



Title	Electrophysiological Studies of Ipsilateral Visual Pathway in Crucian Carp (With 11 Text-figures)
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Citation	北海道大學理學部紀要, 19(3), 530-545
Issue Date	1974-10
Doc URL	http://hdl.handle.net/2115/27577
Type	bulletin (article)
File Information	19(3)_P530-545.pdf



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Electrophysiological Studies of Ipsilateral Visual Pathway in Crucian Carp

By

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(With 11 Text-figures)

The axons of the retinal ganglion cells in the fish are believed to cross over completely at the chiasma and then to reach the contralateral optic tectum. Nevertheless, behavioural (Sperry and Clark, 1949; McCleary, 1960; Ingle, 1965; Mark *et al.*, 1973) and electrophysiological experiments (Mark and Davidson, 1966; Niida, 1973) showed the existence of the pathway by which contralateral visual informations were transferred to the ipsilateral brain halves.

According to the behavioural experiment, it is known that there is a phenomenon of the interocular transfer in the fish. The fish learned to discriminate colours or patterns only with one eye can discriminate them using the untrained opposite eye alone. Mark (1964) and Mark *et al.* (1973) showed that in the commissural system, the tectal commissure is responsible for the interocular transfer of learning.

While, in the electrophysiological experiment, Mark (1964) recorded the visual responses from the fibres of tectal commissure and Niida (1973) showed the existence of the ipsilateral tectal neurones which can be visually driven.

An analysis of electrical activities of the ipsilateral tectal neurone is of special interest because they should give the clue to find out the possible visual pathway to the ipsilateral hemisphere as well as the mechanism of interocular transfer of learning.

From the present work, the neurones with the following properties are found in the ipsilateral optic tectum: the neurone responding to flicker light, the neurone possessing the receptive field of excitatory centre with inhibitory surroundings. Furthermore, visual responses were recorded from the neurones of the torus longitudinalis and ipsilateral valvula cerebelli.

The present paper will give descriptions of the possible visual pathway to the ipsilateral optic tectum, ipsilateral torus longitudinalis and ipsilateral valvula cerebelli, based on response properties of ipsilateral visual neurone and brain lesion.

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Material and Methods

Preparation and its maintenance

Experiments were performed on the crucian carps (*Carassius auratus langsdorfi* Temminck et Schlegel). The fish was initially anaesthetized with the solution of tricaine methanesulfonate (MS-222). The fish was wrapped with tissue paper soaked in water to keep moistened and secured in a U-shaped holder. The optic tectum was exposed by opening the cranial bone, and the meninges covering the tectum was removed with a pair of forceps, assuring a minimal bleeding. After exposure of the tectum, the medulla was severed with iris scissors at the level of the vagal lobe, thus the fish was immobilized. Simultaneously, the contralateral eye was removed. The movement of an ipsilateral eye ball was prevented by destruction of the oculomotor system by stubbing through the corpus cerebelli down to the base of the brain and the eye ball was also physically fixed by application of the adhesive for surgical operation, alkyl-cyanoacrylate (Aron alpha, Sankyo). During the experiment the gill was perfused with aerated water (at 17°C–18°C) through a tube inserted into the oral cavity.

Recording

Tungsten micro-electrodes were used for extracellular recording. The electrodes were sharpened electrolytically to 4–6 μm in the tip diameter and coated with polystyrol. The electrodes with DC resistance of 15–20 M Ω proved to be the best for isolation of ipsilateral single neurones.

Electrical signals of the single neuronal activities were fed to ordinary AC amplifier and to one beam of the cathode-ray oscilloscope, signal from a phototransistor was fed to the other beam and the photic stimulus was monitored.

Visual stimulation

Visual stimulation was given to the fish out of water. The cornea was prevented from drying by coating it with liquid paraffin. As a light source for visual stimulation, a tungsten incandescent lamp was used. Stationary photic stimuli led through light-guide type fibre optics, the aperture of which was 2 mm, were given at the distance of 10 cm from the left eye. Its maximal luminance was approximately 15000 millilamberts at the cut end of the fibres. When necessary, the luminous intensity was changed covering 4 log units by neutral density filters interposed between light source and light guide. The stationary light was turned on and off by electromagnetic shutter which was driven by an electric stimulator (MSE-3, Nihonkoden). Besides stationary photic stimuli, moving stimuli, which were monitored by potentiometer circuits, were employed. In this case, a hemisphere of acrylic plastic (60 cm in diameter) was supported vertically and the stimulus light through the light-guide was moved on the external surface of the hemisphere.

