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ANATOMY AND PHYSIOLOGY OF A BINOCULAR SYSTEM IN THE FROG *RANA PIPIENS*

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SUMMARY

The locations of tectal neurons projecting to nucleus isthmi (n. isthmi) were found by iontophoretic injection of horseradish peroxidase (HRP) into n. isthmi. After retrograde transport, stained tectal somata are found to lie almost exclusively in layer 6 and below of the ipsilateral tectum. Many cells are colored throughout the extent of their dendrites into the fine rami, giving the appearance of a Golgi stain. Nucleus isthmi receives projections from the ipsilateral tectum and from no other region.

Nucleus isthmi units recorded electrically respond to visual stimuli and are arranged in a topographic map of the visual field. There are two types of receptive fields, those with small centers and those with large centers. The small centers are about 3–5° in diameter, similar to type 2 optic nerve fibers. Their response is to many of the same geometric features of stimulus as excite type 2 fibers. The large centers are at least 7–10° in diameter and respond to many of the same features as excite types 3 and 4 optic nerve fibers. The responsiveness of small and large center n. isthmi units is very similar to the elements of the ipsilateral visual field projection onto tectum, i.e. the neuropilar units recorded in layers A and 8 of the tectum when the contralateral eye is occluded. These are in strong contrast to those of tectal cells of layer 6 and below, which have large receptive fields, show far less vivacious response, adapt extremely rapidly to repeated stimuli and are hard to describe in terms of characteristic stimuli because they are unresponsive most of the time. We suggest, therefore, that the axons of tecto-isthmic cells are quite active and that their cell bodies, located in layer 6 and below, only fire occasionally on the firing of their axons.

INTRODUCTION

The retinal projection onto the tectum of the frog is almost entirely crossed. However, when recording electrically in the superficial neuropil of the rostral tectum, it is common to find visually evoked units driven by the ipsilateral eye as well as by the contralateral eye[6]. Keating and Gaze[16] showed that the path from the ipsilateral retina is not direct but relayed. On making lesions of the contralateral tectum and the postoptic commissure, they interrupted that path. Recently Gruberg and Udin[10] described the anatomical connections to and from the n. isthmi and suggested that these connections were those that were severed by Keating and Gaze. The n. isthmi receives a projection from the ipsilateral tectum. In turn, the n. isthmi projects to superficial layers of both the tectal lobes. Isthmic fibers to the contralateral tectum cross in the postoptic commissure. Gruberg and Udin[10] proposed that information from the eye reaches the ipsilateral tectum by way of the n. isthmi. Grobstein et al.[9] and Glasser and Ingle[8] subsequently showed that unilateral destruction of the n. isthmi abolishes all units in the ipsilateral tectum that respond to the ipsilateral eye.

In this paper we show by direct electrical recording the properties and distribution of visual units in the n. isthmi. We will describe how patterns of response of n. isthmi units are similar to those of optic nerve fibers and different from those of tectal cells in the deeper half of the tectum. These results at first suggested that the cell bodies of those tectal neurons which project to the n. isthmi might lie among optic nerve terminals in the superficial half of the tectum. But then we stained these cell bodies by using horseradish peroxidase (HRP) injection into n. isthmi. On comparing the anatomical and physiological results, we were led to a surprising conclusion.

METHODS AND MATERIALS

HRP injections

Horseradish peroxidase was injected by iontophoresis into n. isthmi of 14 adult frogs (*Rana pipiens*, 3–5 cm long, snout to vent). After 1, 2, 4 or 6 days of survival at 22 °C, the brains of these animals were prepared for cutting (40-μm cryostat sections in the transverse plane) and stained by the Mesulam blue reaction[20] as previously described[10]. For controls we used brains that had been injected with HRP directly into the tectum.

Electrical recording

For mapping the visual receptive fields of units in n. isthmi, animals were lightly curarized and centered under a hemispherical aluminum dome (51 cm in diameter) that served as field background. A platinum-black-tipped metal microelectrode[4] was introduced through the caudal pole of the exposed tectum and driven ventrally through the tectum to the upper boundary of n. isthmi. The electrode was then advanced in 40 μm steps, and the receptive fields of the units recorded were described by moving black targets against a background and by turning light off and on. The targets were magnetized and followed the movement of a magnet held to the black of the alminum dome that served as background.

