The paths and destinations of the induced ipsilateral retinal projection in goldfish

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SUMMARY

Adult goldfish had one tectal lobe removed surgically, and several months later, the eye contralateral to the missing tectum was injected with radioactive proline. Radioautographs of the brains were studied to trace the paths and termination sites of the optic fibers.

The optic tract decussated at the chiasm, as normally, but then ran caudally in a large neuroma on the tectum-less side of the brain. Substantial numbers of fibers left this neuroma to enter two or more of five commissures, through which they recrossed the midline. These commissures: transverse, minor, horizontal, posterior and ansate, ordinarily contain few or no optic fibers. All are normally linked with the tectum. Negligible numbers of aberrant optic fibers recrossed the midline elsewhere. On the intact side of the brain, ipsilateral to the injected eye, the optic fibers innervated some or all of the nuclei and areas normally served by contralateral retinal fibers. An earlier behavioral study of these same fish had shown that some of them made reversed optokinetic nystagmus in response to stripe movement seen by the eye projecting ipsilaterally; others failed to respond to stimuli through this eye. In all the reversed responders, a caudal group of retinal projection sites was labeled ipsilaterally. This included the basal optic nucleus and the caudal portions of nucleus dorsolateralis thalami and area pretectalis. In the non-responders, these targets were not labeled ipsilaterally. Together, these results suggest that one or more of these three sites is or are responsible for optokinetic nystagmus in normal goldfish.

INTRODUCTION

In an earlier paper, we used behavioral and electrophysiological methods to demonstrate that adult goldfish could be induced surgically to develop reversed vision through one eye (Easter & Schmidt, 1977). We inferred that new functional connexions had been formed between the retina and visual nuclei on the embryologically incorrect ipsilateral side of the brain.

In this paper, we employ anatomical methods to trace the aberrant fibers
in the same fish. The eyes were injected with a radioactive amino acid and the brains prepared radioautographically (Grafstein, 1967; Neale, Neale & Agranoff, 1972). The fiber paths are interpreted for what they reveal of how regenerating fibers find their new, embryologically incorrect, destinations. The destinations are correlated with our earlier demonstration of visuomotor reversal, and interpreted to show which of the many visual nuclei are involved in optokinetic nystagmus.

**METHODS**

Goldfish (Carassius auratus, 'common' strain), 12–18 cm long tip to tip, were obtained commercially (Ozark Fisheries, Stoutland, Mo, U.S.A.) and maintained in filtered aerated aquaria at 20–25 °C.

Three surgical procedures, derived from Sharma (1973), were used. As they are described in detail elsewhere (Easter & Schmidt, 1977), they will only be briefly summarized here. The fish were anesthetized in a 0.1% solution of tricaine methanesulfonate and operated in air. The brain was exposed dorsally; the telencephalon and one tectal lobe were removed by aspiration, the optic tract to the missing tectum was freed from all its central connexions, and its central stump was positioned near the rostral pole of the ipsilateral tectum. This procedure is designated 'optic nerve transplant' and abbreviated, ONTP. Other animals received additional lesions at the same time, for reasons related to the earlier study. In some, the eye ipsilateral to the missing tectum was removed. These fish are designated 'optic nerve transplant-eye extirpated', and abbreviated, ONTP-EX. In other fish, half the retina from the eye ipsilateral to the missing tectum was removed surgically. These are designated 'optic nerve transplant-half retina extirpated', and abbreviated ONTP-HRX. In summary, all animals had one tectal lobe removed, and the optic nerve which ordinarily served it deflected ipsilaterally. The remaining tectal lobe was innervated by the normal contralateral eye (ONTT, N = 8), or received no contralateral retinal projection (ONTT-EX, N = 2), or received about half the normal complement of contralateral retinal fibers (ONTT-HRX, N = 3). Following surgery, the cranial opening was closed and the animals were returned to their tanks. All were studied with respect to visuomotor behavior and/or the retinotectal map, and the results of those studies are published elsewhere (Easter & Schmidt, 1977). Not all animals which contributed to the earlier report survived to be included here.