Lesion and histology

In order to determine the recording sites of neuronal activities visually driven, electrolytic lesion was made in the brain by passing current through the recording micro-electrode (5–20 μA). Immediately after the process, the brain was fixed with 80% alcohol, embedded in paraffin, then serially sectioned at 15 μm and stained with carbol-thionine.

In addition, to observe nervous structure of the brain, the brain was fixed in the Bodian II solution, embedded in paraffin, cut at 15 μm in transverse and sagittal serial section and stained with a modified Bodian method (Otsuka *et al.*, 1960).

Results

Visual responses from the neurones of the ipsilateral optic tectum

In the previous paper (Niida, 1973), the visual responses from ipsilateral tectal neurones were classified into 6 types. Further careful analysis was made concerning 48 ipsilateral tectal neurones in this experiment. As the result, one type of neurone could be newly obtained, and in addition, the receptive field properties of type 4 neurones were studied.

1) Distribution of recording sites

The positions of the neurones described above were ascertained by making an electrolytic lesion in the ipsilateral tectal layer. To identify the small lesion

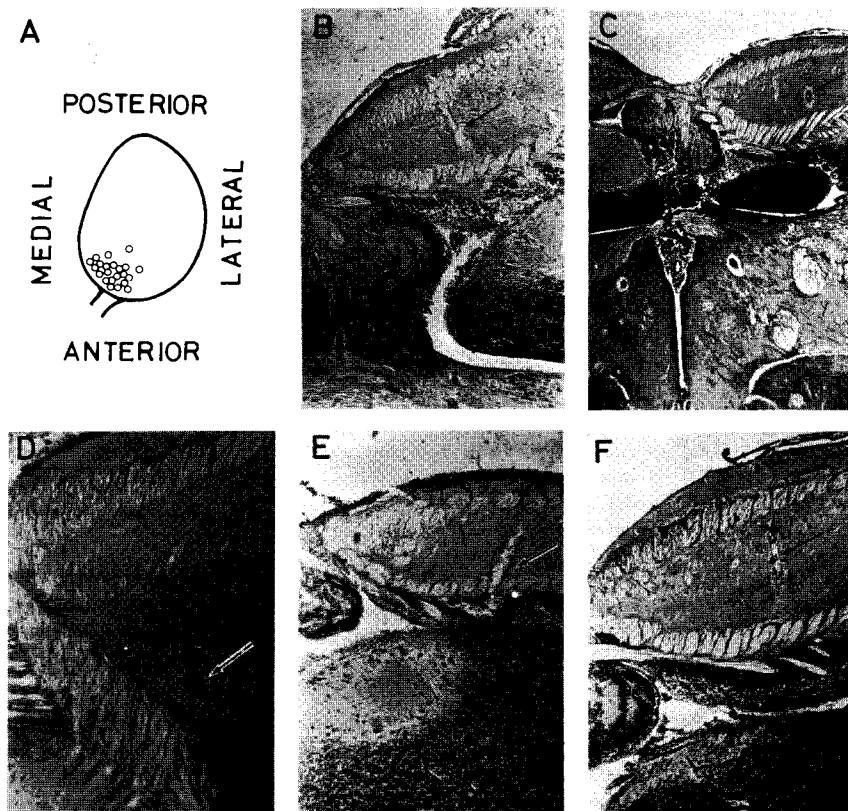


Fig. 1. Positions of the recording electrode in the ipsilateral tectal surface (A) and examples of the electrode lesion in the ipsilateral tectal layer (B to F). B: type 3 neurone; C: type 4 neurone; D: type 5 neurone; E: type 6 neurone; F: type 7 neurone. Arrow: electrode lesion.

in brain sections, criteria are needed to distinguish between actual lesions and stained artifacts. The best indicator of a lesion, which frequently appear as dark stained spots, is its growth and diminution over several consecutive sections. Typical examples thus obtained are shown in Figure 1, where locations of lesions are found in anteromedial or dorsomedial portion. In fact, from these portions, it is easy to obtain the record of visual responses. Figure 1A shows dorsal view of electrode positions in the ipsilateral tectal surface. As is seen from this figure, the visual responses are not obtained at all from lateral and posterior portions. Because most of the receptive field of ipsilateral tectal neurone was not clearly defined in boundary between centre and surrounding area, the analysis of the ipsilateral retinotectal projections have not been attempted systematically in this experiment. However, from the electrode positions in Figure 1A, ipsilateral retinotectal projections are inferred based on the contralateral retinotectal projections which were demonstrated in the previous paper (Niida and Sato, 1972). That is, only receptive fields of far nasal superior area of the left eye are projected onto anteromediodorsal area of the left optic tectum.

