

Retinofugal Pathways in the Longnose Gar *Lepisosteus osseus* (Linnaeus)

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ABSTRACT Retinal projections were studied with autoradiographic and silver methods in the gar, *Lepisosteus osseus*, one of the two surviving members of the holostean actinopterygians. Contralaterally, the retina projects to the preoptic nucleus of the hypothalamus, and, via the medial optic tract, to the dorsal thalamus, medial ventral thalamic nucleus, nucleus pretectalis profundus pars ventralis and pars dorsalis, and the medial portion of the deep layer of the central zone in the optic tectum. The dorsal optic tract projects to the lateral ventral thalamic nucleus, nucleus pretectalis centralis, and the superficial white and gray zone of the optic tectum. The ventral optic tract terminates in the nucleus of the ventral optic tract, the lateral and medial ventral thalamic nuclei, nucleus pretectalis superficialis, nucleus pretectalis centralis, nucleus pretectalis profundus pars ventralis, the basal optic nucleus, and the superficial white and gray zone of the optic tectum. Ipsilateral projections are to similar sites, except for an absence of inputs to the lateral ventral thalamic nucleus from the dorsal tract and to the nucleus pretectalis superficialis, nucleus pretectalis profundus pars ventralis, and the basal optic nucleus from the ventral tract. The presence of ipsilateral retinal projections in gars is compared to their presumed absence in teleosts, and comparisons of retino-recipient targets in gars are made with teleosts and with non-actinopterygian vertebrates.

Lepisosteus and its close relative, *Amia*, inhabit the fresh waters of Central and North America. They are the sole living representatives of the holostean actinopterygians which reached a peak diversity in the Mesozoic and gave rise to the most successful vertebrate radiation to date, the teleosts (Schaeffer, '69; Moy-Thomas, '71).

Recently, a number of anatomical studies on the retinofugal projections of teleosts have been reported (Ebbesson, '68; Campbell and Ebbesson, '69; Roth, '69; Sharma, '72; Vanegas and Ebbesson, '73; Anders and Hibbard, '74). In the species studied to date, retinal projections to a number of contralateral diencephalic and mesencephalic targets have been described. Most of the retino-recipient areas are migrated cell groups, and the anatomical complexity is sufficient to frustrate comparisons not only with land vertebrates but even among living teleosts, as evinced by the range of nomenclature applied to these visual targets in different teleosts

(Jansen, '29; Ariëns Kappers et al., '36; Schnitzlein, '62; Vanegas and Ebbesson, '73). The examination of the visual system of an intermediate taxonomic grade of actinopterygians that does not possess the wide morphological variation of teleosts might facilitate comparisons with both teleosts and land vertebrates.

For these reasons, we undertook a study of the retinal projections in the longnose gar in the hope that, since this species represents a relic population of an earlier actinopterygian grade of organization, its visual system might be more simple than that of living teleosts. Such a study should yield information on the evolution of visual systems not only within the actinopterygian radiation, but should also facilitate comparisons with the visual systems of land vertebrates.

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MATERIALS AND METHODS

Twelve juvenile specimens of *Lepisosteus osseus* (L.) underwent unilateral aspiration of the retina under MS222 (tricaine) anesthesia. After survival times of 6–60 days at 26°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 micra and stored in 2% formalin in a refrigerator, and processed by several modifications of the Nauta (Ebbesson, '70b) and Fink-Heimer I (Fink and Heimer, '67) procedures for the demonstration of degenerating axoplasm.

An additional three specimens were processed for autoradiography following the injection of 50 μ C of L-(4, 5-³H)-proline, 9.4 μ C/ μ l, with a 10 μ l Hamilton syringe and 26 gauge needle fitted with a polyethylene sleeve which limited penetration into the eye to 3 mm. Aqueous radioactive solutions were evaporated to dryness with nitrogen to remove ³HOH and redissolved in 0.86% saline immediately before use. The animals were allowed to survive 24, 48, and 72 hours postoperatively. Autoradiographic procedures were essentially those described by Kopriwa and Leblond ('62). The animals were perfused with AFA (90 cc of 80% ethanol, 5 cc formalin, and 5 cc glacial acetic acid) and the brains were removed and stored in AFA for at least one week prior to dehydration and embedding in paraffin. The brains were then cut in the transverse plane at 15 micra. Kodak NTB3 nuclear track emulsion was diluted 1:1 with distilled water at 40°C, and the slides were dipped into the emulsion and dried for approximately one hour. The sections were exposed for 20 days and then developed in Kodak Dektol and stained with cresyl violet. Selected sections from the 24 hour autoradiographic case were photographed on Kodalith Ortho film, type 3, with a Leitz large-format camera. The distribution of the retinofugal pathways and their terminal fields were charted on these photographs, which were then compared with the anterograde degeneration cases as an aid in separating terminal fields from fibers of passage.

Additional series of sections processed with Bodian, Nissl, Golgi-Cox, and Klüver-

Barrera methods and cut in the three standard anatomical planes were available for study of nuclear groups and fiber tracts in *Lepisosteus* and in a number of species of teleosts.

RESULTS

Following unilateral enucleation, the optimal survival time for silver impregnation of terminal fields was between six and eight days. Survival times longer than eight days revealed degenerating axons of passage but poor, if any, terminal fields except in the optic tectum. Some axonal debris was still present in the tectum with survival times of 60 days. Terminal fields, as determined with the autoradiographic method, were recognized by an increase in grain density. These fields are observable after a survival time of one day and correspond topographically to terminal fields identified with the anterograde degeneration method. With survival times longer than one day following injection of tritiated proline, increased density of grains over the retinofugal fiber tracts also becomes apparent. The course and termination of retinal projections determined with both methods are identical. The levels of the illustrated sections (figs. 2–5) are shown in figure 1. Figure 7 indicates the position and extent of the fields photographed in the remaining figures.

Normal anatomy

In our description, the thalamus is defined as a region lying ventral to the habenula and dorsal to the preoptic area and hypothalamus. In most anamniotes described to date (Ariëns Kappers et al., '36; Herrick, '48) the thalamus has been divided into dorsal and ventral parts. The ventral thalamus usually lies lateral to the sulcus medius thalami and is characterized by multiple laminae of compact cells. In gars, as in *Polypterus* (Nieuwenhuys and Bodenheimer, '66), the sulcus medius does not divide the thalamus into dorsal and ventral components, but runs ventral to a cell free boundary (figs. 2B, 3). The cells of the dorsal thalamus are not as clearly laminated as are those of the ventral thalamus. Finally, the fasciculus retroflexus passes through the dorsal thalamus. These criteria all apply to the regions we have designated as the dorsal and ventral thalami in *Lepisosteus*.

