The Optic Tectum

David Northmore

Department of Psychology
University of Delaware
Newark, Delaware 19716, USA

northmor@udel.edu
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Glossary

Motoneurons
Neurons in the central nervous system that send their axons to muscles, controlling their contraction.

Plasticity of neural connections
The alteration of synaptic connections. Injury to neurons, especially in fishes, prompts regeneration of axons which may grow into normal and abnormal target areas. Developmental and learning processes involve changes in synaptic arrangement and efficacy.

Receptive field
Region of retina or visual field within which stimulation alters the activity of a neuron. An electrode that picks up multiunit activity has a multiunit receptive field (MURF).

Reticular formation
Diffusely organized neuronal groups around the core of the midbrain and brainstem involved in a wide variety of functions. Most relevant function here is as premotor intermediary between tectum and motoneurons.

Retinal ganglion cells
The output neurons of the retina. Their axons, called optic fibers, terminate in tectum and nuclei of the preoptic-thalamic-pretectal (PTP) area.

Retinotopic map, organization or projection
Found in brain areas, like tectum, that receive a spatially ordered set of input fibers from retina, thereby forming a representation of the retina, and the visual field of the eye. A particular case of 'Topographic map'. The retinotectal map is an instance.

Tectal layers in teleosts- listed from outermost to innermost
SM  Stratum marginale
SO  Stratum opticum
SFGS  Stratum fibrosum et griseum superficiale
SGC  Stratum griseum centrale
SAC  Stratum album centrale
SPV  Stratum periventriculare
**Topographic map, organization or projection**

Found in brain areas that receives a spatially ordered set of input fibers from another brain structure e.g. the connections from tectum to nucleus isthmi (NI).

**Visual looming**

The pattern of motion on the retina created by approaching objects. A symmetrical expansion of the retinal image presages collision.

**Abstract**

The optic tectum forms the roof of the midbrain and is the primary visual center in fishes. The retina and input from other sensory modalities (auditory, lateral line, somatosensory, electrosensory) are mapped topographically over tectum, where the locations of objects and events in body-centered space are represented. Tectum, via its connections to premotor centers, controls eye movements, approach and avoidance movements. In teleosts especially, tectum is a highly developed neural processor, indispensible for the sensory discrimination and rapid decisions required for behavioral reactions necessary for survival and reproduction. Its function is discussed in relation to afferent and efferent brain structures.
Introduction

Looking down upon the brain of a sunfish, the optic tectum appears as a pair of rounded lobes between the forebrain and the cerebellum (Fig. 1). A side view shows how the optic nerves from the eyes cross over one another, becoming the optic tracts, each of which enters the front of its corresponding tectal lobe. This simple anatomical examination shows that the information from each eye travels directly to the tectal lobe on the opposite side. Indeed the great majority of the optic nerve fibers, the axons of retinal ganglion cells, terminate in the tectum, making it the primary visual center in the brain.

This review focuses on the functional aspects of tectum - its role as an information processor and controller of behavior - bearing in mind that the view presented will be limited in scope. There are more than 25,000 fish species occurring in widely diverse forms and in every aquatic habitat. While the optic tectum is present in all species, it is developed to different extents. Our knowledge of tectal function derives almost entirely from a handful of teleost species, mainly perciforms, like the sunfish, or cyprinids like...
the goldfish, with much less information available on elasmobranchs, the cartilaginous fishes. To fill some of the gaps in our understanding we must also look at tectum in other vertebrate groups.

The importance of tectum to a teleost fish can be shown by damaging it. Complete ablation renders the animal effectively blind. However, a partial ablation or localized lesion of one tectal lobe produces a loss of responsiveness to visual stimuli over part of the visual field of the opposite eye, showing that visual space is mapped topographically across the tectum. Damage to the tectum in teleosts also results in losses that go beyond blindness, being impaired in their ability to navigate the environment using non-visual senses, bumping into objects in a way that eyeless fish would not because the tectum serves other sensory modalities besides vision. In other vertebrate species, it is known that the tectum, or the mammalian equivalent, the superior colliculus, contains neurons that respond to sound and touch. Animals with exotic senses like infra-red sensitivity (e.g. rattlesnakes) and electroreception (e.g. skates and rays) possess tectal neurons that respond to these modalities too. Fishes have a well developed system of sensitive mechanoreceptors, the lateral line organs, that detect minute water currents, enabling them to localize prey, avoid objects, and school with other fish. This valuable source of spatial information underwater is almost certainly represented in tectum too, but like many aspects of tectal function in fishes has not been investigated.

The varieties of sensory information converging upon the tectum may evoke behavioral responses via its efferent connections to motor centers of the reticular formation. The tectum, in conjunction with other brain areas integrates sensory signals of different modalities, and in ways not yet understood, arrives at a decision to react positively with orientation and approach, negatively with avoidance, or not to react at all.
Figure 2. Laminar structure of teleost tectum, showing layer nomenclature and a few representative cell types. Roman numerals are Meek's types. Colored bands show principal termination layers of different inputs to tectum.