In eight other ONTP animals, we attempted to sever the postoptic commissures at 2–9 months after the ONTP surgery. The animals were anesthetized and the brain exposed dorsally. Then a microknife was inserted in the vicinity of the posterior commissure, blade away from the chiasm, and drawn caudally. These animals were not included in the earlier report.

After a delay of 2–15 months from the initial surgery, the eye connected to the deflected optic nerve was injected with 40 μl of 1-[2,3-3H]proline, 1 μCi/μl (New England Nuclear, Boston, Ma, U.S.A.). The animals were
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killed 2–3 days later, the cranium opened dorsally, and the heads fixed in Bouin's solution, dehydrated through ethanol, embedded in paraffin, and sectioned transversely or sagittally at 10 μm. Sections were mounted on glass slides, in some cases prestained with Luxol fast blue, and prepared for radioautography by a standard method (Kopriwa & Leblond, 1962). The slides were developed after 4–6 weeks and poststained with hematoxylin and eosin. Two normal fish ( uninjected) were also prepared, sectioned sagittally and horizontally, and stained with all three dyes.

The slides were examined under bright field and dark field illumination, and photographed through a 2.5 × objective onto 35 mm film (Kodak Photomicrography Monochrome Film, SO 410). All photographs were in bright field using red light (Kodak Wratten Filter 25). Under these conditions, the nuclei appear gray, the Luxol fast blue-stained myelinated fiber tracts darker gray, and the radioactive fibers black. None of the negatives or prints were retouched.

RESULTS

Neuroanatomy of normal goldfish

As goldfish neuroanatomy has not been summarized in any single reference, we begin with a summary of those aspects which will be directly relevant to our findings.

Sharma (1972a) has described the retinal projections of goldfish, and we follow his description, with three exceptions. First, his conclusion that all optic fibers projected contralaterally must be revised to read ‘most’ optic fibers, as it has recently been shown that some fibers do not cross at the chiasm, and others recross the midline through the posterior and minor commissures to terminate ipsilaterally (Springer & Landreth, 1977). Secondly, he omitted n. pretectalis, which others have described (Peter & Gill, 1975; Schnitzlein, 1962); we believe it is distinguishable and receives retinal fibers. Thirdly, he reported that there was no basal optic nucleus, but it has recently been identified in goldfish (R. G. Northcutt, personal communication), and receives retinal fibers. It is a small nucleus just lateral to the ventricle, ventral to the caudal extremity of n. dorsolateralis thalami.

The contralateral projections may thus be summarized as follows. The optic tract sends small medial fascicles which enter the minor commissure and project to one preoptic hypothalamic nucleus. The main optic tract continues caudolaterally to divide at n. rotundus into dorsomedial and ventrolateral branches. One group of four retinal targets, very near the rostral pole of the optic tectum, includes: n. rotundus, n. lateral geniculatus, n. corticalis and n. pretectalis. Somewhat more medial and ventral is a group of three retinal targets: area pretectalis, n. dorsolateralis thalami, and the basal optic nucleus. Most retinal fibers go to the optic tectum where they terminate in the external layers (Leghissa, 1955; Neale et al. 1972; Sharma, 1972a).
Six commissures: the transverse, minor, horizontal, posterior, intertectal and ansate, are believed to connect the tectum to structures on the other side of the midline (Ariens-Kappers, Huber & Crosby, 1967; Peter & Gill, 1975). The first four are illustrated at the midline in Fig. 1; the ansate is more caudal and the intertectal more dorsal, and are not shown. The horizontal commissure is the most readily identified because of its complicated course and relations, illustrated in Figs. 1–5. It crosses the midline slightly caudal to the transverse commissure (Figs. 1 and 5) and follows a course rather similar to the inverted handlebars on a racing bicycle. Immediately after crossing the midline, it turns to run caudolaterally (Figs. 2 and 5) to the level of n. glomerulosus (Figs. 2, 3 and 4) where it turns dorsally and loops around the nucleus. Soon after passing n. glomerulosus, it splits into two bundles, the more ventral of which heads toward n. rotundus, and is known as tractus rotundus (Figs. 2, 3 and 4). The more dorsal bundle becomes the superior part of the horizontal commissure and runs rostrolaterally to join the deep white layer of the tectum near its rostral pole (Figs. 3 and 4).