Abbreviations

BON, Basal optic nucleus	NPS, Nucleus pretectalis superficialis
DOT, Dorsal optic tract	NVOT, Nucleus of the ventral optic tract
DT, Dorsal thalamus	OB, Olfactory bulb
E, Nucleus entopeduncularis	OC, Optic chiasm
ES, Extracerebral space	PC, Posterior commissure
FR, Fasciculus retroflexus	PGT, Periventricular gray zone of tectum
H, Habenula	SO, Subcommissural organ
ILH, Inferior lobe of hypothalamus	TCd, Tectal commissure, dorsal component
LVTN, Lateral ventral thalamic nucleus	TCv, Tectal commissure, ventral component
MOT, Medial optic tract	Teg, Tegmentum
MVTN, Medial ventral thalamic nucleus	Tel, Telencephalon
NP, Nucleus periventricularis preopticus	TeO, Optic tectum
NPC, Nucleus pretectalis centralis	TL, Torus longitudinalis
NPH, Nucleus periventricularis hypothalami	V, Ventricle
NPPd, Nucleus pretectalis profundus pars dorsalis	VOT, Ventral optic tract
NPPv, Nucleus pretectalis profundus pars ventralis	VT, Ventral thalamus

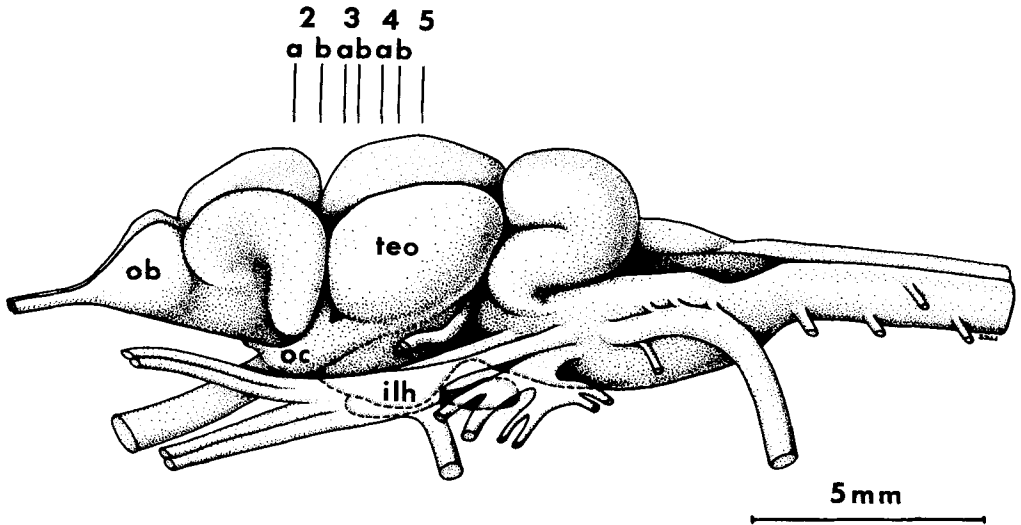


Fig. 1 Dorsolateral view of the brain of *Lepisosteus osseus*. Numbered lines indicate the levels of the transverse sections in figures 2-5.

The pretectal region is that portion of the wall of the neural tube which lies between the thalamus and tectum. A ventrolateral displacement of the rostral tectal poles and consequent distortion of the pretectal and thalamic portions of the neural wall which occurs in teleosts is lacking in gars. Therefore, in *Lepisosteus* it is possible to trace fiber and cell groups of the superficial, central, and deep tectal zones into the caudal thalamus or pretectum. At this level there are three major cell groups — superficial, central, and deep — which are rostral continuations of the respective tectal cellular zones, and are

therefore identified here as pretectal nuclei (figs. 3, 4).

Four major zones can be recognized in the optic tectum of *Lepisosteus*. From deep to superficial, these are (1) the periventricular gray zone (PGZ), (2) a deep white fiber zone (DWZ), (3) the central gray zone (CZ), and (4) the superficial white and gray zone (SWGZ, fig. 6). The majority of cells lie in the periventricular zone, which is composed of a layer of cells (lamina 2) juxtaposed to the ependyma (lamina 1) and an over-lying fiber layer (lamina 3), variably split by a third thinner layer (lamina 4, fig. 6). Most cells

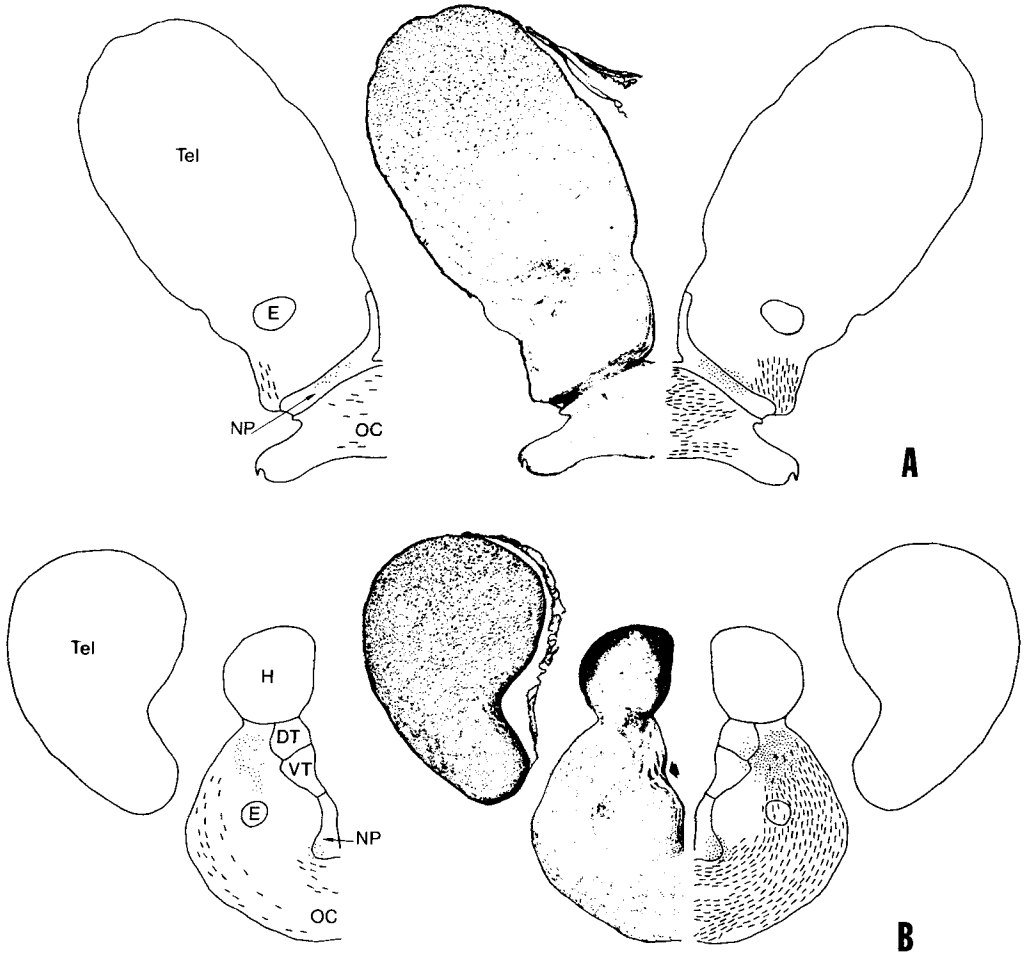


Fig. 2 A, Transverse section through the level of the optic chiasm. In this and figures 3-5, a Nissl preparation is shown in the center, the side ipsilateral to the operated eye is drawn on the left, and the contralateral side is drawn on the right. Retinal fibers of passage are represented by dashed lines and terminal fields by stippling. The pattern of termination is based on an autoradiographic case that survived for one day. B, Transverse section through the level of the rostral diencephalon. Bar scale in this figure and in figures 3-5 represents 1 mm. Ventricular black arrow in 2B-4 marks position of sulcus medius.

in the periventricular zone are piriform, with apical dendrites which extend into the ventral half of the superficial white and gray zone. Unlike the situation in many teleosts, there is no fiber system deep to the periventricular gray.