Anatomical overview

The tectum, the Latin for roof, covers the midbrain. In teleost fishes it is a twin-lobed canopy of neural tissue inflated over a fluid-filled ventricle. The two lobes are connected at the midline by the tectal commissure, and at their bottom edges merge with the tegmentum, the floor of the midbrain (see Fig. 4 B). A well-developed tectum in a highly visual teleost may be 0.8 mm thick with a clearly layered appearance when examined under the microscope. The layering scheme shown in Fig. 2 represents the most common interpretation of tectal structure (see Glossary for the Latin names of the 6 layers). Functionally, the most important distinction is between the superficial layers (SM, SO, and SFGS) which are mainly visual, and the deep layers (SGC, SAC and SPV) which are multimodal and motor. Some layers contain many fibers (SM, SO, SAC), others contain some neuronal cell bodies, fibers and synapses (SFGS, SGC), while the innermost layer (SPV) is composed of densely packed neuronal cell bodies. Some 15 morphologically distinct neuron types have been described in goldfish, a few of which are illustrated in Fig. 2. In elasmobranch fishes, the tectum is less prominent than it is in a typical teleost, being smaller than the telencephalon or cerebellum, and its structure is less well differentiated into distinct cell types and layers. Nevertheless, the same functional distinction between superficial and deep layers seems to apply as it does in teleosts.
Dominant among the neural connections with tectum are the optic fibers coming from the retinas, but tectum is also richly interconnected with many other brain structures. These include (a) 'upstream' structures, the telencephalon and the preoptic, thalamic and pretectal (PTP) areas, (b) midbrain structures, notably the opposite tectal lobe, the torus longitudinalis (TL), nucleus isthmi (NI), torus semicircularis (TS) and (c) 'downstream' structures: the reticular nuclei of the midbrain and brain stem that interface with motor systems. The following sections deal with these structures as part of functional subsystems in which tectum plays a central role.

Figure 3

The retinotectal projection and visual processing

The retinotectal map
Anatomical fiber tracing methods show that the great majority of the optic nerve fibers from one eye cross the midline, enter the opposite lobe of the tectum and form terminal branches within certain tectal layers where they synapse upon tectal neurons. Optic terminals are densest in the SFGS and SO, with some being found in deeper layers, and are distributed in an orderly fashion over tectum so as to make a map of the retina. This retinotectal map is organized so that the front, back, top and bottom of the visual field seen by one eye is represented at the front, back, top and bottom of the opposite tectal lobe.
The retinotectal map can also be investigated by electrophysiological recordings from tectum. A microelectrode inserted into the superficial layers of tectum (principally SFGS) picks up spiking activity that is briskly evoked by visual stimulation in a particular region of the visual field of the opposite eye called the receptive field. The receptive field is usually delineated by flashing small spots of light or moving objects against a contrasting background. Figure 3A shows the roughly circular receptive fields from each of a number of electrode penetrations in the tectum of a sunfish. In this animal, the receptive fields are of fairly similar size and each part of the visual field is represented by a roughly equal area of tectal surface. Thus, the tectum in sunfish, as in goldfish, receives a uniform representation of the entire visual scene. Some species, like the rock basses, have retinas with a fovea, a region of high photoreceptor and ganglion cell density positioned in the eye for detailed forward vision. In these fish, the part of the retinotectal map corresponding to the fovea exhibits smaller receptive fields and a five-fold magnification of frontal vision compared to the rest of the visual field (see Fig. 3B).

**Retinotectal map development and plasticity**

The formation of the retinotectal map during development is of great interest because it provides a model for how ordered connections develop in brains generally. The retinotectal system of fishes has been a fertile field of research since the 1940's when R.W. Sperry, taking advantage of the discovery that optic nerves in fish and amphibians regenerate when severed, showed that optic axons grow back into the tectum restoring the retinotectal map, along with apparently normal visual behaviors. The Chemoaffinity Theory that Sperry propounded, held that individual optic fibers are labeled chemically and grow into tectum to terminate on correspondingly labeled tectal neurons. Much research has since been devoted to discovering the molecular and genetic bases for chemoaffinity underlying path-finding and synapse formation in the retinotectal system (see Further Reading refs. 3 & 16). The facility with which optic axons regrow, and the remarkable neural plasticity that their terminals exhibit within tectum is part and parcel of the continual growth that fish undergo throughout life. Indeed, plasticity is essential to maintain a regular retinotectal map in the face of different patterns of growth in retina and tectum - the retina grows by addition of cells at its circumference whereas the tectum grows by elongation. Of special relevance to this review is that plasticity of the retinotectal projection when experimentally manipulated can provide fresh opportunities to understand tectal function.