In further studies of the physiology of tectal and isthmic neurons, frogs were anesthetized two days prior to the experiment. Then spinal nerves I and II were exposed transpharyngeally and severed bilaterally. The skull was opened in a flap to expose the dura overlying the tectum, and the flap was put back in place. When the frog had recovered from anesthesia, its shoulder girdle was paralyzed. This simple procedure allowed us to work without additional cutting or trauma on unanesthetized, uncurarized frogs that were simply swaddled in extension with wet, light gauze. Recordings were made through electrodes tipped with platinum-black. Active units were studied both in tectum and in n. isthmi. The electrodes had a wide range of tip diameters (2–8 μm). The locations of electrodes were verified by electrolytic lesions and subsequent histological sectioning of the brain.

RESULTS

HRP injections

When HRP was injected into n. isthmi, the locally stained volume was a maximum of about 300–400 μm in diameter (Fig. 1A). With a few eccentric injections there was some local spill-over to adjacent areas generally dorsal to the nucleus.

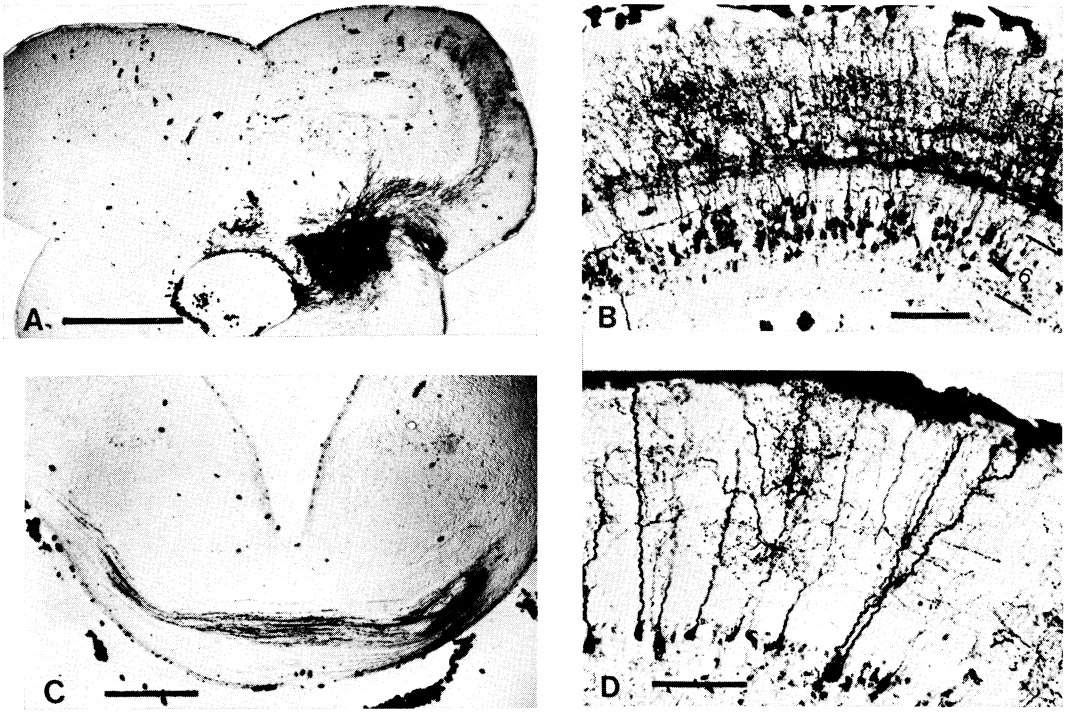


Fig. 1. A: typical n. isthmi HRP injection site. Scale bar 500 μm. B: stained region of rostral tectum showing cells stained primarily in layer 6 with mesh of dendritic trees and axonal arbors in superficial layers. Four-day survival after n. isthmi HRP injections. Scale bar 100 μm. C: anterograde staining of n. isthmi fibers in supraoptic decussation crossing from right (injected side) to left. Scale bar 300 μm. D: field of ipsilateral stained tectal pyramidal cells with apical processes extending to surface. Scale bar 100 μm.