The deep white zone (DWZ) consists of myelinated and unmyelinated fibers (lamina 5). It is continuous across the midline as the intertectal commissure. Laterally and caudally a portion of the deep white fibers form the tectobulbar tracts.

The central gray zone (CZ) consists predominantly of large bipolar cells. It is not a compact zone, but the greatest density of cell bodies is found in the dorsal half of this zone. Thus the central gray can be divided into superficial and deep neuropil regions (laminae 6 and 7). Dendrites of the bipolar cells radiate superficially to ramify in the deep half of the superficial white and gray zone.

The superficial white and gray zone (SWGZ) can be divided into four laminae,

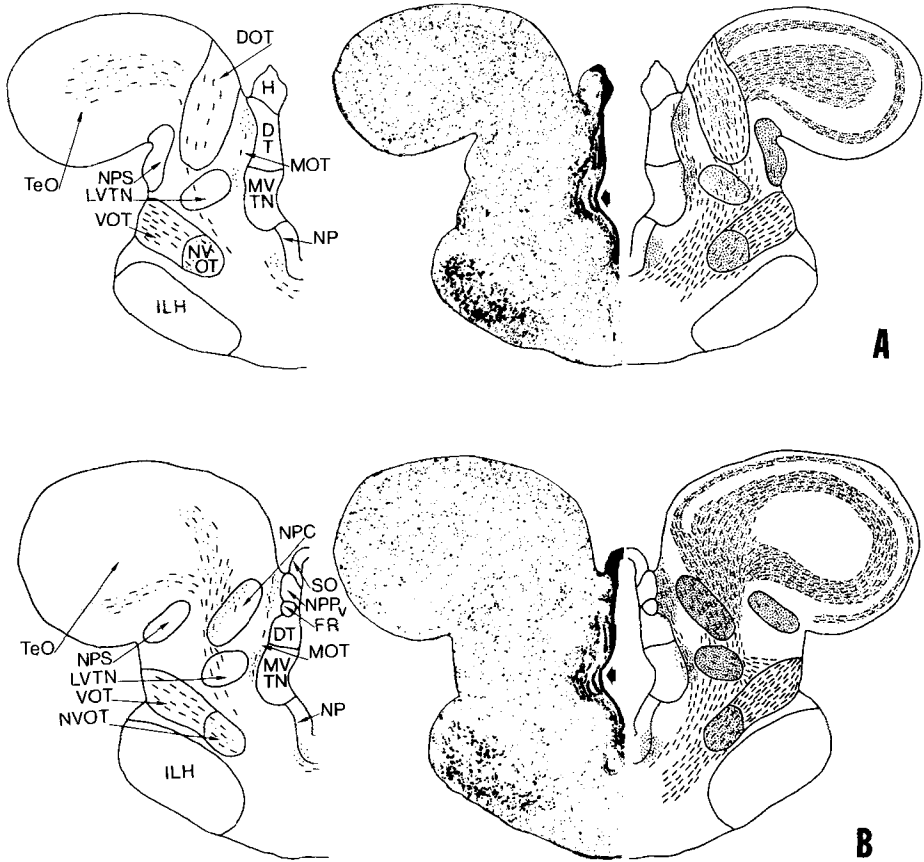


Fig. 3 A, Transverse section through the rostral pretectum. Note continuation of tectal cellular laminae into superficial pretectal nucleus. B, Transverse section through mid-pretectal level.

the most superficial of which is a marginal layer of unmyelinated fibers (lamina 11). Immediately beneath the latter is a small calibre fiber layer containing scattered oval cells (lamina 10). Both autoradiographic and Fink-Heimer preparations reveal these fibers to be of retinal origin. However, the larger well-myelinated fibers that form lamina 9 do not degenerate following removal of the retina, nor were they labeled in our autoradiographic preparations. These fibers exit the tectum rostrally and, in Bodian preparations, can be followed as a distinct tract as far as the pretectum. The last subdivision of the superficial tectal zone constitutes the bulk of this zone. Lamina 8, an extensive neuropil subdivided dorsoventrally by a number of fascicles com-

posed of large-calibre, myelinated fibers, constitutes the major retinofugal target of the tectum.

Contralateral projections

Fibers course caudally in the optic nerve to the optic chiasm where the majority, but not all, decussate and enter the optic tract (fig. 9B). At the level of the decussation (fig. 2), some fibers in the dorso-medial portion of the chiasm peel off and give rise to a terminal field in nucleus periventricularis preopticus (NP). The degeneration is present throughout all of this cell group except for its most caudal pole (figs. 3, 4A). As the optic tract courses dorsally in the rostral thalamus (fig. 2B), the fibers pass through but do not terminate in nucleus entopeduncularis (E),