**Visual processing in tectum**

In the retinotectal mapping experiments of the kind shown in Fig. 3, the spiking activity picked up by an extracellular micro electrode in superficial tectum (SO, SFGS) is not generally resolvable into action potentials of constant waveform that would be indicative of the firing of an individual neuron (or 'single unit'), but instead consists of bursts of action potentials of different amplitudes called multiunit activity. It is evoked by stimuli, such as small spots of light flashed on or off, in roughly circular areas (5-10 degrees across in goldfish) termed the multiunit receptive field (MURF). This activity used to be thought to come from the terminals of optic fibers. However, it can be largely eliminated
by drugs that block synapses suggesting that it comes from the dendrites of tectal cells where optic fibers make synapses.

Microelectrodes may also pick up action potentials indicative of individual neurons in tectum. If such units are visually responsive, their receptive fields generally differ from the relatively small, retinotopically ordered MURFs of superficial tectum, instead taking a bewildering variety of forms. In the various cyprinid and perciform species investigated, tectal cell receptive fields probed with flashed or moving spots of light vary greatly in size, ranging from roughly circular fields 2-5 degrees across to complex fields extending some 160 degrees. The latter may have elongated or irregular shapes, with multiple subregions with differing stimulus preferences, such as the onset or offset of light. Experiments that scan spots of light across receptive fields have shown spikes being elicited from band-shaped regions of space, suggesting that these cells may be selective for complex shapes, perhaps the body markings of conspecifics. While most tectal cell receptive fields are centered appropriately with respect to the retinotectal map, a high proportion (22% in yellow perch) are displaced 45 degrees or more, showing that tectal neurons can perform a large-scale integration of visual pattern.

In the foregoing observations, the cell types being recorded from were unidentified. A few studies recording with intracellular micropipettes have allowed the tectal cells to be stained for identification, but only the simplest characterizations of visual trigger properties have been made, adding little to our understanding of processing by tectum. The properties of some of the identified cells types shown in Fig. 2 will be dealt with in subsequent sections on tectal subsystems. In summary, most tectal cell types respond in some way to light flashes or movement, typically with large receptive fields. Perhaps significant too, is that their firing patterns to light stimuli are temporally complex, exhibiting successive periods of excitation and inhibition.

Answers as to how location, motion, color and shape are processed by the tectum are not to be had from gross lesions of tectum as these have a profoundly blinding effect. Happily, the plasticity of the retinotectal system allows more subtle interventions to be made, throwing some new light on tectal processing. When optic nerve fibers are severed by crushing, they grow back into the tectum and eventually reform a correctly oriented retinotectal map with nearly normal MURFs. The ability of a sunfish to localize a brief light flash by orienting to it is fully restored, at least where visual space is represented by an orderly retinotectal map; where space is represented by a disorderly map as a result of regenerating optic fibers going astray, orientation movements are misdirected. Map orderliness is also important to pattern processing because after optic nerve regeneration, when optic terminals are disorganized and sparser than normal, fish can discriminate coarse bar patterns, but not the fine patterns that they can normally discriminate.

The ability of goldfish to discriminate colors is also restored, apparently to normal, after optic nerve regeneration but this observation alone does not mean that tectum is involved - the PTP nuclei (see below) also receive regenerated optic fibers that could be responsible. However, recordings of tectal activity strongly suggest that tectum is involved in color processing because its neuronal responses evoked by different
wavelengths of light cannot be reproduced by varying the intensity of a single wavelength, as would be the case in a colorblind system. Torus longitudinalis (see below), which is closely interconnected with tectum, is such a colorblind system. Moreover, some tectal cells can be excited by one range of wavelengths while being inhibited by another. Such qualitative response differences indicate a color discriminating system. As in mammalian visual cortex, color processing is likely bound up with pattern and shape processing.

Motion is an important stimulus parameter for exciting tectal neurons in all vertebrates studied. In fish, recordings of neuronal activity in tectum have demonstrated directional preferences: activity is evoked most vigorously by a visual stimulus moving in one direction through a receptive field compared to all other directions tested. Most of the data suggest that directional selectivity is elaborated in tectum, although retinal units may exhibit it also. Visual motion is a valuable source of information assisting the detection and recognition of objects and providing cues to depth, as will be seen in the discussion of the tectum-nucleus isthmi system.

Because the fields of view of the two eyes overlap in the front, some of frontal space is represented in both tectal lobes. A small number of optic fibers serving this part of the visual field, appropriately enough, do not cross over, but terminate in frontal tectum on the same side. This arrangement suggests that the tectum should be able to process images binocularly to help determine the distance of objects like prey, which fish have been shown to do. Neurons that can be driven via either eye, have been found in the tectum of goldfish and trout, but their large and diffuse receptive fields seem unsuited to the demands of stereoscopic depth perception.