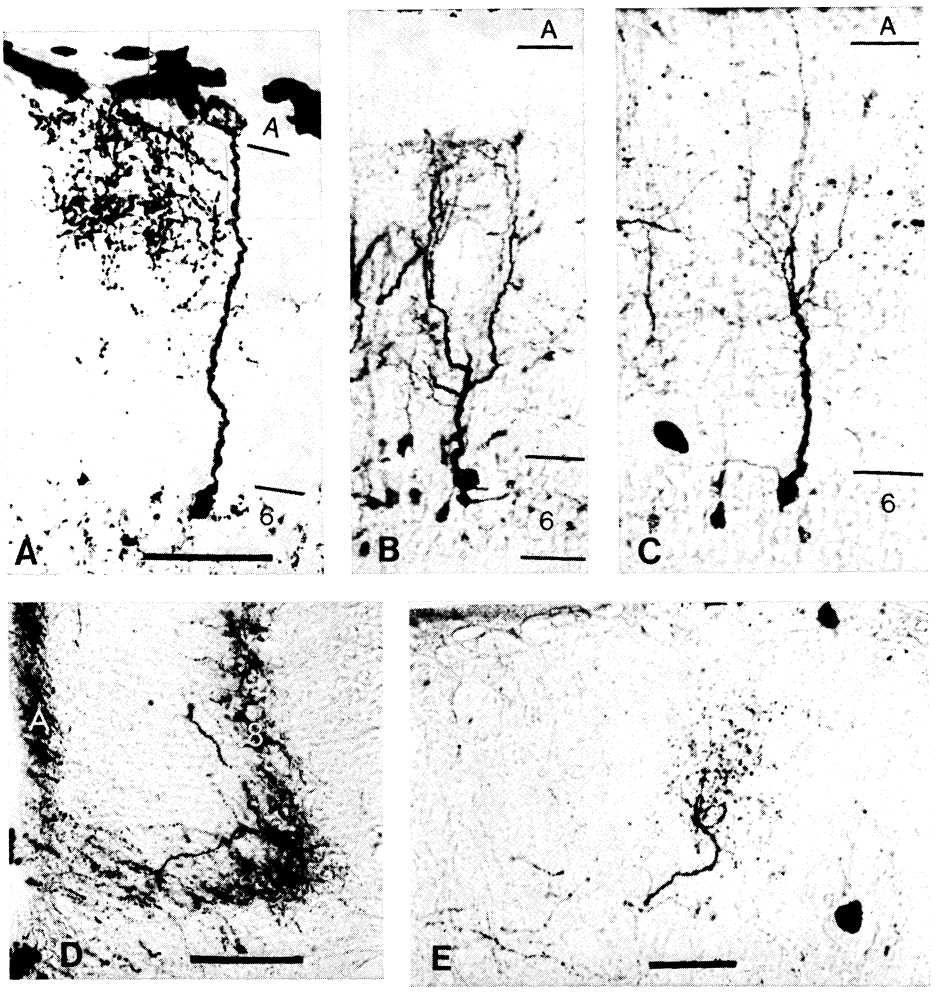


Fig. 2. Top: Golgi-like staining of a variety of pyramidal cells in tectal layer 6 after ipsilateral n. isthmi injection. A: cell with single apical process ending in small bush in layer A (montage of two photographs). B: cell with fine dendritic branches ending in a thin intermediate lamina. C: cell with open branching pattern. Scale bar 100 μm. Bottom: D, contralateral anterior tectum showing two layers of stained fibers in lamina A and 8. Extreme lateral region. Tract runs below on lateral surface. Scale bar 100 μm. E: single axon from n. isthmi terminally branching in superficial ipsilateral tectum. Scale bar 50 μm.

In the ipsilateral tectum we can see stained somata at all survival times, and in each case only a wedge of tectum shows stain (Figs. 1B, 1D). There is no relation between the time of survival and the extent of the region of stained tectal cells. No stained somata are seen in the contralateral tectal lobe or in the contralateral n. isthmi. In fact, except for larger injection sites which clearly include other structures adjacent to n. isthmi, the ipsilateral tectal lobe is the only area to contain stained cell bodies.

The stained somata in the ipsilateral tectal lobe are almost exclusively in the deeper layers of the tectum in layer 6 and below (for layering notation see Fig. 5B).

Stained cells are seen most commonly in layer 6, although other deep cell layers are also represented (Fig. 1B).

A striking characteristic of the HRP-labeled tectal cells is that the reaction product not only lies in the somata but solidly fills the dendritic arbors including the fine branches. These cells look as if they had been treated with a Golgi stain. Almost all the morphological types of tectal cells previously described by classic Golgi stains are seen after injections into n. isthmi. Most cells are of the pyramidal type, but bipolar and ganglionic types are also represented. A very common type of pyramidal cell has its soma in layer 6, and it has a thick, unbranched, untapered apical dendrite which projects radially and ends in a tight bush, approximately 25 μm wide in layer A (Fig. 2A of Potter[22]). In favorable sections, arrays of these bushes can be seen along layer A. Other pyramidal cells have a variety of dendritic profiles ranging from those with terminal branches that end compactly in a single plane to more open types with branches that terminate at different levels (Figs. 2B, C). 'Bipolar' cells are scattered at the extreme medial part of the tectum and in layers 2 and 4.