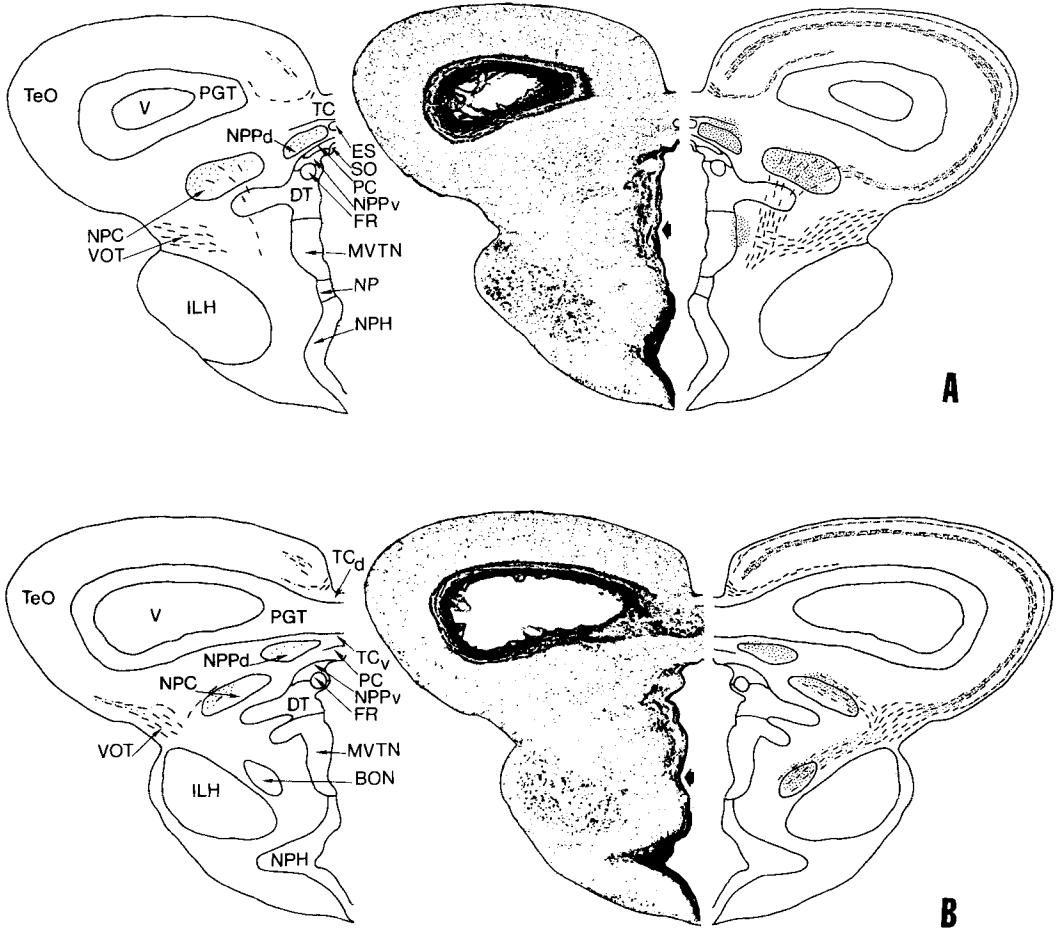


Fig. 4 A, Transverse section through caudal pretectum. B, Transverse section at the level of the basal optic nucleus.

and then turn medially to terminate in a field just lateral to the periventricular cell plate of the thalamus (figs. 2B, 8A).

At more caudal levels (fig. 3) the optic tract splits into three major divisions which we have labeled the dorsal (DOT), medial (MOT), and ventral (VOT) optic tracts. For purposes of description, we will deal first with the medial optic tract and the regions of fiber termination associated with it.

Having given rise to a terminal field in the rostral thalamus, the medial tract continues caudally with fibers terminating in two fields that lie immediately lateral to the cell plates of the medial ventral tha-

lamic nucleus (MVTN) and the dorsal thalamus (DT, fig. 3A). The former zone of terminal degeneration continues further caudally (fig. 4A) than does the latter (fig. 3B). A third terminal field appears at the level of the subcommissural organ (fig. 3B) associated with the rostral portion of the periventricular cell plate of a pretectal group which we have termed nucleus pretectalis profundus pars ventralis (NPPv). As the medial optic tract is traced further caudally (fig. 4A) it divides into two fascicles. The ventral fascicle terminates in a second medial pretectal nucleus, nucleus pretectalis profundus pars dorsalis (NPPd), which lies immediately dorsal to the pos-

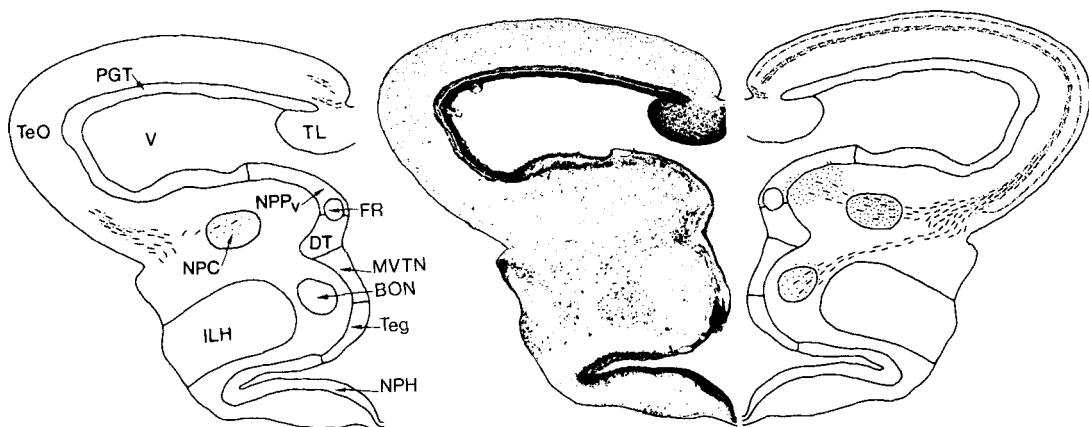


Fig. 5 Transverse section at a mid-tectal level.

terior commissure (PC). The dorsal fascicle enters the deep part of the central zone of the optic tectum (TeO) where it courses laterally just superficial to the periventricular gray zone (figs. 4, 5, 9C).

The remaining divisions of the optic tract split at the level of the rostral pole of the tectum (TeO, fig. 3A). At this level the dorsal optic tract (DOT) turns medially and courses towards the dorsomedial portion of the tectum. It appears to terminate in the rostral portion of the lateral ventral thalamic nucleus (LVTN). At the level of the caudal thalamus (figs. 3B, 4A), fibers of the dorsal optic tract terminate in a large preectal group, nucleus preectalis centralis (NPC). The tract then continues dorsally into the superficial white and gray zone of the tectum (figs. 3, 4, 5). The dorsal tract appears to be the major visual input to the rostral pole of the tectum.

The third division of the optic tract, which we have termed the ventral optic tract (VOT), arises at the level of the rostral thalamus (fig. 3A). Scattered cells, the nucleus of the ventral optic tract (NVOT), are embedded among the fibers of this tract and probably receive optic terminations (fig. 3). Fibers arising from the ventral optic tract turn medially and terminate in the caudal portions of the lateral (LVTN) and medial (MVTN) ventral thalamic nuclei (figs. 3B, 4A). The tract then courses dorsally and gives rise to a dense terminal field in nucleus pre-

ectalis superficialis (NPS, fig. 3). At more caudal levels the ventral tract terminates in three regions — nucleus preectalis centralis (NCP, figs. 4B, 5), the caudal portion of nucleus preectalis profundus pars ventralis (NPPv, fig. 5), and the basal optic nucleus (BON) of the mesencephalic tegmentum (figs. 4B, 5). The remaining portion of the ventral optic tract enters the tectum on its ventrolateral aspect (figs. 4B, 8C, 9E).

Within the optic tectum, the terminal fields can be related to the various zones which are recognized in normal material. As the dorsal and ventral optic tracts enter the tectum they both divide into dorsal and ventral components, which remain within the superficial white and gray zone. The more superficial optic fibers form tectal lamina 10, among which oval-shaped cells are scattered. The terminal field (T1, fig. 6) associated with these fibers is localized in this lamina and may extend into the ventral-most portion of the marginal layer (lamina 11). The ventral optic component forms numerous fascicles which terminate in lamina 8. Small groups of large-calibre myelinated optic fibers mark the ventral boundary of the superficial white and gray zone. The terminal fields of these retinal ganglion cell axons (T2, fig. 6) do not extend into the central tectal zone (CZ). While these retinal fibers from the dorsal and ventral optic tracts do not terminate in the central or deep tectal zones, the terminal field of the medial

