

Research Reports

THE ROLE OF THE OPTIC TECTUM IN VARIOUS VISUALLY MEDIATED BEHAVIORS OF GOLDFISH

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SUMMARY

Five visually mediated behaviors were assessed following ablation of one or both lobes of the optic tectum in goldfish. Three of the behaviors disappeared following tectal ablations: optomotor response (swimming with the stripes in a rotating striped drum), food pellet localization and shadow-induced deceleration of respiration. Two of the behaviors persisted following tectal ablation: optokinetic nystagmus (movement of the eyes with the stripes in a rotating striped drum) and dorsal light reflex (tilting of the vertical axis toward the brighter of two laterally placed lights). The unexpected result that lesioned fish tracked the stripes with their eyes, but did not swim after them as normal fish did, suggests that the tectum serves a pre-motor function in addition to its sensory role. In addition, the results demonstrate that selected behaviors can be used to establish whether functional tectal or non-tectal connections are made by regenerating goldfish optic nerves.

INTRODUCTION

Over the past several decades, the regenerative powers of the visual systems of fish and amphibians have been extensively studied¹⁰. The earliest, simplest, and in some respects still the best method used to assess reestablishment of function was behavioral². The animal was presented with a visual stimulus at various times following section of the optic nerve, and the appearance of a response indicated that synaptic contacts had been reformed. Usually, the synapses were assumed to be in the tectum, the largest of the retinofugal projection sites. But many other areas also receive direct retinal input²³, and it is possible that some behaviors do not depend on the retino-tectal projection. The belief that different visual functions depend on different visual centers is well established in other species³.

Accordingly, we have assessed the role of the tectum in 5 visually mediated behaviors in goldfish. We have made lesions in one or both lobes and determined if the behaviors survived the lesions. In the succeeding paper, this information is used to study optic nerve regeneration in fish, both behaviorally and anatomically²⁶.

METHODS

Goldfish were obtained from Ozark Fisheries, Stoutland, Mo. and were maintained in filtered, aerated aquaria. The initial data on optokinetic nystagmus (OKN) and the dorsal light response (DLR) were obtained by S.S.E. on large goldfish (15–20 cm tip to tip) maintained at 20 °C. The data on the optomotor response (OPM), food pellet localization (FPL) and shadow-induced deceleration of respiration (SDR) were obtained by A.D.S. and B.W.A. on smaller fish (10–15 cm tip to tip) maintained at 30 °C.

Surgical procedures

The fish were anesthetized by immersion in an aqueous solution of tricaine methanesulfonate (250 mg/l), and all surgery was performed in air. The cranium was opened dorsally and a flap of bone reflected caudally. The intracranial fatty material overlying the brain was removed by aspiration to expose the optic tectum; one or both lobes were then removed by aspiration. Following this, a piece of gelfoam or surgical cotton was inserted inside the cranium, the flap returned to its original position and cemented in place with dental acrylic. For the smaller fish a flap of cranium was hinged rostrally by a three-sided cut and replaced following surgery. Any fish that evidenced abnormal swimming after surgery was discarded.

One or both eyes were removed under anesthesia, in some cases at the same time as the tectum. To temporarily blind fish, lidocaine hydrochloride (5–15 μ l of 1 or 2% solution, Elkins Sinn, Inc.) was injected intraocularly through a 30-gauge needle.

OKN

Eye movements were monitored with the aid of small polyethylene stalks attached by suction to the corneas; as the eyes moved so did the stalks. The horizontal eye movements of fish clamped in a sponge-lined holder inside a transparent, water-filled chamber were automatically followed with a flying spot scanner^{6,7}. OKN was elicited by rotating a striped cylindrical drum outside the fish's chamber. The drum was 1 m in diameter, with vertical black and white stripes which subtended about 7° at the center of the drum and rotated at speeds of 1–60°/sec in either direction. Normally, the drum was visible to the fish over 100° in the vertical plane and 280° horizontally. This field could be decreased by masking the outside of the fish's chamber. The drum was illuminated with room lights.