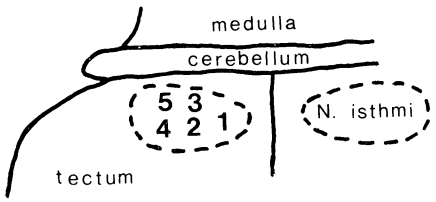
Additional stained fibers can be traced in the anterograde direction from n. isthmi to the ipsilateral tectum. Fibers enter the ipsilateral tectum from a superficial tract of the lateral tegmentum immediately ventral to the tectum. On entering the tectum the fibers travel by way of layer 7 and layer G. Axons turn toward the surface from those layers. At various levels they branch to form terminal bushes. Occasionally individual arbors can be seen in isolation (Fig. 2E). In each stained brain only a band or wedge of tectum shows many stained axon arbors in the superficial tectum. Invariably, below these stained axons are stained somata in the deeper layers. Some of the cells have dendrites which penetrate to the superficial layers. On the other hand, stained cells from the deeper tectal layers can be found in regions that do not have an overlying band of stained isthmo-tectal fibers.

HRP-stained fibers of n. isthmi can also be traced from the injection site forward along the lateral surface of the tegmentum to a crossing in the supraoptic decussation (post-optic commissure) of the anterior diencephalon (Fig. 1C). In the 4- and 6-day animals, fibers of this type can be followed further into the contralateral diencephalon where they run back caudally to the tectum into distinct superficial laminae, layer A and layer 8 (Fig. 2D).

In some brains a few fibers can also be seen crossing at the same transverse level as the injection site and spreading into the contralateral n. isthmi. No somata are stained, so it is unlikely that these stained fibers originate in n. isthmi.

Visual map in n. isthmi

The electrical recordings reveal a systematic map of the visual space onto the nucleus (Fig. 3). Generally, as the electrode moves in ventral steps, there is a dorso-nasal shift in the locus of receptive fields for the units recorded. The visual map in the nucleus covers the frontal visual field of the animal, extending out to 90° from the longitudinal axis.



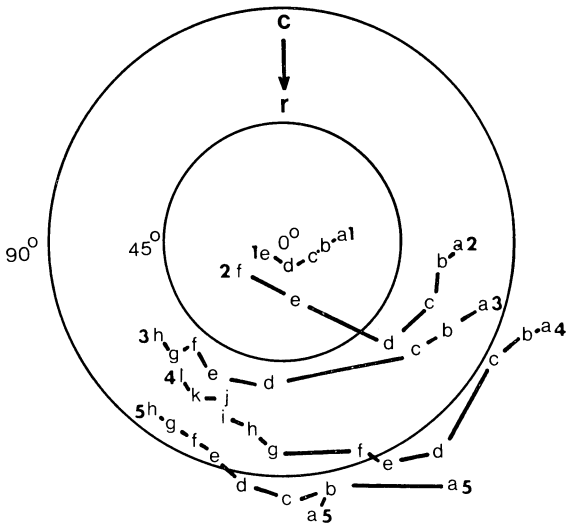


Fig. 3. Above: dorsal surface of caudal tectum showing sites of 5 electrode penetrations. Below: map of visual field of n. isthmi on hemispherical dome. For each electrode penetration, letter 'a' corresponds to location on dome where visual field of n. isthmi units are first encountered. In penetration 5, two distinct foci of units were found at the dorsal boundary of the n. isthmi. Subsequent series of letters represent center of receptive fields of succeeding units after 40 μM ventral movement of recording electrode. Arrow points axially in rostral direction. 90° corresponds to equator of hemisphere. 0° corresponds to the apex of the hemisphere directly over the left eye.

Unit properties of n. isthmi and ipsilateral tectum

Electrically recorded units in n. isthmi of unanesthetized, uncurarized frogs are of two general classes. One type has small receptive fields 3–5° in diameter and responds to much the same features that excite type 2 optic fibers[18]. It responds vigorously to the movement of small objects 0.5–2° in size within the excitatory receptive field (Fig. 4c). There is little response to changes in ambient light. In addition, it possesses not only a 'surround' but, under certain conditions, a much larger receptive field (such as when the blood circulation is compromised) and so differs noticeably from the type 2 elements found in optic nerve. The isthmic units are not quite as vigorous or protracted in firing as type 2 units, and with repeated stimuli there seems to be a greater habituation than in the optic nerve fibers they resemble.