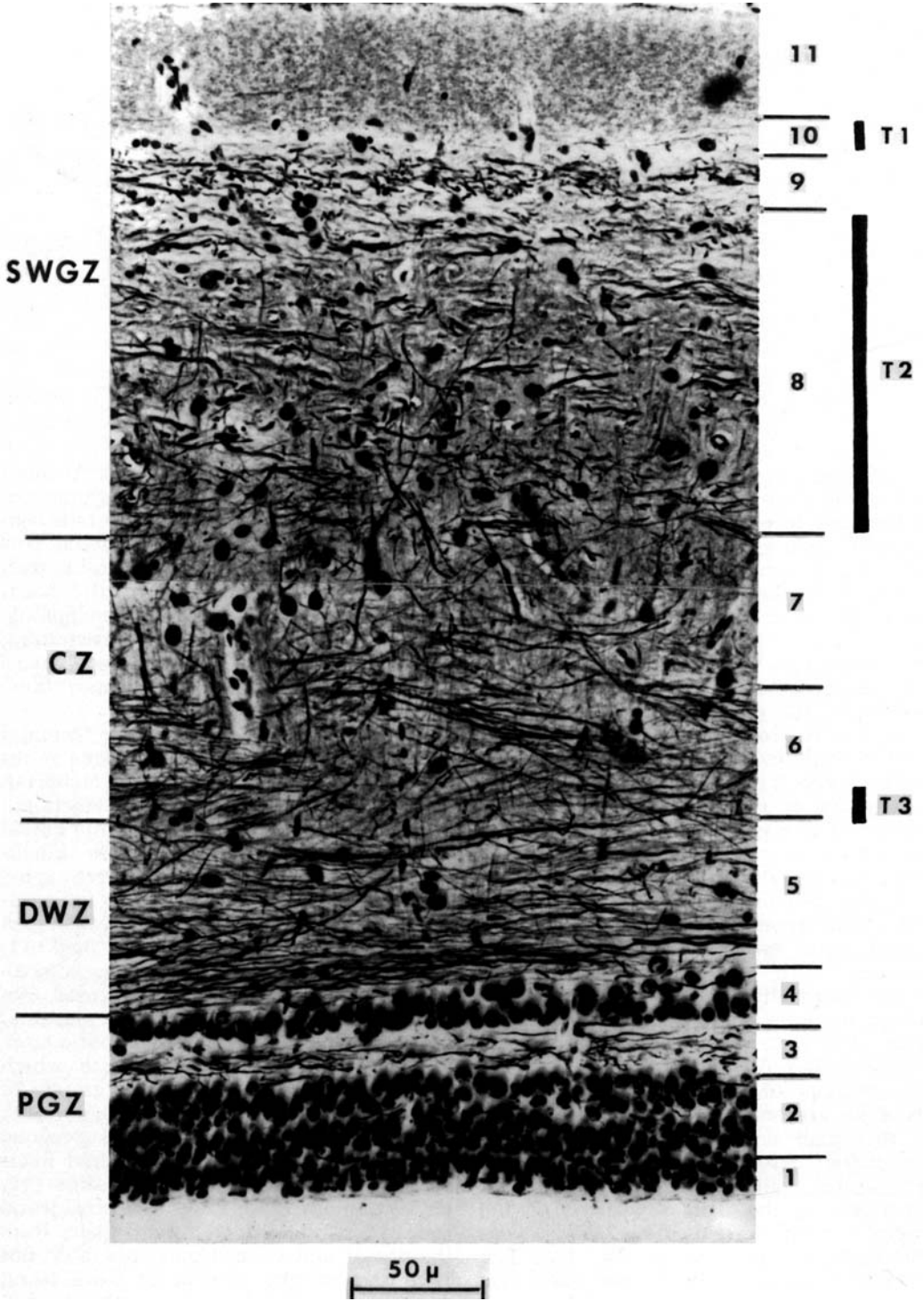


Figure 6

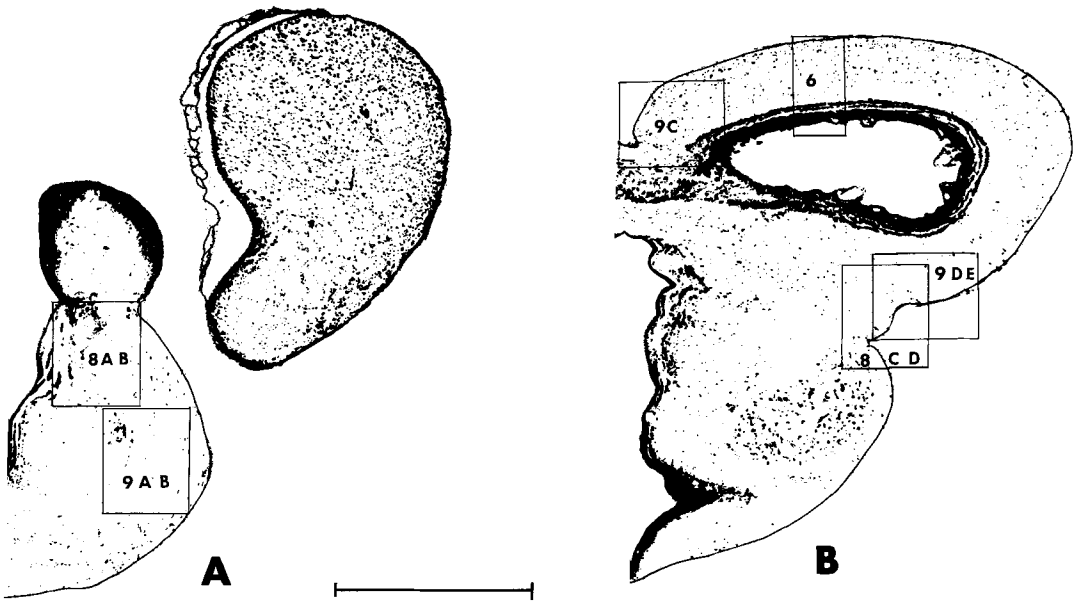


Fig. 7 Photomicrographs of the rostral diencephalon (A) and rostral tectum (B) indicating the orientation and extent of figures 6, 8, and 9. Bar scale represents 1 mm.

optic tract (T3, fig. 6) is located on the ventral border of the central zone (CZ), in a position to synapse on the proximal dendritic shafts of the piriform cells of the periventricular gray zone (PGZ).

Ipsilateral projections

While the ipsilateral projections of the retina are consistently less dense than those to contralateral sites, most of the regions in the diencephalon, pretectum, and tectum which receive contralateral projections also receive an ipsilateral input. All three divisions of the optic tract are present on the ipsilateral side.

At the level of the optic chiasm (fig. 2A), some of the fibers do not decussate but remain on the ipsilateral side (fig. 9A)

and turn dorsally. There is a terminal field among the cell bodies of nucleus periventricularis preopticus (NP), and the caudal extent of this terminal field is similar to that seen on the contralateral side (figs. 2B, 3).

The medial optic tract (MOT) terminates in the periventricular cell plate of the dorsal thalamus (DT, figs. 2B, 3A, 8B), the medial ventral thalamic nucleus (MVTN, fig. 3), the rostral part of nucleus pretectalis profundus pars ventralis (NPPv, fig. 3B), and nucleus pretectalis profundus pars dorsalis (NPPd, fig. 4) on the ipsilateral side. The medial optic tract then courses caudally and dorsally from the pretectal region and enters the medial aspect of the tectum and courses along the ventral boundary of the central zone (figs. 4, 5), as does the contralateral medial optic tract.

