

GUITARFISH POSSESS IPSILATERAL AS WELL AS CONTRALATERAL RETINOFUGAL PROJECTIONS

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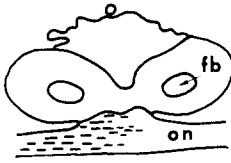
Autoradiographic analysis of the primary retinal projections in the thornback guitarfish reveals both contralateral and ipsilateral projections to diencephalic, pretectal, and tegmental nuclei and the optic tectum. A total of 12 retino-recipient cell groups receive ipsilateral as well as contralateral inputs.

To date, all studies using Fink–Heimer or autoradiographic methods in elasmobranch fishes have revealed only contralateral retinofugal projections, except for an ipsilateral projection to the rostral preoptic area [2–4, 7, 8]. Ebbesson and Meyer [2] recently reported that the retinal projections of a guitarfish, *Rhinobatos*, appear completely crossed, like those of sharks. However, this study employed only the Fink–Heimer method, which is not as sensitive as the more recently developed autoradiographic method, particularly in elasmobranch fishes.

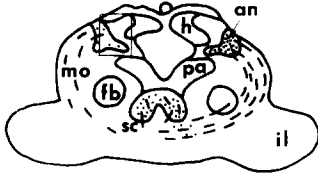
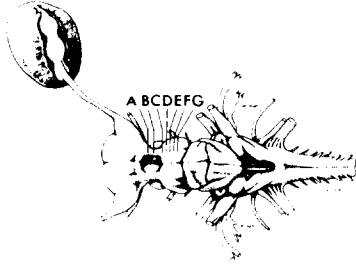
As part of an ongoing analysis of the visual system of the thornback guitarfish, *Platyrrhinoidis triseriata*, we examined the primary retinal projections using the autoradiographic method and here report that in the thornback there are 12 distinct retinal targets, and each of these neural populations receives ipsilateral as well as contralateral retinal inputs.

Six adult thornback guitarfish received intraocular injections of 50–100 μCi of [^3H]proline (50 $\mu\text{Ci}/\mu\text{l}$) under MS222 anesthesia and survived 4, 6, 8 or 10 days at 14–18°C before being reanesthetized and perfused with 0.7% saline followed by AFA. The brains were dehydrated, embedded in paraffin and sectioned in the transverse plane. Sections were coated with NTB-3 emulsion and exposed for 30–40 days at 7°C before development in Dektol and staining with cresyl violet.

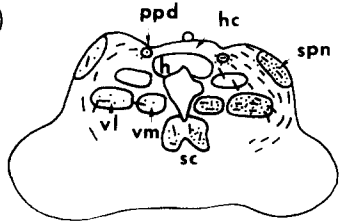
The majority (perhaps 90%) of the labeled optic nerve fibers decussate in the optic chiasm (Fig. 1A). As the fibers emerge from the chiasm a dense field of terminals occurs in the suprachiasmatic nucleus of the hypothalamus (Fig. 1B, C) whose cells are easily recognized extending ventrally into the caudal half of the chiasm to form paired tongue-like extensions of the preoptic area.



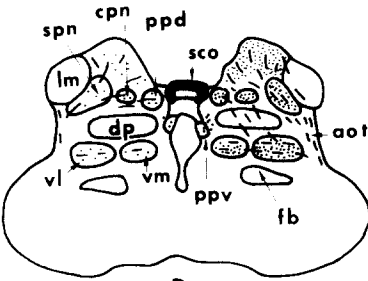
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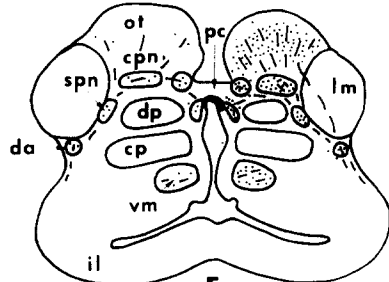
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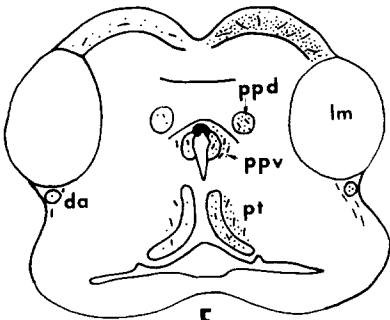
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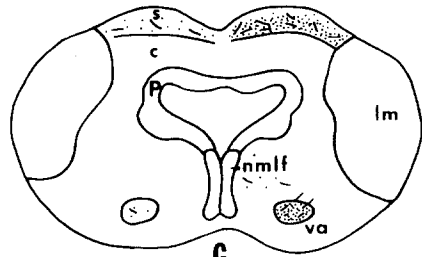
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E