In some instances OKN was also examined in the drum used to evoke OPM (40 cm diameter, 9° stripes, 90°/sec velocity of rotation). Individual fish were clamped in a restraining device and centered in a transparent circular tank (29.5 mm diam. \times 10.5 mm high) suspended in the rotating cylinder by a central shaft and containing water at 20 °C. Stalks were attached to the eyes and eye movements were videotaped

from above, at 60 frames/sec. Eye positions were then taken (6 samples/sec) from the TV monitor during playback.

OPM

Individual fish were placed in the tank just described and were allowed to adapt to the apparatus for 2 min with the drum rotating. This was followed by the measured test, in which the total amount of time spent swimming with and against the stripes during a 3 min interval was recorded with timers. Then the direction of the drum was reversed, and a new 3 min test was scored.

FPL

In order to establish that FPL was visually mediated, we embedded some pellets in a clear vinyl plastic which isolated them chemically but not visually from the fish. Normal sighted fish snapped at the pellets; fish blinded by bilateral enucleation did not. The response is therefore visually mediated. This conclusion is supported by the results of the next paper²⁶ in which FPL disappears following optic nerve crush and reappears along with other visually mediated behaviors as the optic nerve regenerates its central connections.

When food pellets are tossed into the tank, normal fish either catch them as they sink or soon after they hit bottom. Typically, the pickup from the bottom was accomplished with the body nearly parallel to the floor. Fish blinded by bilateral enucleation never caught sinking pellets, but frequently picked them from the bottom while making apparently random foraging movements with their bodies nearly perpendicular to the tank floor. When our experimental animals captured pellets as the normals did, they were scored positively.

SDR

Fish were clamped in a foam restraining device inside a metal tank, and respiration was continuously monitored with a thermistor near the mouth¹⁸. A hand-held piece of opaque black plastic was slowly passed over the open box obscuring the light from a fluorescent ceiling fixture. Normal fish respond to the stimulus by breathing less frequently (Fig. 6A). The response was quantified by computing the percent respiratory deceleration; [respiratory rate during the stimulus—respiratory rate during a comparable interval immediately prior to the stimulus/prestimulus rate] \times 100. Each fish received only one stimulus presentation, since repetitive stimulation leads to temporary habituation.

DLR

When fish occupy an asymmetrical radiance field, they tilt toward the more luminous side²⁰. This is usually interpreted as an adaptive response which aids camouflage by keeping the animal's dorsal surface perpendicular to the brightest part of the radiance field, hence the name "dorsal light reflex". When one eye is blinded, either by removal, by lidocaine injection or by optic nerve crush, a goldfish tilts toward the sighted side, reflecting the imbalance of the two optic nerve signals. It is most evident immediately following surgery. The presence or absence of DLR was