The projections of the dorsal division of the ipsilateral optic tract are similar to those of the contralateral dorsal tract (DOT), except that the lateral ventral thalamic nucleus (LVTN) and lamina 10 of the ipsilateral optic tectum do not receive an ipsilateral retinal input (figs. 3-5). The terminal field in the rostral part of the central pretectal nucleus (NCP) is limited

Fig. 6 Photomicrograph of transverse section through the optic tectum of *Lepisosteus*. Bodian preparation from a mid-dorsal position at a rostro-caudal level similar to tectal level seen in figure 5. The extent of retinal terminal fields within the tectum is indicated by bars at the right: T1 (dorsal component) and T2 (ventral component) of dorsal optic tract, and T3 (terminal field of medial optic tract). Numbers 1-11 indicate tectal laminae and the letters indicate tectal zones: PGZ, periventricular gray zone; DWZ, deep white zone; CZ, central zone; SWGZ, superficial white and gray zone.

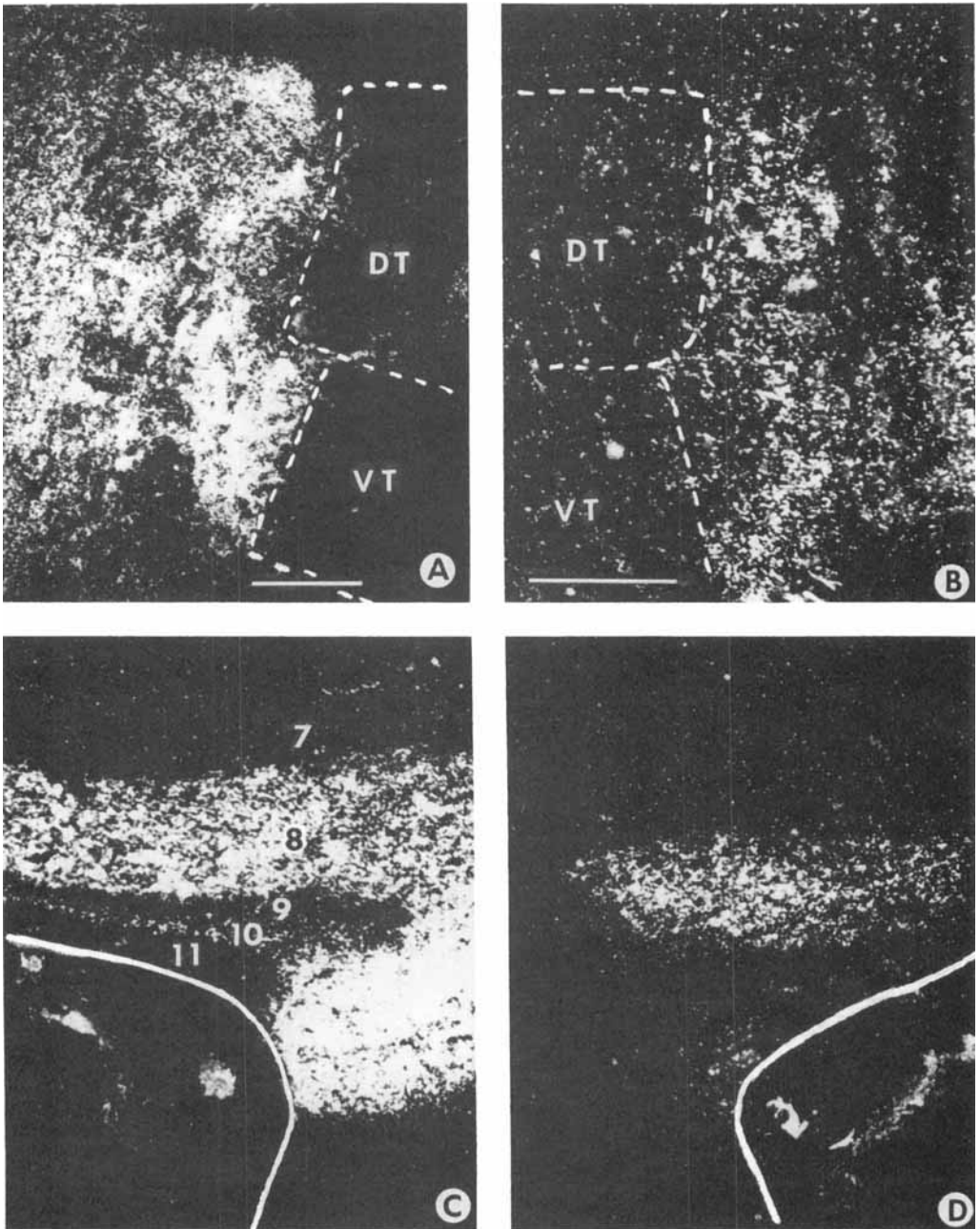


Fig. 8 Dark field photomicrographs of autoradiographs following unilateral intraocular injection of tritiated proline. A, Contralateral thalamus at same level as that shown in figure 2B. B, Ipsilateral thalamus at same level as that shown in figure 2B. C, Contralateral ventrolateral optic tectum at same level as that shown in figure 4B. D, Ipsilateral ventrolateral optic tectum at same level as that shown in figure 4B. Dorsal surface is toward the top in all figures. Bar scales represent 100 micra. Magnification of B, C, and D are identical. Dotted lines in A and B indicate lateral extent of cell bodies of the dorsal and ventral thalamus. White lines in C and D mark the pial surface of the optic tectum and 7-11, the laminae of the optic tectum.

to the dorsal half of this nucleus (figs. 3B, 4A). The dorsal optic tract then courses into the medial half of the rostral tectal pole in the superficial white and gray zone and appears restricted to lamina 8 (figs. 3-5). These ipsilateral retino-tectal fibers occupy a very restricted area of the dorso-medial tectal roof and could not be traced beyond a mid-tectal level in the rostro-caudal plane.

The ventral optic tract on the ipsilateral side terminates in the nucleus of the ventral optic tract (NVOT, fig. 3) and in the caudal portion of the central pre-pectal nucleus (NCP, figs. 4B, 5). However, nucleus preectalis superficialis (NPS, fig. 3) and the caudal part of nucleus preectalis profundus pars ventralis (NPPv, figs. 4, 5) do not appear to receive an ipsilateral retinal projection. The ventral optic tract enters the lateral aspect of the optic tectum in the superficial white and gray zone and extends to the caudal pole of the optic tectum (figs. 4B, 5, 8D, 9D). Like the ipsilateral dorsal optic tract, the ipsilateral ventral optic tract only terminates in lamina 8, but its terminal extent appears twice as extensive in transverse sections as that of the ipsilateral dorsal optic tract, and this terminal field runs the entire length of the optic tectum.

The ipsilateral basal optic nucleus (BON, figs. 4B, 5) does not receive a retinal input.