**Neuroanatomy of the experimental brains**

We shall describe animals from all groups together, as we noted no consistent intergroup differences.

**Extent of the lesions.** The lesions were all restricted to one side, apart from the missing telencephalon. In the thirteen fish with intact postoptic commissures, 90–100% of one tectal lobe had been removed. In the eight with sectioned postoptic commissures, only the rostral 30–05% of the tectum was gone. Damage to non-tectal areas was not so easily identified, owing to the presence of a large neuroma associated with the regenerated optic tract.

Our description of the paths and destinations is drawn from the thirteen animals with intact postoptic commissures. The other eight are described separately in a more restricted context.

**Paths of the optic fibers.** The optic fibers from the ‘deflected’ nerve crossed the midline at the chiasm, and entered the diencephalon in the optic tract on the contralateral (lesioned) side (Fig. 9). They formed a neuroma several

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**Figures 1–4**

Calibration line accompanying each set of figures: 500 μm.

Fig. 1. Sagittal section through a normal goldfish brain at the midline. Rostral to the right, dorsal upward in Figs. 1–4, 6–8. Hematoxylin, eosin and Luxol fast blue. No radioautography.

Fig. 2. Sagittal section through the same brain as in Fig. 1, 450 μm lateral to midline.

Fig. 3. Sagittal section through the same brain as in Figs. 1 and 2, 490 μm lateral to midline.

Fig. 4. Sagittal section through the same brain as in Figs. 1–3, 520 μm lateral to midline.
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hundred \( \mu m \) in diameter, as seen on the left in Fig. 11. This includes, but is much broader than, the space normally occupied by the transverse commissure. The neuroma attenuated caudally, until in some animals, at the level of the middle of the intact tectum, it disappeared. In other cases, it extended still more caudally, occupying the region of the descending tectal efferents (Ebbesson & Vanegas, 1976; Sligar & Voneida, 1976). In two cases, the labeled tract extended past the ansate commissure and was found in association with a pathway unknown to us as far caudally as our transverse sections went, i.e. well into the medulla.

Bundles of radioactive fibers originated from the neuroma and recrossed the midline predominantly in five commissures. The transverse and minor were labeled in all 13 animals, the horizontal in nine, the posterior in six, and the ansate in two. These numbers indicate that the more rostral commissures, those closest to the chiasm, were more frequently invaded. Only two animals showed fibers crossing elsewhere. In one, the intertectal commissure was lightly labeled. In the other, label appeared in a region of the ventral mesencephalon which did not correspond to any commissure known to us.

In all cases, the label could be traced through serial sections and was seen to follow the commissure in question. Figures 6–8 show one series of roughly sagittal sections to illustrate this point for the horizontal commissure, whose normal course and relations were described above. This brain was not stained with Luxol fast blue, so the tracts are darkened only by the silver grains. The optic chiasm and the three post chiasmatic commissures can all be identified in Fig. 6, which should be compared with Fig. 1. All are labeled. Figures 7 and 8 show more lateral sections; in Fig. 7, the ventral part of the horizontal commissure has been caught on its way caudolaterally, and the superior branch is shown over most of its length on the way from n. glomerulosus to the deep white layer of the tectum. Likewise, tractus rotundus is shown connecting to n. rotundus. In Fig. 8, several sections more laterally, the loop around n. glomerulosus is shown. These illustrations were all from the intact side of the brain.