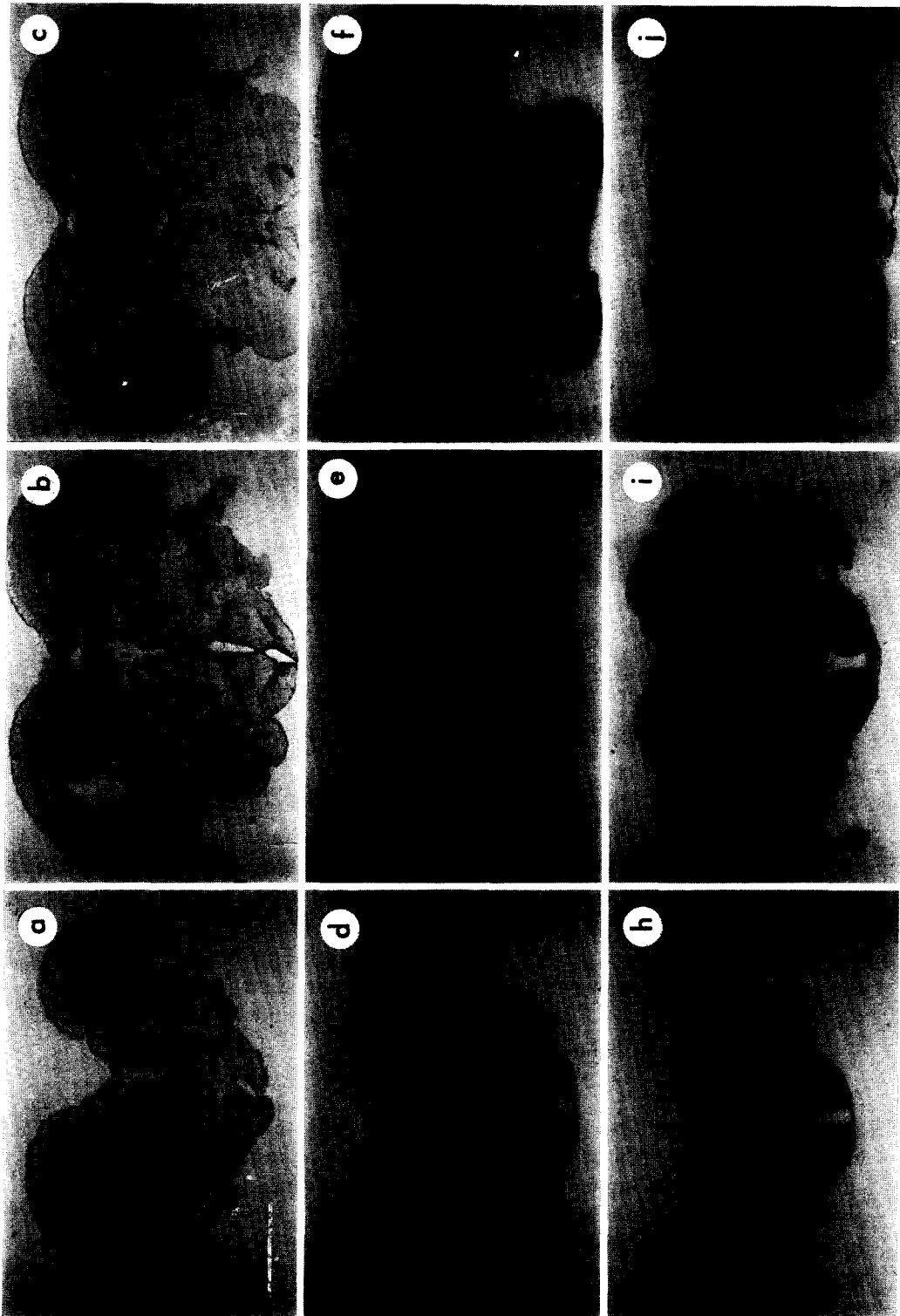


Fig. 1. Histology showing a normal goldfish tectum at rostral (a), midtectal (b) and caudal (c) levels. Unilateral tectal ablation at three different levels in d, e and f; bilateral tectal ablation in h, i and j. Scale 1 mm.

examined by simply observing the fish immediately following their recovery from anesthesia.

Histology

Most brains from ablation experiments were examined histologically with standard paraffin techniques. In some cases, one eye was injected with [^3H]proline several days before sacrifice²⁶. These brains were assessed radioautographically to assure that retinal projections to non-tectal sites had not been surgically interrupted²³, and that ipsilateral projections had not yet been established²⁴.

RESULTS

Extent of surgical lesions

Surgical lesions were examined histologically and were found to be quite complete. Fig. 1 shows 9 frontal sections throughout 3 comparable rostrocaudal levels of brains from 3 types of experiments: unoperated, unilateral and bilateral tectal ablations. The superficial portions of structures underlying the tectum were in some instances damaged. However, the extent and nature of this damage were highly variable between fish. Since the extent of the tectal ablations was uniform, and since the behavior indicated very little between-subject variability, we feel that the altered behavior of the fish reflected the absence of the tectum.