From what is known about visual processing in the fish tectum, it seems clear that it does not work in the hierarchical fashion of mammalian visual cortex, where the visual stream ascends from one cortical region to another with a progressive enlargement of receptive fields and a progressive elaboration of trigger features. Structurally, the tectum in fishes is rather uniform across its surface, although some anatomists have seen evidence of a repeating, columnar organization. Pattern processing underlying the complex visual discriminations that fish are capable of, most likely depends on tectum, at least in teleosts, because it is the only high resolution visual center. Evidently, spatial information from the retina, such as object shape and location which is preserved by the orderly, topography of the retinotectal map is immediately broken up in tectum and recoded in ways yet to be deciphered.
Figure 4. A. Dorsal view of goldfish brain. Reproduced by kind permission of M.A. Gibbs. B. Goldfish brain cross section. Adapted from Meek J. (1983) Brain Research Reviews 6: 247-297 with permission C. Left tectum and TL showing paths of marginal fibers from 5 points in TL. Dashed curve on tectum is representation of visual field equator. D. Right visual field showing equator (dashed line), tectal MURFs (small circles), TL receptive fields (larger areas). Cb cerebellum, IC intertectal commissure, OB olfactory bulb, OT optic tectum, Teg tegmentum, Tel telencephalon, TL torus longitudinalis, TS torus semicircularis, VCb valvula of the cerebellum.

**Tectum - Torus longitudinalis subsystem**

The torus longitudinalis, TL, which occurs only in teleost fishes, consists of a pair of elongated cell masses connected to the medial margins of the tectum, lying just below the intertectal commissure, a thin band of fibers that connects the two tectal lobes (Fig. 4 A, B). Large numbers of small neurons in each TL (100,000 in goldfish) send an abundance of fine, unmyelinated axons into the SM, the most superficial layer of the adjacent tectum, where they course in parallel over the tectal lobe (see Fig. 4 C, Fig. 5). Indeed, SM, is filled with these TL axons, called marginal fibers, together with the dendrites of tectal neurons (mainly type I) onto which they synapse. The synaptic contacts made by the marginal fibers may outnumber all other inputs to tectum. The type I neurons, with cell bodies in SFGS, have extensively branched dendritic trees that receive marginal fiber synapses. This arrangement is strongly reminiscent of cerebellum where Purkinje cells...
receive synapses from the parallel fiber axons of granule cells. Type I cells also receive retinal input on their basal dendrites in SFGS and send a short axon into SGC. A return pathway from tectum to TL is made by Type X cells in SGC whose dendrites ramify at the SFGS/SGC boundary and in central SGC where the type I axons also terminate.

Figure 5

![Diagram of Tectum-TL circuitry](image)

Figure 5. Tectum-TL circuitry, showing a cross section through one TL and part of adjacent tectum. A retinal ganglion cell transmits to the main visual layer of tectum, SFGS. A type X cell receives visual signals and relays to the dorsomedial TL, which transmits luminance information over tectum in SM. This is received by the dendrites of Type I neurons, which are also activated by retinal input. Corollary discharge of eye movements is relayed via the ventrolateral TL in SM and also received by Type I dendrites.

Anatomical studies in various species show that TL is composed of two main divisions that will be called here dorsomedial and ventrolateral that have different connectivity and function. Electrophysiological studies have confirmed the existence of a precisely ordered loop between dorsomedial TL, tectum and back again, and have also shown that dorsomedial TL deals with a specific kind of visual information. A microelectrode inserted into dorsomedial TL, picks up sustained firing activity that is related in an inverse way to the illumination of the opposite eye, such that activity is high in the dark and is reduced by illumination. This sustained dimming activity can also be evoked by dark objects. It shows a clear retinotopic character so that an electrode in the front of TL picks up activity to dimming in the front of the visual field; positions farther back in TL have dimming receptive fields farther back in the visual field (see Fig. 4 C,D).
Dorsomedial TL responds to dimming with a considerably longer latency than does superficial tectum.

Electrical stimulation of a point in TL sends impulses along a beam of marginal fibers across tectum (see Fig. 4 C). This beam passes over a point in SFGS with a MURF that overlaps the receptive field of the TL point that was stimulated (Fig. 4 D). To complete the loop from tectum back to TL, type X cells connect topographically to dorsomedial TL. It is noteworthy that this tectum-dorsomedial-TL loop appears to be concerned only with dimming and with retinal location of a light stimulus; it is totally unconcerned with stimulus color, shape, or motion. That dimming is a separate visual submodality is underlined by the existence of a class of dimming retinal ganglion cells. Moreover, when the optic nerve regenerates after being cut in goldfish, dimming responses are the first to reappear in tectum and simultaneously in TL, followed significantly later by other kinds of visual responding (e.g. light onset).