F



G



The decussating optic fibers course laterally and dorsally, forming the marginal optic tract, with many of the optic fibers streaming through the forebrain bundles (Fig. 1B, C). The marginal optic tract first terminates in the rostral half of the dorsal thalamus, among the cell bodies of a densely packed plate of cells termed the anterior thalamic nucleus (Figs. 1B and 2B). More caudally, the anterior thalamic nucleus is replaced by a periventricular plate (pars ventralis) and a slightly migrated cell group (pars dorsalis) of the periventricular or deep pretectal nucleus (Fig. 1C–F); both parts of this nucleus receive a direct retinal input. At this same level (Fig. 1C), a new population of large neurons, embedded in the marginal optic tract, has previously been termed the superficial pretectal nucleus [7, 8].

Many fibers of the marginal optic tract turn medially at these levels (Fig. 1C–F) and course through the ventrolateral and ventromedial nuclei of the ventral thalamus. Both of these nuclei appear to receive retinal terminals; our autoradiographs reveal labeled fascicles, as well as dense grain puffs, scattered throughout both nuclei. A substantial number of the labeled optic fibers continue medially and caudally to terminate among the cells of the posterior tuber (Fig. 1F).

As the marginal optic tract courses toward the optic tectum, it divides into dorsal and ventral tracts which innervate the optic tectum. At this point of bifurcation of the marginal optic tract (Fig. 1D), a third pretectal nucleus, the central pretectal nucleus, is embedded among the optic fibers and receives retinal terminals. At the same level, the superficial pretectal nucleus is displaced medially by the rostral pole of the lateral mesencephalic nucleus (Fig. 1D) whose size rapidly increases caudally (Fig. 1E–G). This nuclear complex is extremely well developed in most batoids, its size restricting the lateromedial extent of the optic tectum in these fishes. Although a number of optic fibers course through the rostral pole of the lateral mesencephalic nucleus en route to the optic tectum, there is no evidence that this nucleus receives a direct retinal input.

An accessory optic tract (Fig. 1D) arises from the ventrocaudal edge of the marginal optic tract as the latter enters the optic tectum. This accessory tract first



Fig. 1. Charting of the primary retinofugal projections revealed by injection of [^3H]proline. A–G: transverse sections through the diencephalon and mesencephalon at levels indicated on the dorsal view of the brain. Stippling indicates terminal fields and dashed lines fibers of passage. Contralateral retinal projections are charted to the right and ipsilateral projections to the left. Bar scale equals 2 mm. An, anterior thalamic nucleus; aot, accessory optic tract; c, central tectal zone; cp, central posterior thalamic nucleus; cpn, central pretectal nucleus; da, dorsal accessory optic nucleus; dp, dorsal posterior thalamic nucleus; fb, forebrain bundles; h, habenular nuclei; hc, habenular commissure; il, inferior lobe; lm, lateral mesencephalic nucleus; mo, marginal optic tract; nmlf, nucleus of the medial longitudinal fasciculus; on, optic nerve; ot, optic tectum; p, periventricular tectal zone; pa, preoptic area; pc, posterior commissure; ppd, pars dorsalis of the periventricular pretectal nucleus; ppv, pars ventralis of the periventricular pretectal nucleus; pt, posterior tuber; s, superficial tectal zone; sc, suprachiasmatic nucleus; sco, subcommissural organ; spn, superficial pretectal nucleus; va, ventral accessory optic nucleus; vl, ventrolateral thalamic nucleus; vm, ventromedial thalamic nucleus.

terminates in a small cell group immediately ventral to the lateral mesencephalic nucleus (Fig. 1E, F) and termed by us the dorsal accessory optic nucleus; the accessory optic tract then continues caudally and medially to terminate in a much larger cell group (Fig. 1G) lateral to the nucleus of the medial longitudinal fasciculus and oculomotor nucleus. We term this cell group the ventral accessory optic nucleus.

Optic fibers entering the tectum do not course in its most superficial layer, as claimed by earlier descriptive studies [1], but enter in the deeper half of the superficial zone (Fig. 1F, G) where many turn dorsally to terminate more superficially.