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**Figures 5–8**

Fig. 5. Horizontal section through the brain of a normal goldfish. Rostral to the right. Hematoxylin, eosin and Luxol fast blue. No radioautography.

Fig. 6. Nearly sagittal section through the brain of an ONTP-EX goldfish. The plane of section was tilted slightly with respect to both the vertical and the transverse axes, but passed through the midline in the region of the postchiasmatic commissures. Hematoxylin and eosin. Radioautograph; labeled fibers appear black.

Fig. 7. Nearly sagittal section through the same brain as in Fig. 6, 450 \( \mu m \) lateral to midline, on the intact side of the brain. The dark band (lower left) is a fold in the emulsion.

Fig. 8. Nearly sagittal section through the same brain as in Figs. 6 and 7, 490 \( \mu m \) lateral to midline, on the intact side.
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brain. Sections through the lesioned side of this same brain showed a similar, symmetric labeled pathway.

The same pathway was charted in the brains cut transversely. An example appears in Fig. 11, through the n. glomerulosus, including the tractus rotundus and the superior and inferior parts of the horizontal commissure.

We emphasize that the optic fibers were quite selective in the pathways that they occupied. We have tried to make this point by describing where they were found; it is also instructive to consider where they were not found. Three fiber tracts which, because of their proximity to labeled fibers, might be expected to have been invaded, were not. First, the so-called tectocerebellar tract (Franz, 1912) shown in Figs. 3, 4 and 7, would seem to provide a natural conduit for fibers running caudally in the superior part of the horizontal commissure. Second, the habenular commissure (Peter & Gill, 1975) is only tens of μm dorsal and rostral to the posterior commissure; it might therefore be expected to receive optic fibers whenever the latter did. Third, the non-myelinated post-chiasmic commissures (subhorizontal, preinfundibular, and postinfundibular (Ariens-Kappers et al. 1967)) lay very near the myelinated ones, and near the optic chiasm. The absence of label in these three locations shows that the proximity of a pathway was not sufficient by itself to bring in aberrant fibers.

Once the fibers had recrossed the midline to the side ipsilateral to their retina of origin, they associated with the optic tract (ONTP, ONTP-HRX) or occupied its remains (OPTP-EX). Thus, the fibers which came through the horizontal commissure entered the dorsomedial branch (Fig. 7) from which many probably entered the dorsal tectum. In most cases, the foreign optic

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**Figures 9-11**

Fig. 9. Transverse section through the brain of an ONTP goldfish. Dorsal is up, the lesioned side to the right. The optic tracts have crossed, and the fibers from the radioactive eye have entered the (right) tract contralateral to the injected eye. Others pass through the transverse commissure. Hematoxylin, eosin and Luxol fast blue. Radioautograph.

Fig. 10. Transverse section through the brain of an ONTP goldfish, at roughly the same rostrocaudal level as in Fig. 9. Dorsal is up, the lesioned side to the right. This fish had had postoptic commissures sectioned just prior to injection of radioactive proline into the experimental eye. The experimental tract was labeled but unmyelinated, while the normal tract was myelinated but unlabeled at this level, therefore, they both appear nearly equally dark in this photograph. Note the build-up of label near the break and a few hundred μm lateral to it on the experimental side. Hematoxylin, eosin and Luxol fast blue. Radioautograph.

Fig. 11. Transverse section through the brain of an ONTP goldfish, about 1-5 mm caudal to the optic chiasm. Dorsal is up, the lesioned side to the left. Most of the labeled fibers from the contralateral eye are in the neuroma, but some have exited to occupy the three labeled tracts, which are heavily labeled on that side, less so on the intact side. The intact tectum is heavily labeled. Hematoxylin and eosin. Radioautograph.
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fibers remained fasciculated separately from the normal optic tract, and formed a separate but contiguous bundle.