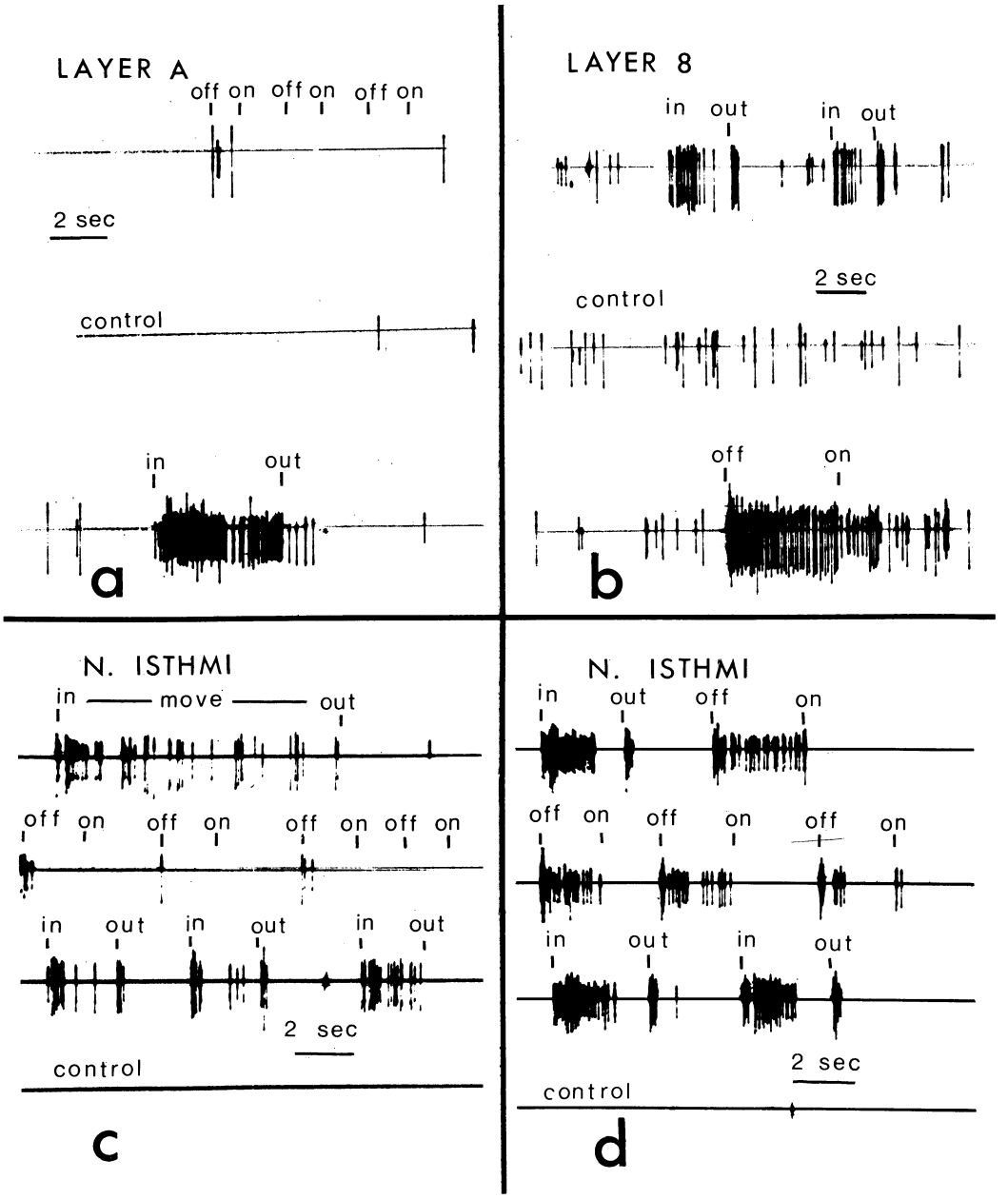


Fig. 4. a: visual units of tectal layer A with contralateral eye occluded. Top trace, little response to change in background illumination; middle trace, control; bottom trace, movement of 1° spot into, within and out of 4° receptive field area. b: visual units of tectal layer 8 with contralateral eye occluded. Top trace, movement of a 1° spot into, within and out of a 10° receptive field area; middle trace, control; bottom trace, response to changes in background illumination. c: units similar to layer A but within n. isthmi. Top trace, movement of a 1° spot into, within and out of a 5° receptive field area; 2nd trace, little response to change in background illumination; 3rd trace, repeated movements into and out of receptive field area; bottom trace, control. d: units similar to layer 8 of tectum but recorded within n. isthmi. Top trace, movement of a 1° spot into, within and out of an 8° receptive field area; 2nd trace, sequence of turning off and on background illumination; 3rd trace, repeated movements into and out of receptive field area; bottom trace, control.