OKN

The role of the tectum in OKN was assessed in 8 large fish. First one eye was

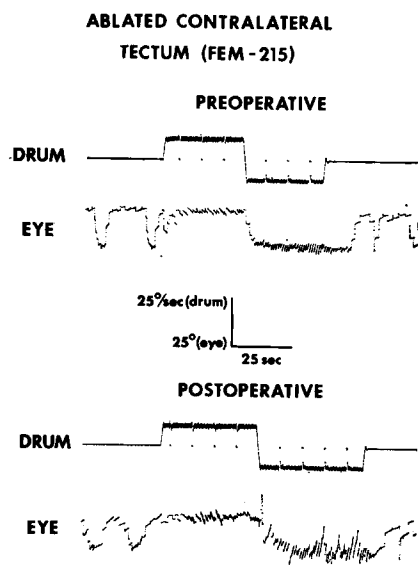


Fig. 2. Record of right eye movements before (above) and after (below) removal of the contralateral tectum; the left eye had been removed one week earlier. Drum: upward deflection of upper trace indicates counterclockwise rotation; downward, clockwise. Eye: angular orientation of right eye in the horizontal plane (lower trace); upward, counterclockwise; downward, clockwise.

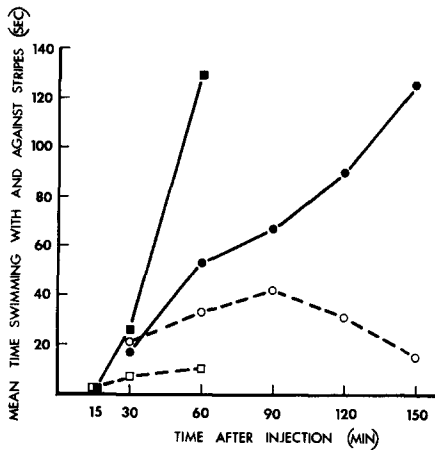


Fig. 3. Mean time swimming with (■—■) and against (□---□) the clockwise moving stripes following binocular injection of 5 μ l of 1% lidocaine ($n = 4$) and time swimming with (●—●) and against the stripes (○---○) following a binocular injection of 5 μ l of 2% lidocaine ($n = 4$). Each of the 8 fish was tested repeatedly at each time point.

removed (4 left, 4 right), and after a week for recovery, the OKN made by the remaining eye was recorded. A typical record, shown in the upper half of Fig. 2, is completely normal^{6,7}. The ipsilateral tectum was then ablated, and the 7 surviving fish were tested for OKN 11 days later. This interval was chosen to allow sufficient time for recovery from the incidental surgical trauma, but not for generation of connections to the ipsilateral tectum²⁴. All 7 fish responded normally to the rotation of the striped drum as shown in the lower half of Fig. 2. Since we anticipated that the ablation might have spared the anterior pole of the tectum, which serves the anterior visual field^{12,22}, we masked this region and found that a normal OKN was also elicited by drum movement seen only in the temporal and lateral fields alone.

Six of these fish survived two additional days, at which time the remaining eye was injected with [³H]proline, then sacrificed 2 days later, and the brains prepared for radioautography. Of the 6 fish, 4 had no tectum remaining on the experimental side, while the other two had small fragments on the anterior pole. The tectum ipsilateral to the remaining eye was not labeled. All of the non-tectal nuclei on the contralateral side which normally receive input from the retina were labeled. The surgery had therefore selectively removed the tectum without interfering with other retinal projections, nor had any new ones developed. In smaller fish maintained at 30 °C, ipsilateral projections are formed within 2 weeks after surgery.

In a separate experiment, we removed both lobes of the tectum in 9 smaller fish and left both eyes intact. Upon testing 1 week later all fish made OKN. The histology confirmed that the ablations had been complete.

