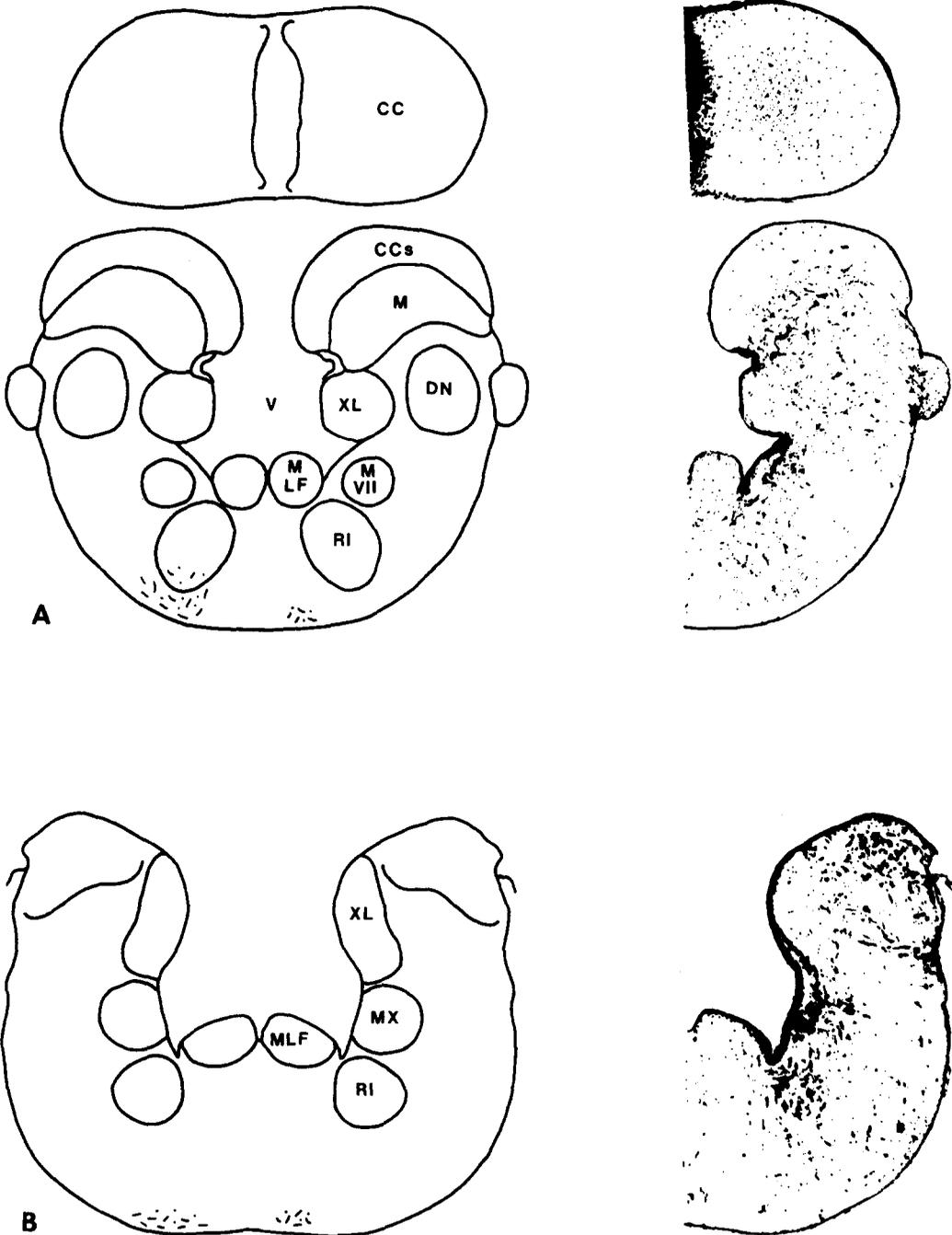


Fig. 7. A: transverse section through a mid-medullary level. B: transverse section through a caudal medullary level. Descending tectobulbar pathways do not extend beyond this level.

on the ipsilateral side, terminating sparsely along the ventral portion of the lateral tegmental nucleus (LT, Fig. 5A) and in nucleus lateralis valvulae (LV, Fig. 5B). The fiber bundle courses through and terminates heavily in nucleus isthmi (NI, Fig. 6A) and then continues caudally in a ventral bundle (Figs. 6B and 7). A component of the degenerated tectobulbar fibers crosses to the contralateral side at the level of the lateral tegmental nucleus (Fig. 5A) and continues caudally in a ventral bundle (Figs. 5B–7) which lies medial to the homotopic position of the ipsilateral descending bundle. Both these descending bundles terminate along their course on the long, ventrally extending dendrites of reticular formation neurons (RS and RI, Figs. 6B and 7). The descending tectobulbar tracts do not reach spinal levels and were not traced caudal to the level indicated in Fig. 7B.