Very similar units are recorded in layer A of the tectum when the contralateral eye is occluded (Fig. 4a).

The other type of unit has larger receptive fields, at least 7–10° diameter, and responds to the same features that excite types 3 and 4 optic fibers. It responds well to both small convex objects and large edges and also to general changes in illumination (Fig. 4d). Units of this type correspond closely to units recorded in layer 8 of the tectum when the contralateral eye is occluded (Fig. 4b).

DISCUSSION

Anatomical relationship of tectum to n. isthmi

Our HRP injections into n. isthmi show that the ipsilateral tectum is the only input to the n. isthmi. The present study, combined with earlier proline and degeneration studies[10], shows that the n. isthmi projects only to the tectum. Thus, it appears that n. isthmi is exclusively connected to the tectum. A similar arrangement exists in the pigeon, where the n. isthmi pars parvocellularis is in exclusive reciprocal connection with the ipsilateral tectum. A major difference between the frog and the pigeon is that no projection from n. isthmi to contralateral tectum has been found in the pigeon[13,14].

One source of possible ambiguity in interpreting our histological results is that a major efferent tectal tract passes immediately lateral to the n. isthmi. It is thus possible that some of the HRP-stained neurons in the tectum have axons running in that tract and do not terminate in the n. isthmi. It is known that axons of passage will take up HRP and transport it to their cell bodies if they are cut or disrupted. However, previous injections of HRP in the caudal tectum, through which most of this tract passes, does not lead to staining of tectal cells anywhere but in the immediate vicinity of the injection sites. Thus we conclude that the stained cells of the tectum do project to n. isthmi.

Physiological relationship of n. isthmi to tectum

Several laboratories, notably that of Keating and Gaze[16], have observed that the visual fields of both eyes map onto the neuropil of each tectal lobe. In particular, the small receptive field components (3–5°) look remarkably similar for both visual fields in the same tectal hemisphere. Keating and Gaze found by ablation experiments that the first stage of the pathway from retina to ipsilateral tectum includes the contralateral tectum but not the intertectal commissure, the posterior commissure, or the deep tegmental commissural system. Our recent HRP study showed how n. isthmi links the two tectal lobes[10]. We proposed that this link is the second-stage relayed pathway Keating and Gaze had been looking for. Grobstein et al.[9] and Glasser and Ingle[8] subsequently found that ablating n. isthmi abolishes the ipsilateral visual field in the tectum.

Note there are a small number of direct ipsilateral retino-tectal fibers (see, for instance, Neary[21]), but these are so sparse that they cannot account for the many units activated in the tectum when the ipsilateral eye is stimulated. Using a cobalt method to fill the optic nerve of *Rana esculenta*, Lazar[17] found that 'in particularly successful