**Commissural lesions.** We have suggested, from the pattern of label at the chiasm, that optic fibers first crossed to the side of the brain contralateral to their origin. If so, then all the radioactive fibers in the labeled commissures must have run from the tectumless side to the intact side. We tested the validity of this inference by cutting the commissures in eight other ONTP fish, 2–9 months after the initial surgery, by which time the aberrant projection had been formed. Immediately following the cut, the experimental eye was injected with \( ^{3}H \)proline, and the animals resuscitated. Several days later, they were killed, and radioautography was carried out. We anticipated that we would find a discontinuity of label at the site of the cut, with label on the side still connected to the retinal ganglion cell somata, and no label on the disconnected side.

The knife track was easily identified histologically by the clot and gliosis. Not all commissures were cut in all animals; briefly, eight commissures were sectioned completely, two partially. In all complete breaks, there was an abrupt discontinuity, with all the label on the side contralateral to the injected eye. The grain density was notably higher at the site of the cut than it was a short distance along the labeled tract, as shown in Fig. 10. This local build-up probably reflects a damming of the axoplasmic flow, and has been reported with \( ^{3}H \)leucine, catecholamines, and various enzymes (Dahlström, 1965; Heslop, 1975; Lubinska, Niemierko, Oderfeld-Nowak & Sware, 1964; Ochs & Johnson, 1969; Ochs & Ranish, 1969). The two partial sections showed label on both sides of the cut, but only on the tectumless side was there a local build-up. These results are inconsistent with the idea that optic fibers coursed in both directions. They ran exclusively from the tectumless side to the intact side.

We conclude that the fibers crossed at the chiasm and recrossed through two or more of five commissures, three of which (transverse, horizontal, and ansate) ordinarily contain no retinal fibers, and two of which (minor and posterior) ordinarily contain very considerably fewer than after the regrowth. All five of the commissures connect to the tectum.

**Termination sites of the optic fibers.** In this section, the terms, ‘ipsilateral’ and ‘contralateral’ are used with reference to the injected eye. We scanned the radioautograms in search of nuclei or areas with high grain density, and we assumed that these represented projection sites of the optic fibers. We recognize that the presence of fibers in a region is a necessary, although not sufficient, condition for the existence of synapses there.

The fibers projected predominantly to sites normally innervated by optic fibers.

The ipsilateral tectum was labeled in all fish (Figs. 7, 8, 11, 13–15), confirming Sharma (1973). The tectal layering in the optic fiber and external
plexiform layers was qualitatively normal, but in the ONTP animals, it was thicker, probably because of the abnormally high number of retinal fibers resulting from the binocular input. In some fish, the ipsilateral tectal label was patchy (Levine & Jacobson, 1975). In those animals which had remnants of the contralateral tectum, these remnants were labeled normally.

Of the non-tectal visual nuclei, the lateral group of four was labeled ipsilaterally in all fish. The nuclei were not readily discernible on the contralateral side, owing to the very high grain density overlying the neuroma. It is conceivable that this high grain density represented hyper-innervation of intact nuclei (Schneider, 1973; Sharma, 1973), but it may only have indicated a high density of fibers. The more medial group of three was labeled ipsilaterally in ten animals, unlabeled in three.

It should be possible to infer from this material and from the behavioral results (Easter & Schmidt, 1977) which of the visual nuclei is (or are) responsible for optokinetic nystagmus. We reason that the animals which made reversed optokinetic nystagmus should have that nucleus innervated ipsilaterally, normal responders should have it innervated contralaterally, and non-responders should not have it innervated on either side. We examined the radioautograms of ten reversed responders (five ONTP, three ONTP-HRX, and two ONTP-EX), and of three non-responders (ONTP). None of the thirteen responded normally. Since all animals, reversed- and non-responders alike, had ipsilateral projections to the tectum and the group of four, we conclude that these projection sites must not be involved in optokinetic nystagmus. This leaves the medial group of three as a more likely candidate. The rostral portions of area pretectalis and n. dorsolateralis thalami were labeled in all. The caudal extension of these two and the basal optic nucleus (all served by the same branch of the ventrolateral optic tract) were innervated ipsilaterally in all reversed responders, and in a few, contralaterally as well. They were not innervated on either side in the non-responders. We conclude that optokinetic nystagmus depends on the projection to one or more of them.