Microelectrode recordings from ventrolateral TL yield distinctly different neural signals: bursts of firing that are synchronized with saccadic eye movements. There is evidence that TL is signaling the direction and extent of every eye movement, and presumably relaying this information to tectum via a different and deeper set of marginal fibers than those carrying the dimming signal from dorsomedial TL. These saccadic bursts are 'corollary discharge' signals, meaning that they derive from eye movement commands; they are not actual eye movement commands because ablation of TL has no effect on the eye movements that a fish makes spontaneously. The source of the saccadic information is not tectum, but other inputs to TL, possibly nuclei in the midbrain near the midline where oculomotor nuclei reside, or nuclei connected with the cerebellum.

The role of the TL-tectum loop can only be guessed at. Comparative studies suggest that TL is highly developed in species that live in turbulent environments. One such, the squirrel fish, has a marginal layer that makes up nearly half the thickness of the tectum. It lives in and around coral reefs, moving between brightly lighted and dim recesses in surging water. The TL-tectal loop may be involved in adjusting the visual processing of tectum under these circumstances.

A further clue to function is the association of marginal fibers with the type I cells that strikingly resembles parallel fiber systems elsewhere in the central nervous system, notably the cerebellum, and the electrosensory lobe of mormyrid electric fish. In the latter case, the neural circuitry learns to predict the consequences of the fish's own movements on the electoreceptor signals and enables the brain to discount them, perhaps thereby improving the detection of objects in the environment using its electric sense. The TL-tectal system may be doing something similar for vision according to the following scenario. Neural activity in dorsomedial TL can be thought of as a picture of the environment seen through the opposite eye. This picture is monochromatic, it is without motion enhancement, it over-represents the visual horizon, and is transmitted continuously, but with some delay, via the marginal fibers over the tectum. When the fish makes an eye movement, a corollary discharge is generated along the length of the ventrolateral TL and transmitted across tectum via the deep marginal fibers. At the same
time, the eye movement shifts the luminance distribution in the scene across the retina, which in turn, shifts the activity pattern within the main retinal termination layer, the SFGS. This activity change is picked up by the dendrites in SFGS of type I cells which fire in response; simultaneously the dendrites of type I cells in SM are excited by a pattern of marginal fiber activity representing a) the visual scene before eye movement and b) the corollary discharge representing eye movement direction and amplitude. Learning takes place by strengthening and/or weakening of the marginal fiber synapses so that after a period of experience, the activity of all the type I cells constitutes a prediction of how the scene will look after the eye movement, based on what it looked like before. Subtraction of the predicted pattern from the current pattern, would highlight changes in the scene that are not self-produced, and are therefore significant.

Figure 6.

**Tectum-Nucleus isthmi subsystem**

A cross section through the brain of a teleost fish, just in front of the corpus of the cerebellum reveals a cell mass below the TS, surrounded by fibers exiting the tectum. This is the nucleus isthmi (NI). It is well developed in highly visual fish, but is still present even in blind cave fishes, however it has not been found in elasmobranchs. It
consists of a shell of tightly-packed neurons surrounding a core containing dendrites, incoming fibers and synapses (see Fig. 6). The incoming fibers are mainly from the tectal lobe on the same side and make excitatory synapses within the core on the dendrites of the neurons whose cell bodies lie in the shell. The latter send their axons back to tectum on the same side. Anatomical tracer studies have shown that tectal neurons project to NI in topographic fashion, and that NI neurons project back to tectum topographically.

Introducing a microelectrode into NI immediately confirms that tectal input confers visual responsiveness upon NI. Extracellular microelectrodes pick up bursts of high amplitude spiking activity that occur spontaneously or are evoked by visual stimuli shown to the opposite eye. Flashed spots of light can evoke spike burst responses but they habituate with repeated presentation. Movement is a much more effective stimulus, but its effects also habituate. NI, therefore, is excited by change or novelty. It is interesting that although the anatomical connections from tectum to NI are topographically organized, the visual responses are not: visual stimuli anywhere in the field of the opposite eye can elicit NI bursts.

The movements that especially excite NI in goldfish and sunfish are approaching objects. A checkered ball stimulus that approaches the fish evokes bursts of activity that steadily increase in vigor. When the ball stops, the activity drops off, and when it moves away, there is a brief burst of activity followed by relative silence. Averaging over several approach trials reveals a ramp up in neural activity; faster approach gives a correspondingly faster ramp up, suggesting that NI activity signals the closeness of the ball. The ramp up is somewhat independent of the size of the ball, showing that the response is not simply a function of retinal image size. On the face of it, the NI-tectum circuit appears to be signaling the closeness of objects derived from monocular motion cues. NI also responds to stimulation via non-visual stimuli (somatosensory, auditory, lateral line), modalities that tectum also processes.