OPM

The investigation of OPM employed tectal lesions, eye removal and temporary blinding by intraocular injection of lidocaine. The time course of the lidocaine-

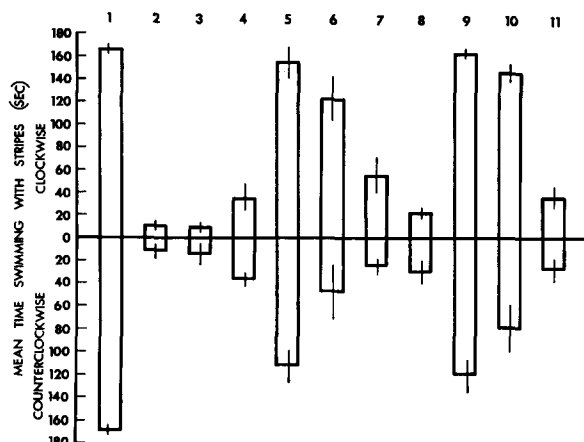


Fig. 4. Mean time swimming with the clockwise or counterclockwise moving stripes. 1, normal fish ($n = 5$); 2, normal fish with still stripes ($n = 5$); 3, normal fish that received a binocular injection of lidocaine ($n = 5$); 4, bilateral enucleation ($n = 5$); 5, right eye removed ($n = 5$); 6, right eye removed and caudal half of right tectum ablated ($n = 5$); 7, right eye removed and rostral pole of left tectum remaining ($n = 5$); 8, both eyes intact and both tecta completely ablated ($n = 9$); 9, left tectum ablated and both eyes intact ($n = 5$); 10, group 9 with lidocaine in the right eye; 11, group 9 with lidocaine in the left eye. Standard errors of means are indicated.

induced blindness and the effects of two different doses are presented in Fig. 3. Injections took effect within 5 min and the blindness lasted from 15 to 30 min, depending on the dose. These results were confirmed using OKN. In addition, lidocaine injection was found to abolish the b-wave of the electroretinogram, a sensitive retinal indicator of post-receptoral activity³. Systemic effects of lidocaine were ruled out by experiments described below.

Fig. 4 gives the results of our investigations of the role of the tectum in OPM. The principal findings are contained in columns 1, 4, 8 and 11. Normal fish swam with the stripes more than 160 of the 180 sec (column 1). These same fish, following bilateral enucleation, swam with the stripes less than 40 of the 180 sec (column 4). Fish with eyes and non-tectal centers intact, but with both tecta removed, responded like the bilateral enucleates (column 8); loss of tectum was equivalent to loss of eyes. Fish with one tectal lobe intact, the other missing, and the eye contralateral to the intact lobe blinded by lidocaine, responded like the enucleates (column 11). Thus, the presence of a tectal lobe was not sufficient to mediate OPM; a functional retinotectal projection was necessary.

The results in Fig. 4 are now described in more detail. Column 1 illustrates normal behavior with the drum moving. Column 2 shows the diminished circling behavior when the drum was stationary, which indicates that the moving stripes elicited the unidirectional swimming response. Column 3 illustrates the blinding effects of lidocaine, with results similar to those obtained by bilateral enucleation (column 4).

The effects of unilateral lesions are shown in columns 5, 9, 10 and 11. In column 5, the right eye had been removed, and the animals responded to both directions of

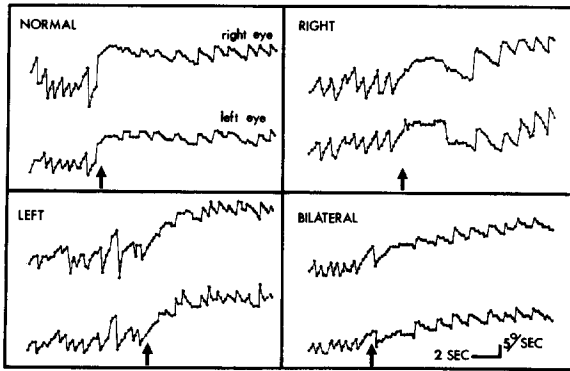


Fig. 5. Representative OKN from videotape playback in normal fish, fish with both eyes intact and right tectum ablated, fish with both eyes intact and left tectum ablated and fish with both eyes intact and both tecta completely ablated. Stripes were moving clockwise to the left of the arrow and counter-clockwise to the right of the arrow.

rotation. The movement of the stripes from rear to front (clockwise movement seen by the left eye) was the more effective, in keeping with results from other animals^{4,7}. Column 9 shows results from animals with both eyes intact, but the left tectum ablated. The directional asymmetry of the response is like that of column 5, supporting the notion that eye and contralateral tectum are equally important in this behavior. These same fish received injections of lidocaine into the right eye, and continued to respond (column 10), supporting the idea that the retinal projection is of no use if it has no tectum to report to. In column 11, both retinofugal pathways were inactivated, and the response disappeared.