**DISCUSSION**

We have confirmed Sharma (1973) in our observation of the consistent innervation of the ipsilateral tectum. On the other hand, we have seen very little recrossing in the intertectal commissure, and a great deal elsewhere. We have confirmed Levine & Jacobson (1975) in noting that the tectum was frequently labeled non-uniformly, that fibers occasionally extended very far caudally into the medulla, and that they crossed the midline in the posterior commissure.

**Effects of different lesions.** The experimental surgery differed within and between the groups in two respects: the extent of the tectal lesions and the state of the other eye.
Although much of the lesioned tectum – the caudal portion – was still intact in some of the ONTP animals, all had extensive ipsilateral retinal projections. Even when contralateral tectal remnants existed, and were labeled, the ipsilateral projection was not restricted to the part corresponding to the region missing on the other side. This is different from the result in amphibians, in which only the fibers destined for the missing regions moved ipsilaterally (Meyer & Sperry, 1973; Udin, 1975). In an earlier electrophysiological study (Sharma, 1972b), in which similar lesions had been made in goldfish, fibers which normally terminated in the rostral tectum moved to positions in the remaining caudal half of the same lobe, thus compressing the entire contralateral projection. The ipsilateral tectum was not mapped in that study, but the results reported here suggest that a new ipsilateral retinotectal projection must also have been formed. If it was retinotopic, as seems likely (Easter & Schmidt, 1977; Sharma, 1973), the one eye would have two tectal projections; a compressed map contralaterally, and one with normal magnification ipsilaterally. It would be interesting to know which projection dominated the animal’s behavior.

Surprisingly, the completeness of the ipsilateral retinal projection from one eye did not seem to be affected by damage to the other eye. The fibers regenerated ipsilaterally even when the normal complement of contralateral fibers was in place. This confirms Sharma (1973) and has been found in amphibians also (Ingle, 1973; Meyer & Sperry, 1973; Misantone & Stelzner, 1974), but is quite different from the case in neonatal hamsters (Schneider, 1973). In the hamster, an extensive ipsilateral retinotectal projection was developed only when the contralateral eye had been removed at birth. Evidently, interfiber competition for terminal space is a more exclusive process in this species than in fish and amphibians.

Ipsilateral projection sites and reversed visuomotor behavior. In attempting to infer which of the retinal projection sites was responsible for optokinetic nystagmus, we have eliminated the tectum and one group of four nuclei because animals without reversed responses had ipsilateral fibers projecting to them. This group includes some pretectal nuclei which one of us had previously implicated in optokinetic nystagmus on the basis of an ablation study (Easter, Landreth & Northcutt, 1974). We now believe that the earlier conclusion was incorrect, probably because the ablations interrupted fibers to the more caudal group of three which was not known at that time. In support of our revision, we point out that induction of a reversed response is a more powerful tool in correlating anatomy and behavior than destruction of the normal response, because the former approach avoids the problem of fibers of passage.

The basal optic nucleus has been implicated in frogs as the retinal projection site through which optokinetic head nystagmus is mediated (Lazar, 1973). For that reason, we favor it as the most likely candidate of the three that we have suggested in goldfish. It is not homologous with the nucleus of the optic tract, the functionally analogous nucleus in rabbits (Collewijn, 1974, 1975a, b).
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Choice of pathways. Other workers have described the pathways taken by
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REFERENCES


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List of Abbreviations

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<tr>
<td>hor.comm.</td>
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<td>optic tract, norm: normal, exp. experimental</td>
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