The neural circuitry of the NI-tectum subsystem involves the type XIV cells of tectum, the source of tectal input to NI (see Fig. 6). These complex neurons which are the most numerous of the tectal cell types have cell bodies in the SPV and a long dendritic trunk that ascends to the superficial layers (SO, SFGS) where they pick up retinal input. They also have dendritic branches that ramify in deeper layers (SGC), probably picking up non-visual inputs that arrive there. The type XIV output axons originate at the SFGS/SGC boundary and then split, with one axonal branch running upwards, eventually to a nucleus of the pretectal area, the other axonal branch running downwards, branching again to make terminals in SGC, and then leaving tectum to make excitatory synapses on the dendrites of NI cells in the core of the nucleus. The loop is completed by the NI neurons that send axons back into the SGC of tectum.

Two factors seem to be responsible for the complete absence of any topography in the visual responses of NI, despite anatomical evidence to the contrary. The first, is the likely existence of electrical synapses within the core of NI, providing low resistance pathways between neighboring NI neurons that tend to synchronize activity across the
nucleus. Experimentally such synchronization is observed: two well-spaced electrodes within NI pick up almost identical signals, showing that NI behaves as an integrated unit. The second factor, is a layer of possible connectivity between type XIV cells in the upper SGC formed by type XIV dendrites and type XIV axon branches that seem to be arranged to spread activity laterally across tectum.

The feedback from NI to tectum has interesting effects on activity in deep tectum, the significance of which is still unclear. Spiking activity recorded extracellularly at one point in SGC correlates highly with NI spiking; it also correlates highly with any other point in SGC because of the connectivities just discussed that nullify the topography. Even more remarkable is that when NI and SGC activity is correlated, as occurs in bouts of several 100's of milliseconds, NI and SGC spikes synchronize together within a fraction of a millisecond. While the relationship of this synchrony to stimulation or to behavior is unknown, it appears that precise timing of neural events is critical to processing in deep tectum, whereas precise spatial topography is not.

The function of the tectum-NI loop is still a matter of surmise. The fact that NI's responses, which are evoked by novelty, motion, and especially approaching objects, are broadcast throughout tectum, suggests an alerting or attentional role. This is supported by experiments showing that the response of one NI to stimuli seen by the opposite eye can be reduced or 'distracted' by a more salient stimulus presented to the other eye. There is evidence in fish and frogs that NI may modulate optic nerve input in the upper layers of tectum, accentuating the response to visual stimuli. In birds, too, NI has been proposed to play an attentional role. In teleosts, NI's influence is strongly manifest throughout deep tectum, perhaps allowing an assessment of particularly salient events by means of a comparison of NI signals with all current sensory representations in tectum, whatever their sensory modality, and selecting one as an object for attention or behavioral response.

**Multimodal Processing and Torus Semicircularis**

When the optic tectum is peeled away, one sees lying along the midline, the valvula of the cerebellum, a tongue-like protrusion of the cerebellum, and flanking it, two crescent-shaped bodies, the torus semicircularis (TS) (see Fig. 4 B). Its corresponding structure in mammals is the inferior colliculus, an auditory center. On anatomic grounds, TS is another potentially important partner with the optic tectum, having reciprocal connections with it. Each TS sends axons to both tectal lobes, but each tectal lobe sends axons to TS only on the same side. TS is a large nucleus, but only a relatively small proportion of TS cells provide input to the deep layers (SGC, SAC, SPV) of tectum. TS has a diverse set of inputs, some of which are sensory in nature: auditory, lateral line, somatosensory. In electric fishes (Gymnotids and Mormyrids), TS is large and well differentiated into lamina or subnuclei to process the information provided by the electrosensory receptors about surrounding objects and the electric signals of conspecifics. Other inputs to TS come from the cerebellum, the forebrain, and the opposite TS. Inputs to TS from the optic tectum arise on the same side from type XII and type XIII cells whose cell bodies lie in the deep layers (SGC, SAC).
Microelectrode recordings in TS reveal neuronal responses representing its various sensory inputs. Many neurons in TS of goldfish and trout are visually responsive, presumably as a result of tectal input. Indeed, the response characteristics of these neurons - very large receptive fields; unreliable responses to light flashes; preference for motion but without directional preference; and a propensity to habituate - reflect the visual responses recorded in deep tectum that are so closely correlated with NI activity. Other TS neurons are responsive to acoustic and/or lateral line stimulation, and some combine this acousticolateral responsiveness with the kind of visual responsiveness just described. In such bimodal neurons, the two modalities can combine in different ways, in some, responding to stimuli of either modality, in others to both in an additive fashion; sometimes the interaction is nonlinear, requiring that both stimulus modalities be present for a response. The feedback pathway from TS to tectum is therefore a conduit for introducing multimodal responsivity into deep tectal circuits. So far, there is very little physiological data on multimodal processing in tectum of fishes, although it has been studied in amphibians where visual and lateral line inputs combine to activate deep tectum. The benefit of combining different modalities within tectum may be that events and objects such as prey or conspecifics can be more easily detected and more rapidly responded to, if the mappings of the different modalities overlap in tectum allowing them access to common motor mechanisms.