Columns 6 and 7 show the effects of partial tectal lesions. When the caudal half of the right tectum and right eye were removed, the response was unaffected (column 6), but when the caudal three-quarters were removed, the response was severely diminished, yet still present (column 7).

We conclude that OPM is dependent on the existence of one functional retino-tectal pathway. It was not sufficient, as it was with OKN, to have intact and functional pathways from the retina to non-tectal visual nuclei. This difference in the neural requirements of the two quite similar behaviors might be doubted on the grounds that the two responses were assessed in different drums on fish of different sizes, maintained at different temperatures. Therefore, we tested OKN in the OPM drum using small, warm fish with intact brains or with unilateral or bilateral tectal ablations. Fig. 5 shows the records obtained from analysis of the playback of the videotape. OKN was normal, even at the higher velocity in the smaller drum.

FPL

This behavior was assessed on many of the same fish included in Fig. 4. Normal fish, those with one retinotectal pathway intact and those with partial tectal lesions all showed the behavior. In contrast, fish with bilateral tectal ablations did not, even when the plastic pellets were left in the tank for 15 min. These fish also failed to detect the pellets after swimming near them. It is therefore unlikely that the ob-

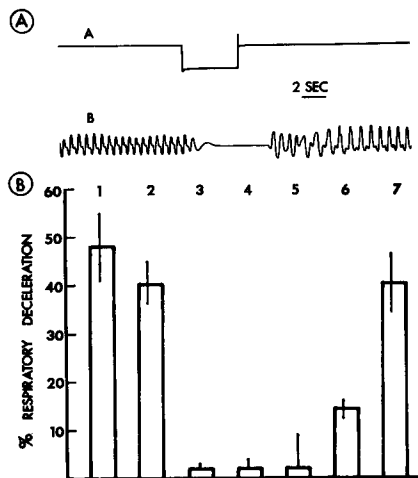


Fig. 6. A: shadow-induced respiratory deceleration produced by passing a black piece of plastic (A_A) over a fish; A_B, respiration recorded by a thermistor placed near the mouth of a fish. Deceleration ensues shortly after shadow onset and persists for several seconds after the normal stimulus condition has returned. B: percent respiratory deceleration produced by moving shadow in normal fish (column 1; n = 17); one eye and contralateral tectum removed (column 2; n = 12); both eyes removed (column 3; n = 15); ipsilateral eye and tectum removed (column 4; n = 12); both eyes intact and both tectal lobes ablated (column 5; n = 5); right eye removed and rostral quarter of right tectum remaining (column 6; n = 6); right eye removed and caudal half tectum ablated (column 7; n = 5).

served results can be explained by an increased threshold for, rather than by a loss of FPL. We conclude that, as with OPM, the ability to localize food using visual cues also depended upon the tectum.

SDR

The effects of tectal lesions on SDR are given in Fig. 6. Fig. 6A shows a sample record; Fig. 6B summarizes the responses of several experimental groups. A marked deceleration is seen in normal fish (column 1). Fish with one eye removed show a similar response (column 2), while fish with both eyes removed (column 3) did not, which rules out non-retinal photoreceptors as the detectors⁵. Fish with an ipsilateral eye and tectum removed (column 4) did not respond, which shows that the projection from retina to contralateral tectum is essential. When both tectal lobes were removed, but both eyes left intact, the fish failed to respond to the stimulus (column 5). Partial tectal ablations that spared the rostral fourth of the tectum attenuated the response (column 6), while lesions which spared the rostral half tectum did not (column 7). Thus, SDR also depended on the integrity of at least part of the retinotectal pathway, much like OPM and FPL.