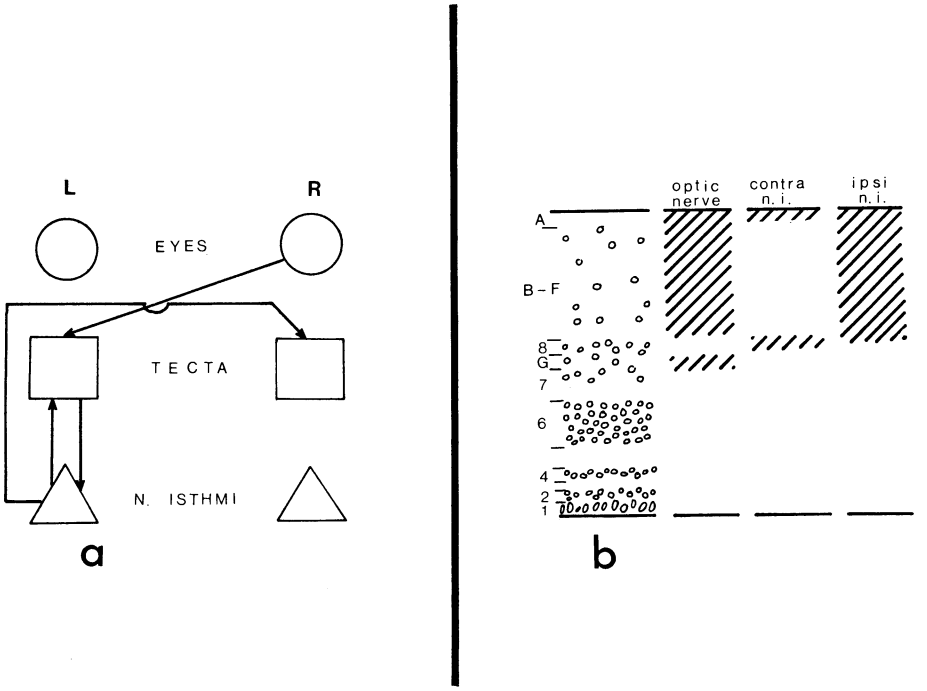


Fig. 5. a: visual pathway from right eye to right tectum. b: layers of tectum extending from layer 1 (the ependymal cell layer adjacent to the ventricle) to layer A (the most superficial layer). The shaded areas are the distribution of terminals of optic nerve fibers, contralateral n. isthmi fibers and ipsilateral n. isthmi fibers.

preparations a few fibres can be found in the mesencephalon'. These fibers are restricted to layers F and 8 of the intermediate neuropil of the rostral tectum. No ipsilateral fibers are found in layer A. In addition, Gaillard and Galand[5] electrically recorded from the left tectum of *Rana esculenta* after cutting the right optic nerve and right optic tract. In 100 penetrations with their microelectrodes they found a total of only 18 units located in the intermediate neuropil. None of these units responded to changes in background illumination. Thus the direct ipsilateral retino-tectal fibers appear to be a negligibly small subset of the ipsilateral retino-tectal system.

As we described, the units recorded in n. isthmi are quite similar in type of activity and nature of receptive field to the units found in the outer neuropil for the ipsilateral representation on the tectum. Thus by recording, as by ablation, n. isthmi is now reasonably identified as the relay between the tectal lobes and thereby we are faced with an exquisite problem. To realize its full poignancy, it is useful to lay out the connections starting from the eye, using R and L for 'right' and 'left', and assert simply that the path from the opposite eye is the mirror image (Fig. 5A).

(1) The outer neuropil of L tectum receives mapping projections of optic nerve fibers almost exclusively from the R eye (Fig. 5b).

(2) The outer neuropil of the L tectum receives fibers from both n. isthmi. The R n. isthmi projects the field of the L eye onto the L tectum. At any point along the

surface of the tectum an electrode, thrust in, encounters representation of a more or less specific region in the visual space around the frog (Fig. 5b).

(3) Into this neuropil of terminals that map the visual fields, the apical dendrites of deeper tectal cells project radially. The cell bodies of many of these neurons lie in a thick layer (layer 6) many cell bodies deep, just beneath the outer neuropil. These somata are, typically, pyramidal and studded with short basal dendrites. Coursing through the cellular layers are thin sheets of nerve fibers. We do not know their provenance, and their origins are probably scattered[23].

(4) The axons of the tectal cells of layer 6 and below arise primarily from the apical dendrites in an intermediate zone centered on layer 7 lying between outer neuropil and the thick layer of cell bodies. These axons are the tectal output and go to all places to which the L tectum projects, including the n. isthmi (L).

(5) The n. isthmi (L) receives a direct projection from the cells of the deeper layers (layer 6 and below) of L tectum. No other fibers enter n. isthmi (L) except those from L tectum. There is a physiologically recorded map of the visual field in the n. isthmi (L). The map is in accord with anatomical findings[10,15]. Furthermore, the n. isthmi (L) projects its map back to the outer neuropil of L tectum in registration with the visual field map. Even further, the n. isthmi (L) projects in an orderly mapped way to the R tectum in addition to the L tectum, and to *nowhere else*.

This orderly connectivity sounds, at first, idyllic. But it now plunges us into physiological nihilism. With the anatomical background as given cursively above, let us turn to the recordings from the tectum. These are open to some doubt as to provenance and mechanism but, for the moment, let us take the neuropil records simply as data. In the outer layers one records elements of small receptive fields, fairly sensitive, vivacious, non-adapting in the sense that stimuli do not evoke significantly lesser responses on repetition[11,18]. Among these smaller active elements, for the nonce call them 'terminal structures' or 'glomeruli', are those attributable to contralateral n. isthmi in that they display the visual field of the eye ipsilateral to the tectal lobe under study. These are almost as active as like elements of small receptive field representing the contralateral eye. But since the n. isthmi receives fibers only from tectal neurons, the information necessary for the responsiveness of the 'glomeruli' from n. isthmi must be available in the tectal output.