Ipsilateral retinofugal fibers in the thornback guitarfish were observed in 5 of the 6 animals and were traced laterally into the marginal optic tract where they course throughout its entire mediolateral extent. Thus they do not form a single, compact fiber bundle. The ipsilateral anterior thalamic (Fig. 2A) and suprachiasmatic nuclei exhibit the highest density of ipsilateral terminals, but grain densities at least 3–4 times higher than background were observed ipsilaterally over all nuclei receiving contralateral retinal inputs. Ipsilateral optic fibers were seen in both the lateral and medial optic tracts, and the entire rostral half of the superficial tectal zone appears to receive an ipsilateral retinal input. Labeled fibers and terminals were not

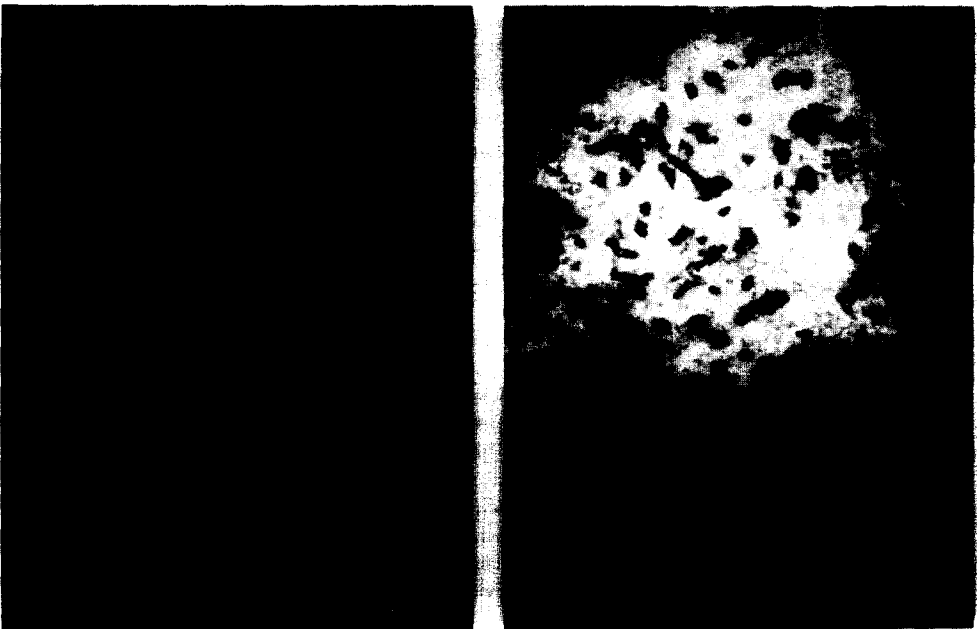


Fig. 2. Dark-field photomicrographs of ipsilateral (A) and contralateral (B) retinal projections to the anterior thalamic nucleus. Orientation and extent of photographed field indicated by rectangle in Fig. 1B. Bar scale equals 150 μm .

observed caudal to the tectal level charted in Fig. 1G. Thus it is possible that the ipsilateral retinotectal projection is restricted to the rostral half of the tectum as in many mammals. However, it is also possible that longer survival times may reveal a retinotectal projection to the caudal tectum.

We believe that the ipsilateral labeling is due to direct retinal projections rather than transneuronal transport because: (1) we can trace ipsilaterally labeled optic fibers directly from the labeled optic nerve, which would not be possible if labeling were due to transneuronal transport; (2) transneuronal transport has not been observed in ectotherms before 11 days survival [5, 6] at temperatures approximately twice those of our guitarfish; (3) if such transport were occurring, label should be obvious in tectal recipient nuclei that do not receive retinal input, and this is not apparent in our material; and (4) tecto-tectal transport via the tectal commissure would be restricted to the central tectal zone, whereas our material reveals labeled retinal inputs to the superficial zone.

The number of nuclei receiving retinal inputs in the thornback guitarfish complements that revealed by autoradiography in sharks [7, 8]. The retinal projection to the caudal ventral thalamus that one of us reported in *Squalus* [8] likely corresponds to the posterior tuberal target in the thornback guitarfish.

Differences in the results reported in these autoradiographic studies and earlier Fink–Heimer studies are due somewhat to the limitations of the latter method and are partly interpretational as regards the varying number of accessory optic nuclei recognized. Ebbesson and co-workers [2–4] recognized a single retino-recipient dorsal thalamic nucleus, which they believe runs the entire length of the thalamus, whereas we recognize two distinct nuclei (anterior thalamic and superficial pretectal nuclei). Preliminary data on the thalamotelencephalic projections in the thornback guitarfish [9] indicate that the anterior thalamic nucleus – and not the superficial pretectal nucleus – projects to the telencephalon.

All autoradiographic studies to date indicate the existence of an accessory or basal optic tract and nuclei, although these structures were not recognized in two of the three earlier Fink–Heimer studies [3, 4]. It is highly unlikely that these differences are due to species variation, and we believe that further autoradiographic studies will likely reveal well developed accessory optic pathways in most sharks.

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