DISCUSSION

Tectal projections in gars

The present study demonstrates the presence of extensive projections, both ascending and descending. Some of these projections and their targets are of particular interest in that they may well be independent or unique evolutionary developments within the actinopterygian radiation.

The medial zone of the actinopterygian tectum is confluent with a specialized structure, the torus longitudinalis, which is not present in land vertebrates. Degeneration is present in the core of this structure following lesions through the gar tectum, as has been reported in teleosts^{4,12,21}. These results are, however, probably due to interruption of fibers of passage and not indicative of a tectobulbar projection. Studies in the carp, *Cyprinus*, carried out by Ito and Kishida¹⁵ with both degeneration and retrograde transport methods, show that while the torus longitudinalis projects only to the tectum, its major afferent input is from nucleus lateralis valvulae and the valvula of the cerebellum, via the tractus mesencephalocerebellaris anterior; a portion of these fibers traverse the stratum album centrale of the tectum to reach the torus longitudinalis, and only a few labeled cells were found in the tectum following injection of HRP into the torus. The present study also demonstrates the presence of a tectal projection to nucleus lateralis valvulae, and Finger⁵ has demonstrated projections of the latter nucleus to the valvula in catfish.

We can thus postulate that a circuit is present such that the tectum projects to nucleus lateralis valvulae which in turn projects to the valvula. Nucleus lateralis valvulae and the valvula both then project to the torus longitudinalis, which finally projects back upon the tectum. As the degeneration seen in the torus longitudinalis following tectal lesions in gars, and also in some teleosts⁴, appears to be homotopically organized, it is probable that the ascending fibers from nucleus lateralis valvulae and the valvula traverse the tectum in a rostrocaudally ordered manner. As the fine structure of the torus longitudinalis closely resembles that of the granular layer of the cerebellum¹⁴, and the torus may be involved in opticostatic correlation¹⁵, the presence of a topographic arrangement of its ascending input would not be surprising.

Two additional features of this system are unique within bony fishes. The valvula

itself is a protuberance of the corpus cerebelli that extends rostrally into the space of the midbrain ventricle; it is a unique specialization, present only in the advanced actinopterygians — teleosts and holosteans — and absent in chondrosteans and all non-actinopterygian vertebrates. Secondly, the projection of the tectum to nucleus lateralis valvulae does not correspond to any known tectocerebellar system in land vertebrates. Tectocerebellar fibers have been reported in pigeons²², but this projection may represent an independently evolved system or result from invasion of pretectal or thalamic structures which project to the cerebellum^{6,16}. In most land vertebrates, the cerebellum does receive visual information, but via the tecto-ponto-cerebellar projection system¹⁰. While this tecto-tecto-valvular circuit may be subserving functions similar to those of the mammalian pontocerebellar system, it would appear to be independently evolved within actinopterygians.

Among the ascending projections, there are also possibly unique features. Tectal projections have been found to the entopeduncular and prethalamie nuclei, but the homologues of these nuclei in non-actinopterygians are unclear. In gars, there is no evidence of retinal projections to these nuclei, but retinal fibers do traverse parts of them and could form en passant synapses. That tectal fibers should reach such rostral targets is surprising, but since these nuclei lie well rostral and dorsal to the supraoptic decussation, the possibility that the tectal fibers within them are merely part of the decussating system is an unlikely one.

Gars may also have retinal afferent fibers arising in the tectum. Degenerated fibers were seen in the optic chiasm and nerve. However, they could not be traced directly into the nerve in our material and were not present consistently in all cases, so the possibility that they are aberrant fibers from the supraoptic decussation cannot be discounted.

Comparisons with other bony fishes

Among actinopterygian fishes, the efferent projections of the tectum have been studied in only a very few species, all of which are teleosts except the gar. These species include two advanced perciforms, *Eugerres* and *Holocentrus*⁴, the very specialized blind cave-fish *Astyanax*²¹, the goldfish *Carrassius*¹², and the catfish *Ictalurus*²⁰. In light of the great number of extant species of teleosts and the extensive range of variation in their adaptive zone, it would be premature to analyze in detail the relatively minor differences in the patterns of tectal projections which have been reported among them. These differences may be due to species variation, to interpretation of experimental material, and/or an artefact of nomenclatural differences. The latter problem is particularly severe within bony fish; normal, cytoarchitectonic variation among species is pronounced, and thorough analyses of neuronal groups in a variety of species, as has been initiated in gars¹, need to be carried out. Until such analyses are completed, along with more experimental studies of projections in a more wide-ranging sample of species, comparisons of results will continue to be difficult.