DLR

Following unilateral tectal ablation and recovery from anesthesia, the fish did not tilt in the direction of the control (ipsilateral) eye. When the ipsilateral eye and tectum were removed, the fish did tilt toward the side with the eye. Eye removal eliminates retinal input to the pretectal nuclei, as well as to the tectum, while tectal ablation

does not interfere with retinal input to pretectal nuclei. Thus, the tectum does not appear to play a major role in DLR. These results do not exclude the possibility that some tilting occurred following tectal ablation, since only qualitative assessments of DLR were made.

DISCUSSION

In studies of the visual system in which visual function is secondary to anatomical and electrophysiological considerations, there may be a tendency to view the ability of the animal to see on a single continuum from full vision to blindness. Consideration of findings in a number of animal studies suggests otherwise since selective lesions can effect one visual function with little effect on another²¹.

The present finding, that OPM in the goldfish depends upon an intact tectum while OKN does not, was unexpected. Both OPM and OKN are elicited by the same stimulus and both responses serve to reduce movement of the retinal image. Despite the presumably identical function of the two responses, it appears that pursuit by swimming (OPM), unlike pursuit by eyes (OKN), is mediated by the tectum. That the tectum is a pre-motor center for OPM, in addition to being a primary sensory center is not surprising. Direct stimulation of the tectum is known to elicit head turning in trout¹ and codfish¹⁶, and it is generally believed to be a major integrating center in these animals²⁷.

Apparently OKN is not dependent upon the tectum, but must derive from visual signals to one or more of the other retinal projection sites. It could be argued from these results that OKN is not dependent upon a specific set of retinofugal connections, but upon the existence of some minimum number of connections from retina to anywhere in the brain. This alternative was ruled out by another set of experiments⁸ in which we left the tectum intact and made small lesions in the brain stem. Fish with such lesions did not make OKN which suggests that OKN requires relatively few, but specific, functional connections between retina and brain. This conclusion raises the question of whether the tectum by itself can mediate OPM, or whether the tectum and brain stem sensory nuclei are both necessary.

Our finding that OKN survived tectal ablation agrees with other reports in two mammals: rabbit⁴ and monkey¹⁹. Our other result, that OPM did not survive tectal ablation, is consistent with an early report in fish²⁵, but seems inconsistent with two previous reports on amphibians. Lazar¹³ worked with adult frogs and found that horizontal head nystagmus in response to rotation of a striped drum survived tectal ablation. Mark and Feldman¹⁴ used larval frogs and found that when the drum moved the tail bent in the direction of rotation, without altering the relative movement between the animal and the drum. In one frog, this response was still observed following tectal ablation. Neither of these responses constituted OPM as defined in the present study since neither led to a displacement of the whole animal with respect to the stripes.

The dependence of FPL on an intact tectum is consistent with results obtained from hamsters²¹ and frogs^{11,17}, in which it was essential for localization and acquisition of small objects.

Conditioned deceleration of heart rate²² or respiratory rate²⁸ has been obtained with visual stimuli that differed from the one we used in producing SDR. In these experiments, the tectum seemed to play a role as it does in SDR.

DLR does not depend upon the tectum and may perhaps require the integrity of the same brain stem sensory nuclei that mediate OKN. The preliminary finding that tectal ablation abolished DLR in the catfish¹⁵ may be attributable to species differences.

Partial tectal ablations failed to abolish the tectally mediated responses. Since, in all cases, the caudal tectum had been removed, these results argue against a significant role for the caudal tectal structures in OPM, SDR or FPL. This is an important exclusion, in view of the existence of large efferent tracts that exit the caudal-lateral tectal border in teleosts⁹, which might have been implicated in the ultimate transmission of information leading to OPM. In addition, these data suggest that tectal regions may be equipotential for mediation of these behaviors and that function is unimpaired as long as some minimum amount of tissue remains.

In summary, we have shown that the optic tectum is essential to performance of 3 of 5 behaviors studied. These results suggest that selected visually mediated behaviors can be used to determine when and whether a goldfish optic nerve has formed functional connections to a specific brain structure. In the following paper, restoration of several of these behaviors following optic nerve regeneration in goldfish is examined and correlated with the growth of optic nerve fibers into the tectum.

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