TS in teleost fishes, in its role as auditory center, contains directionally selective neurons that respond to underwater sound vibrating in a particular direction. TS also contains neurons that respond to the much lower frequencies of water movement that stimulate the lateral line organs. There is a rough topography in TS so that an object causing a water disturbance near the animal will activate a population of TS cells that is specific to the location of the object. In fishes that sense objects like prey through the small electric fields that they generate, different populations of TS cells will be activated by different positions of the field source. Lastly, somatosensory signals conveying touch and pain arrive from the spinal cord, and also go directly to tectum. In each of these modalities, TS elaborates and refines differential sensitivities to the important stimulus dimensions (frequency, direction, position etc.), relaying to the deep layers of the tectum on both sides, and potentially providing information on the whereabouts of events or objects. When these objects can be simultaneously visualized, there will be correlations between the visually evoked activation in tectum and the TS signals. Plasticity of the TS connections in tectum could then generate a topographic map that is in register with the visual map, which is what is found in other vertebrate groups, but yet to be properly demonstrated in fish tectum.
ASCENDING CONNECTIONS - WITH PRETECTUM, DIENCEPHALON, TELENCEPHALON (PTP)

Between the optic tectum and the forebrain are a number of nuclei forming the brain regions called the preoptic area, the thalamus, and the pretectum (PTP). It is inappropriate to detail all of these here (there are 10 or more), especially as there is considerable variation in nuclear composition of the region between species, and in the nomenclature used to described them. The importance of this region for present purposes is that some nuclei receive direct retinal input, some relay visual information on to the telencephalon or on to the tectum. In addition, some of the nuclei receive tectal input and relay to the telencephalon, many with reciprocal connections back from tectum and telencephalon. The region can therefore be seen as a way station for retinal information traveling to telencephalon, and for tectally-processed information, probably multimodal, traveling to telencephalon. Finally, telencephalic regions provide an input to tectum, both directly and via the PTP. The direct telencephalic input is concentrated in SO and in the middle of the SGC of tectum where it could contact the dendritic branches of intrinsic neurons like the type I, as well as several types with output axons (X, XII, XIII, XIV) (see Fig. 2).

The fact that our own sensory abilities of recognition and localization are performed by telencephalic cortical areas raises questions about the relative importance of the telencephalon versus the tectum in fishes. In teleost fishes, the ablation of the entire telencephalon has little effect on behavior, at least to the casual observer. Goldfish, for example, after telencephalic ablation successfully identify prey objects and pursue them, so their vision is not obviously impaired. However, after total tectal ablation, they appear completely blind, indeed more disabled than eyeless fish because their use of non-visual senses for navigating their environment is also impaired.
The very few physiological studies on the PTP nuclei in teleosts show that most of the visually responsive neurons have large receptive fields. Some PTP nuclei do have small receptive fields but contain relatively few cells and these nuclei possess nothing like the detailed retinotopic map that tectum boasts. Evidently, the extra-tectal pathways via PTP to telencephalon lack the necessary 'bandwidth' for detailed vision and may lack access to motor systems for sensorimotor behavior. The sensory information sent to telencephalon by tectum is probably important for the higher order tasks that telencephalon performs, such as spatial place learning or the recognition of conspecifics and their displays. This tectally-processed information is likely to be highly abstracted, rather than a detailed point-by-point representation of the scene, given what we know about the diffuse character of deep tectal activity, the source of telencephalic input.

The situation in elasmobranchs may well be different. It has been reported that sharks after tectal ablation are still capable of behaviorally discriminating between visually presented shapes. There are also other indicators of the relatively greater importance of telencephalon versus tectum in elasmobranchs. Species of shark that depend heavily on vision, as judged by their mode of hunting in well-lit habitats, have tilted their brain development more toward telencephalon than tectum; highly visual teleosts, on the other hand, seem to have done the reverse.

Figure 8.

Figure 8. Eye movement vector map on right tectal lobe in goldfish. Arrows show the direction of eye movements evoked by electrical stimulation of different points in tectum. Tel = telencephalon, OT = tectum, Cb = cerebellum. Reproduced from Salas C. et al. 1997. Neuroscience 78, 271-288 with permission.
Descending connections and motor control

The behaviors that depend upon tectum are initiated or guided by sensory input and require a fair degree of spatial resolution. These behaviors include food and prey seeking, navigating around obstacles in the environment, avoidance of approaching objects, schooling and the ability to swim with a moving textured background (the optomotor response). The tectal outputs mediating these behaviors stem from neurons such as the type XIII with cell bodies in the SGC and dendrites distributed in SFGS and SGC. These neurons send their axons down into the reticular formation of the midbrain and brain stem on both sides, making synapses upon cell groups that activate motoneurons, either in the oculomotor nuclei for eye movements, or in the spinal cord for body movements.