A general pattern does emerge, however, when all the data are considered. The tectum has bilateral descending projections to a number of brain stem nuclei, including the reticular formation, and, in most cases, bilateral ascending projections to

TABLE I

Proposed homologies among ray-finned fishes and land vertebrates

<i>Gars</i>	<i>Teleosts (Schnitzlein, 1962)</i>	<i>Amniotes</i>
Anterior thalamic nucleus	dorsolateral and dorso-medial thalamic nuclei	dorsal lateral geniculate nucleus and/or anterior thalamic nuclei
Dorsal posterior thalamic nucleus	mesencephalic tegmentum	nucleus rotundus
Central posterior thalamic nucleus		
Preglomerular complex	preglomerular and glomerular nuclei	part of ventral thalamus?
Parvocellular part of superficial pretectal nucleus	lateral geniculate nucleus	pretectal nuclei
Magnocellular part of superficial pretectal nucleus	nucleus rotundus	
Nucleus isthmi		

pretectal and diencephalic nuclei. Aspects of these projection systems are considered in detail below.

Comparisons with land vertebrates

To facilitate our discussion, we have listed the nuclei we will discuss in Table I. We have included the names currently used in teleosts, as well as our proposed homologies of the gar nuclei to those of land vertebrates. While the visual system in actinopterygian fishes has some independently derived features, its overall pattern is strikingly similar to that of land vertebrates. One similarity of particular interest is a projection to nucleus isthmi. This nucleus has reciprocal tectal connections in other non-mammalian vertebrates^{8,13,24} and may be the homologue of the recently studied mammalian parabigeminal nucleus¹¹. In gars, nucleus isthmi also projects reciprocally back to the tectum (Northcutt, unpublished data).

There is also close correspondence between bony fish and other vertebrates in the organization of tectal projections to the thalamus and pretectum. Before analyzing these ascending projections, we must consider two nuclei which lie rostral to the tectum in fish and which have usually been labeled the lateral geniculate nucleus and nucleus rotundus¹⁹. Homology of these nuclei to nuclei in land vertebrates of the same name is implied by this nomenclature. As suggested previously by Northcutt and Butler¹⁷, however, this is probably an erroneous assumption, and both these teleostean nuclei are probably comprised by the magnocellular and parvocellular portions of the gar superficial pretectal nucleus. That the superficial pretectal nucleus lies at the pretectal rather than the thalamic level is supported by the data on retinal afferents¹⁷ and tectal afferents, and by the finding that the central pretectal nucleus, which lies just medial to it, projects reciprocally back into the tectum (Northcutt, unpublished data), as does the pretectum in frogs²⁴. Additionally, in goldfish neither lesions nor injections of tritiated amino acids reveal any projections from the superficial pretectal nucleus to the telencephalon (Northcutt and Braford, unpublished data).

When the retinal¹⁷ and tectal projections are considered together, a pattern of visual organization is seen in gars which closely resembles that in other vertebrates. In gars the non-telencephalic area rostral to the tectum can be roughly divided into 3 zones rostro-caudally — rostral, middle and caudal. The retina projects to the rostral (anterior thalamic nucleus) and caudal (pretectum) zones¹⁷, and the tectum projects to all 3 zones. Thus the middle zone receives tectal, but not retinal, input. Tectal projections to the contralateral side decussate in the supraoptic decussation, as they do in land vertebrates².

Within the middle zone, 3 specific nuclei — the rostral part of the preglomerular complex, and the dorsal posterior and central posterior nuclei, receive tectal projections. The preglomerular target lies ventrolateral to the optic tract fibers, and it is not known whether dendrites extend from this nucleus and receive retinal input. Nevertheless, the relationship of the entire preglomerular complex to the hypothalamus makes it unlikely that it is homologous to the nucleus rotundus of land vertebrates. On the other hand, both the dorsal posterior and central posterior nuclei are likely candidates for such an homology. If, as in some land vertebrates^{9,18}, the visual midbrain–thalamic relay lies dorsal to the auditory relay, the dorsal posterior nucleus would appear to be the most likely homologue of nucleus rotundus. In reptiles and birds, nucleus rotundus projects to the dorsal ventricular ridge of the telencephalon. If the dorsal posterior thalamic nucleus of gars also projects to the telencephalon, the proposal of such an homology would be greatly strengthened.

Further rostrally, the anterior thalamic nucleus receives both retinal and tectal inputs. If this nucleus is found to project to the telencephalon, it would very likely be a homologue of the land vertebrate dorsal lateral geniculate nucleus. Finally, the caudal zone also receives both retinal and tectal input, and for reasons discussed above, corresponds to the pretectal region.

Thus, while at first glance, brain organization in bony fish appears to differ markedly from that in land vertebrates, there are in fact many similarities in the sensory organization of the thalamus and pretectum. Such similarities were also found by Finger⁵ in the organization of cerebellar inputs. Whether similar patterns of connectional organization are present in the telencephalon of actinopterygians remains to be determined.

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