DISCUSSION

Ipsilateral retinofugal projections

A major finding of this study is a substantial retinal projection not only to the ipsilateral diencephalon, but also to restricted portions of the ipsilateral optic tectum. While ipsilateral retinofugal pathways have been reported for a number of non-mammalian taxa (*e.g.*, Scalia et al., '68; Halpern and Frumin, '73; Northcutt and Przybylski, '73; Repérant, '73; Butler, '74; Northcutt and Butler, '74a; Cruce and Cruce, '75), none of the teleosts examined to date possess ipsilateral retinofugal pathways (Ebbesson, '68; Campbell and Ebbesson, '69; Roth, '69; Sharma, '72; Vanegas and Ebbesson, '73; Anders and Hibbard, '74). The presence of such pathways in gars, remnants of the holostean radiation, poses the possibility that such pathways may have arisen in these forms independently. If the ipsilateral retinal

pathways should prove to be related to a binocular visual field as they have in many land vertebrates, their presence in a rapidly moving, highly visual predator like the gar would not be surprising. Considering the vast range of ecological adaptations, study of teleosts should allow the resolution of the hypothesis that ipsilateral retinofugal projections have evolved a number of times. For example, members of the teleost family Belonidae show remarkable convergence in body shape and feeding behavior to gars. If belonids were found to possess ipsilateral retinofugal pathways, this would strongly support the independent development of similar visual pathways in widely divergent taxa.

A second possibility is that bilateral retinofugal projections were present in the ancestral vertebrate stock from which the actinopterygians, as well as other vertebrate radiations, evolved. Within the actinopterygian radiation, there are three grades of organization represented by living species—the chondrosteans, holosteans, and teleosts. The presence of ipsilateral as well as contralateral retinofugal pathways in the chondrostean actinopterygians would support this latter hypothesis, and would further pose a question as to the biological significance of the loss of ipsilateral retinal projections in some or all of the living teleosts and many land vertebrates.

Comparisons with teleosts

An examination of the recent literature on the retinofugal pathways of teleosts does not reveal a clear or consistent picture regarding the number or course of the trajectories of these pathways. Based on descriptions and illustrations in the literature, it is clear that topographically different pathways have been given identical names, *e.g.*, fasciculus medialis tracti optici of *Holocentrus* (Campbell and Ebbesson, '69) and *Cichlasoma* (Anders and Hibbard, '74). Comparison is further complicated by similar topographical neural groups receiving visual input by what appears to be different pathways, *e.g.*, retinal projections to the region of Schnitzlein's nucleus dorsolateralis (Schnitzlein, '62) in *Carassius* (Sharma, '72) and nucleus opticus dorsomedialis in *Eugerres* (Vanegas and Ebbesson, '73). Many of the apparent inconsistencies may in fact

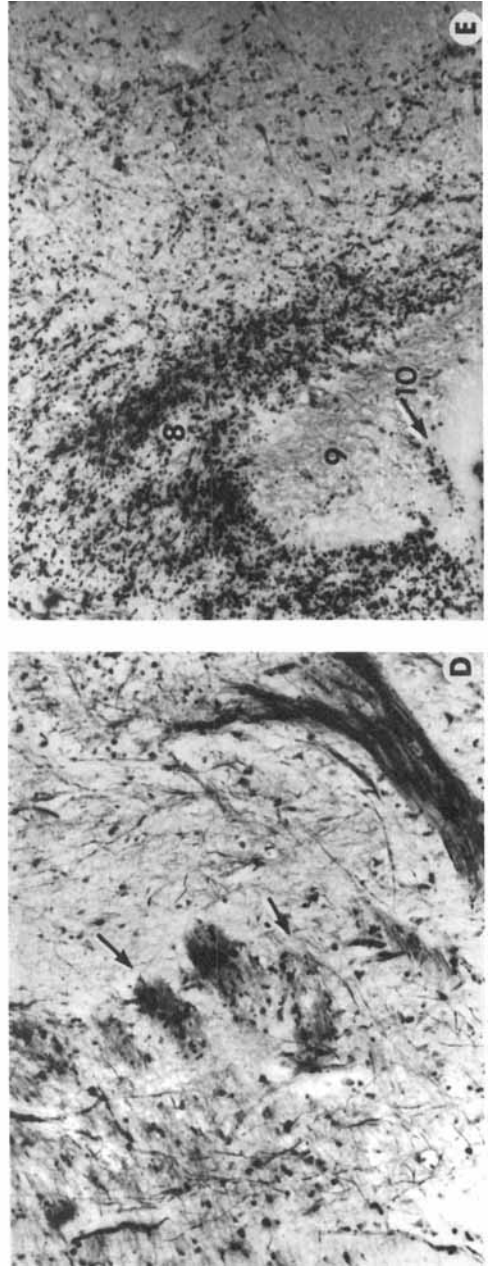
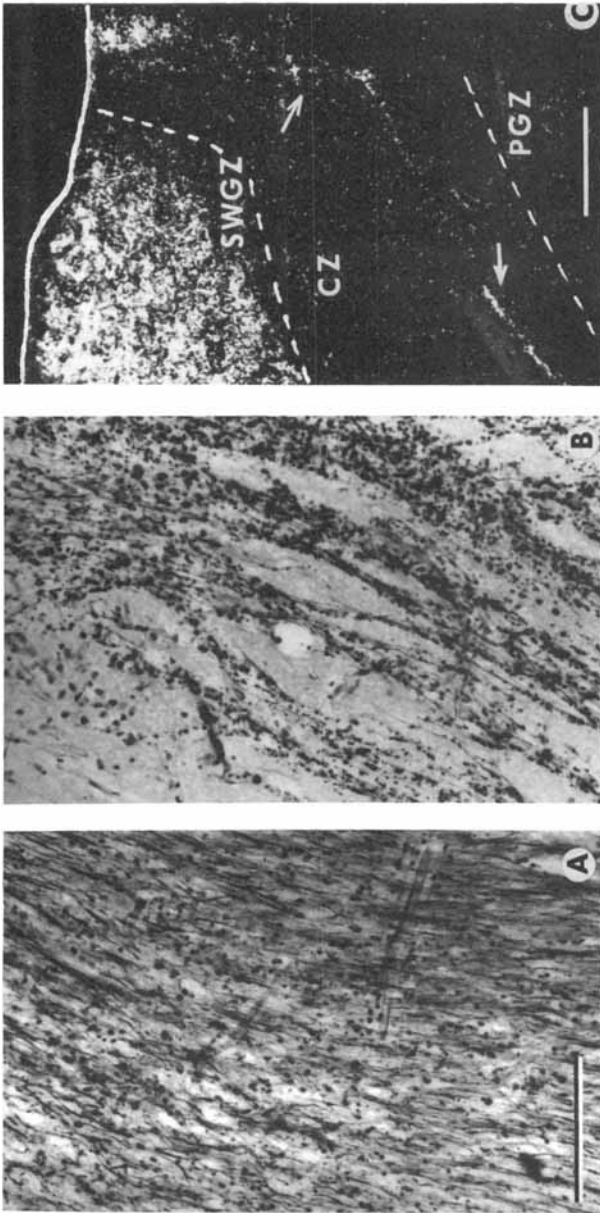


FIGURE 9

be actual biological variation in the species examined, as teleosts are noted for their incredible range of biological adaptations. However, the small size of the brains in these forms and the complexity of their visual systems complicate analysis with anterograde degeneration methods, particularly since frozen sections are utilized and every single section is usually not stained or analyzed.