In the absence of direct recordings of the tectal output neurons, the transformations that take place between topographic sensory mappings and muscle movements, can only be inferred, mostly from experiments involving electrical stimulation. Trains of electrical shocks evoke behavioral responses most easily in the deep layers of tectum (SGC, SAC). Despite the artificiality of electrical stimulation delivered to a point in tectum, the behaviors elicited in a free-swimming fish may look natural, coordinated and even purposeful. Stimulation of rostral tectum causes convergence of the eyes and forward swimming in a pattern resembling food searching. Stimulation at sites farther back produce contraversive turning (opposite to the side of stimulation) of eyes and body, similar to a strike at a fly cast, and at high stimulus intensities, movements resembling escape.

By electrically stimulating the tectum of restrained goldfish and measuring the evoked eye movements, it has been possible to draw a detailed 'vector map' showing the direction and amplitude of eye movements evoked from different regions of one tectal lobe (Fig. 8). The largest, 'medial zone' of tectum elicits movements of both eyes in a contraversive direction. As the stimulation point is moved toward the midline, a greater vertical eye movement component appears; as it is moved caudally, a greater horizontal component appears. This is what would be expected if stimulation is directing movement toward corresponding points in the retinotectal map, where medial tectal positions represent upper field and caudal tectal positions represent caudal field. Stimulation in the 'posterior zone' gives eye movements that are almost entirely horizontal; in the 'anteromedial zone' eye movements do not follow a fixed vector but move toward a 'goal' in frontal space, and in the most anterior region, the two eyes converge inwards. In should be pointed out that because goldfish, like most other fishes, do not possess a retinal fovea, these eye movements are not 'fixating' in the sense that our eyes do when scrutinizing something, but are part of a coordinated eye-body movement that orients the whole fish.

While these experiments show conclusively that it is the place of tectal stimulation that determines the direction of the fish's orientation and motion, it is not understood how 'place' might be translated into an 'intensive' neural code i.e. one that specifies the force and duration of muscular contractions. The tectal output fibers do not project to the reticular nuclei with any obvious topography, except that rostral tectal fibers terminate
preferentially in rostral reticular areas of the midbrain, a region that seems to contain vertical eye movement generators, while caudal tectal fibers terminate in caudal reticular areas containing horizontal movement generators.

The translation from 'place' to 'intensitive' coding appears to be modifiable, perhaps through experience. This is shown by experiments involving plastic rewiring of the retinotectal system. When the optic nerve is crushed and allowed to regenerate into a tectal lobe whose caudal half has been removed, the visual field eventually comes to be represented in compressed form on the remaining rostral half. Sunfish after such surgical rearrangement oriented with normal accuracy to flashed lights in the parts of the visual field that were represented in a compressed retinotectal map. Accurate orienting could also be performed with an expanded retinotectal map produced by removing half the retina and allowing the remaining half to spread its connections across an intact tectal lobe. Evidently a vector map like that in Fig. 8 is not fixed in the tectum but can be expanded or compressed in compensatory fashion, perhaps by changing the gain of the intensitive code. A continual adjustment of this kind through trial-and-error experience would be valuable for keeping prey catching and other motor behaviors well calibrated to the position of objects in space.

The tectum in fishes, as in other vertebrate groups, also plays a part in initiating avoidance and escape behaviors. Moving shadows, especially overhead, and looming objects elicit flight reactions that can be abolished by tectal lesions. Similar defensive reactions can be produced by strong electrical stimulation of tectum. Visual looming stimuli, detected by tectum, probably enabled by NI, activate the giant Mauthner cells in the brainstem that trigger a very rapid and vigorous body flexion, moving the fish out of harm's way.

**Conclusions**

The basic function of tectum in fishes, as in most other vertebrates groups, is to form moment-to-moment representations of the immediate surroundings, using primarily the visual modality, with back up from the somatosensory, auditory, lateral line, and electrosensory modalities. These body-centered representations - as distinct from the world-centered (allocentric) representations that telencephalon develops - connect with motor centers, enabling fish to react swiftly in an appropriate direction, whether it be in prey capture, avoidance of objects or predators, or in complex social maneuvers. Interactions among tectum, its satellite nuclei, PTP, and telencephalon help pick out salient objects or events for a possible response. Retinal input provides a detailed and panoramic 'image' of the surroundings to the superficial layers of tectum, making tectum a likely site for pattern recognition. There are units in tectum with oddly-shaped receptive fields that may represent selectivity for important image shapes but no evidence so far of a systematic parsing of features in a hierarchy of specialized regions such as is found in mammalian visual cortex. Virtually nothing is known of the learning capabilities of tectum in fishes, although it has the requisite machinery such as long-term potentiation of synaptic strengths and NMDA receptors. It does, however, demonstrate plasticity of its retinal input connections and possibly its motor output connections, which may be vital.
for keeping sensorimotor functions in good calibration, especially as the bodies and brains of fishes continue to grow throughout life.

Further Reading