Yet what characterizes tectal cell records from layer 6 and below, is a phlegmatic response[11,19]. This is based on over 200 penetrations of large-diameter, platinum-black-tipped electrodes into the tecta of uncurarized, unanesthetized frogs. Tungsten and bright platinum–iridium electrodes of small diameter and small area can be used for extracellular tectal recording. However, in our hands such electrodes behave exactly as is expected from their tip impedance (as a port) and show only a small sample of what lower impedance tips see (Gesteland et al.[7]). The receptive fields of those cells that respond at all (and they are uncommonly few, considering the densely packed ranks) are fairly large, certainly larger than about 10° for the most part. The cell firing most often adapts rapidly, that is, there is a much smaller response to a repeated stimulus. A few, of odd nature, seem capricious in response over a wide field, signalling first one kind of feature, then another. Some few are certainly orderly, but not of high feature resolution, e.g. detecting particular kinds of boundary, etc.

Identification of cells versus fibers in a neuropil is difficult. Not every spike, even if large, means one is recording from a cell. Our argument is based on making lesions where we recorded. We did not find, for example, that electrodes, recording small receptive-field units, ever lay in layer 6, however morally certain we were at the time that we were in that layer. The lesions, and they alone, were the only certain method we had of knowing our position. Such lesions never revealed small receptive-field units at that depth in our uncurarized, unanesthetized frogs.

But what is most impressive, truly, is the taciturnity of most of the tectal cells. There seem so few that notice visual events. By itself this torpor scarcely deserves comment were it not that the fibers of n. isthmi are so responsive, so delicate in their assessment of spatial configuration, so well-tuned to definite and significant visual features, so moderately adapted on repeated stimuli, so small in receptive field size among those that project to the outer reaches of the outer neuropil. Yet we have shown above that the tectal neurons which project to n. isthmi are from layer 6 and below. Since the sole input, on which isthmic neurons produce firing patterns, comes from those tectal neurons, we seem confronted by a miracle. Can it be that the occasional mutter of a rare tectal neuron is so fraught with meaning as to govern the fine detailed map redisplayed by the neurons of n. isthmi in tectal neuropil? One does not like to attribute such great intelligence to single neurons in a frog's head as would shame a whole frog. And the blunt truth is that looking at the n. isthmi output, having recorded from tectal cells, is like seeing a whole complex image recreated from an occasional corrupt sample. On the whole, we do not trust in revelation, which is the production of relevant output without input information. Ordinarily one might have laid the activity of n. isthmi to some other input, for generally there is a tertium quid to any system. But here we have gone to some pains to show that there is no other input for n. isthmi than from tectal neurons.

The answer, we suggest, is that tectal axons fire vigorously and sensitively, but the cell bodies do not. We have now recorded enough in layers 7 and 8 to recognize that the output from tectum is enormous, small-field and large-field, and that several kinds of combinatory receptive fields exist. But none of this could be told from cell-body activity any more than in many invertebrates (see, for instance, Tauc[24] and Hagiwara and Bullock[12]). This should occasion no surpise. Since the 1950s we have known that the orthodromic impulse begins in the axon and inconstantly spreads back to the cell body, which has a much higher threshold[1–3]. Certainly in the case of small cells this property is even more pronounced than in the large ones.

While expediency as well as received opinion promotes the recording of cell bodies whose signals, when they occur, are large enough to impress anyone with their saliency, the fact that even in large cells the time series of cell spikes is a subset of the time series of axonal spikes ought to have stayed as a caution in our awareness. The problem, after all, is not so much to get impeccably noise-free signals as to find what the message is that goes down the axon. And so the frog tectum can be held up as a minatory gesture to show that clean records and faith are not enough. Nor is it apparently different in mammals, as anyone can say who has worked in the dorsal half of the spinal cord, or recorded in the spinothalamic tract spike-train responses of a

sort never seen in the somata of origin. We should be quite surprised to find that a cortical structure can, without evidence, be deemed an exception. And our impression now is that without axonal studies there is no reason to suppose that the cells one records in brain anywhere are a fair sample of those cells that are there, or that the spike train recorded from a cell is that to be found in its axon. This comment applies especially, we believe, to cortices, including that of mammalian telencephalon.

In conclusion, we have found that electrically recorded units in n. isthmi are very similar to tectal units of layer A and 8 that are driven by the ipsilateral eye. The ipsilateral tectal cells which project to n. isthmi are the only input to the nucleus. These cells are located in the deeper tectal layers and have very sluggish response characteristics. We propose, therefore, that the axons of tecto-isthmic cells are fairly active, and that their cell bodies only fire to small subsets of the impulse trains on their axons, as is the case with invertebrate neurons.

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