All teleosts examined to date possess a retino-preoptic pathway as the most rostral component arising from the optic tract. Gars also possess such a retino-preoptic component (figs. 2, 3). Most studies have also reported a second pathway that separates from the optic tract and courses medially to terminate in the dorsal thalamus and periventricular pretectal fields as far caudally as the posterior commissure (Campbell and Ebbesson, '69; Vanegas and Ebbesson, '73; Anders and Hibbard, '74). This pathway is usually termed the dorso-medial optic fascicle of Jansen ('29). Gars possess a visual pathway, the medial optic tract, that is similar in several features to this teleost pathway. It too terminates in a periventricular pretectal field (figs. 3, 4). Most studies have not recognized a dorsal component of this pathway which in gars continues into the dorso-medial optic tectum to terminate just dorsal to the periventricular gray, but have reported that the deep tectal component arises out of the dorsal and ventral optic tracts after they enter the tectum. However, Landreth et al. ('75) have reported a pathway iden-

tical to that in gars in the teleost, *Hemichromis*.

In both gars and teleosts the majority of the retinofugal fibers course in dorsal (medial) and ventral (lateral) optic tracts. In gars a number of medium sized cells are embedded in the ventromedial edge of the ventral optic tract. These cells may be homologous to nucleus opticus ventromedialis of *Eugerres* as described by Vanegas and Ebbesson ('73). Gars also possess an accessory or basal optic tract and nucleus (figs. 3B, 4). A similar tract and nucleus have been described in *Holocentrus* (Campbell and Ebbesson, '69) and *Cichlasoma* (Anders and Hibbard, '74).

The greatest differences in the retino-recipient targets between gars and teleosts appear in the pretectum. In gars the tectal zones continue rostrally into the diencephalon to form superficial, central and deep pretectal nuclei (fig. 3). The superficial and central nuclei receive fibers from both the dorsal and ventral optic tract while the deep nucleus receives input solely from the medial optic tract. In teleosts the same topographical region of the brain wall contains a complex group of nuclei usually labeled from the pial surface toward the ventricular surface as: nucleus geniculatus lateralis, nucleus rotundus, nucleus pretectalis, and nucleus pretectalis dorso-medialis. All of these nuclei in teleosts have been reported to receive retinofugal projections (Ebbesson, '68; Sharma, '72).

The superficial pretectal nucleus of gars is formed by an outer layer of small oval cells and a deeper layer of large and medium sized cells. It is possible that this nucleus is the homologue of both the teleost lateral geniculate and rotundal nuclei. However, far more details of its organization must become available before this speculation can be resolved. Certainly the suggestion that the teleost pretectal nucleus is homologous to the gar central pretectal nucleus and that the teleost dorso-medial pretectal nucleus is homologous to the gar deep pretectal nucleus is on safer ground, based both on topography and on the manner in which these nuclei receive their retinal projections.

There are marked similarities in the optic tecta of both gars and teleosts. Both possess a marginal layer of small, unmyelinated axons which are non-retinal in

Fig. 9 Photomicrographs of retinofugal pathways degenerated after retinal removal as stained by the Fink-Heimer I method (A, B, D, and E) or traced after intraocular injection of tritiated proline (C). A, Ipsilateral optic tract degeneration at a rostral thalamic level. B, Contralateral optic tract degeneration at same level as A. C, Medial optic tract entering contralateral optic tectum and coursing in the deep part of the central tectal zone (arrows mark course of deep optic tract). D, Degenerated optic tract fibers (arrows mark degenerating fascicles) entering the ipsilateral rostral ventrolateral optic tectum. E, Degenerated optic tract fibers entering the contralateral rostral ventrolateral optic tectum. Numbers indicate tectal laminae which are degenerated, as in figure 6. The dorsal surface is toward the top in all figures except C, in which the dorsal surface is to the left of the figure. Bar scales represent 100 micra. Magnification of A and B are identical, as is the magnification of C, D, and E. Surgical survival time for A, B, D, and E was 12 days. Survival time for C was three days.

origin. Both possess optic tracts which enter the tectum and divide into a small dorsal component which terminates at or just within the boundary of the marginal and external plexiform layers, and a major ventral component which terminates within the external plexiform layer. Both groups possess a central zone of bipolar neurons that extend into the external plexiform layer. Finally, both groups possess a retinofugal pathway that terminates in the deep white zone immediately above the cell bodies of the periventricular gray zone.

In summary, the visual systems of gars and teleosts are very similar in many respects, as might be expected from their phylogenetic relationship. The major differences between the two groups are (1) the relative development of the pretectal area, (2) the presence of ipsilateral retinofugal pathways, and (3) the apparent absence in gars of a ventrolateral deep periventricular visual projection to the tectum.

Comparison with non-actinopterygian vertebrates

It will not be possible to complete satisfactory comparisons of actinopterygian retinofugal projections with those of other vertebrates until we unravel the homologues of the actinopterygian medial optic tract and pretectal nuclei. In all other non-mammalian vertebrates examined, the lateral geniculate nuclei are located far rostrally in the thalamus and are the most rostral retinofugal thalamic targets to receive input. On this basis it is tempting to suggest that the rostral thalamic periventricular cell plate (figs. 2B, 3A), which receives retinal input via the medial optic tract, represents the homologue of the lateral geniculate nucleus. However, the medial visual pathway continues caudally to end in periventricular pretectal fields as well as the deep rostromedial periventricular tectal gray. Such a pathway has not been reported in other vertebrates (Riss and Jakway, '70; Ebbesson, '70a, '72). Certainly the caudal part of the pathway appears to have arisen *de novo* in actinopterygians and should be considered as a unique adaption in these forms.

If the rostral periventricular thalamic plate is considered as a possible homologue of the lateral geniculate nucleus of other

vertebrates, a second problem arises. Teleosts possess a well developed neural complex located just beneath the rostral pole of the optic tectum as seen in transverse sections. This complex has been divided into a lateral nucleus geniculatus lateralis and a medial nucleus rotundus (Schnitzlein, '62). As noted earlier, these nuclei in teleosts receive retinal input and topographically correspond to the cell complex termed the superficial pretectal nucleus in gars (figs. 3, 4). It is possible that both the gar superficial pretectal nucleus and the teleost nucleus geniculatus lateralis and nucleus rotundus correspond to a lateral pretectal nucleus such as nucleus geniculatus pretectalis of reptiles (Butler and Northcutt, '73). This reptilian pretectal nucleus receives both retinal and tectal inputs (Butler and Northcutt, '71a,b; Northcutt and Butler, '74a,b). These points have not been raised in an attempt to prove that the teleost nuclei termed lateral geniculate and rotundus cannot be the homologues of both similarly named nuclei in other vertebrates, but to point out that at our present state of knowledge regarding actinopterygian visual organization, these nuclei could just as reasonably be considered pretectal nuclei. We believe this is a real possibility and that only continued studies will unravel the diencephalic complexity of actinopterygians and allow comparisons with other vertebrates.

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