2) General characteristics of ipsilateral tectal neurone

Type 4 neurones: These neurones are characterized by possessing the clearly defined receptive field composed of the excitatory centre with inhibitory surroundings. A typical example is shown in Figure 2A. When a part of area within the centre of the receptive field was illuminated with a spot of light, the impulse frequency of this neurone decreased gradually, then it remained at a constant level. During this course, if the surroundings of the receptive field were also illuminated by another spot of light, the centre activity could be completely suppressed. When the light applied to the surroundings were turned off, this suppression was lifted and the activity reappeared. Thus, this type of neurones can be regarded as being similar to the class 1 neurone of the contralateral eye, which was reported elsewhere (Niida and Sato, 1972).

Type 7 neurones: Figure 2B shows the behaviour of these neurones. This type neurones exhibited irregularly maintained discharge in the dark and their receptive field was not clearly demarcated as those of 6 type neurones reported previously (Niida, 1973). Impulse frequency of this discharge was not modified by the stepwise change of light but by flicker light stimulation: increase in frequency of flicker resulted in increase of the response. The volley of impulses appeared to synchronize with each light flash. Because the response pattern of this neurone was not modified by change in the intensity of light, it can be said that this type of neurones are sensitive exclusively to the flicker light.

Visual responses from the neurones of torus longitudinalis

Visual responses of single neurone from torus longitudinalis, which belongs to the region of mesencephalon, were observed following to the section of tectal commissure. When an electrode was driven down along the anteromedial edge

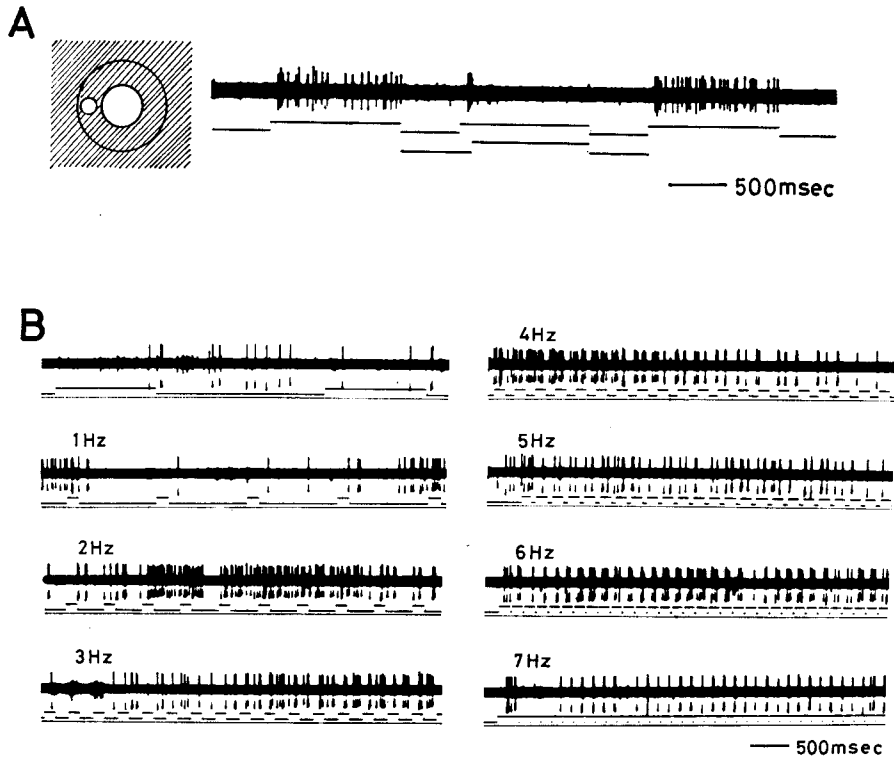


Fig. 2. Typical response pattern of type 4 (A) with diagrammatic representation of the receptive field and type 7 neurone (B). A: when the centre of the receptive field is illuminated by a spot of light, "on"—discharges are elicited but simultaneous illumination applied to the surrounding area suppresses the activities of the centre. B: this neurone does not respond to the transient change in stimulation but responds well synchronizing with flicker light. Lower trace of the records indicates stimulation monitored with phototransistor, upward; light-on; downward: light-off.

of the ipsilateral optic tectum, the neurones responding to visual stimuli could be isolated. But at the posterior medial edge, no visual response could be obtained. Recordings from torus longitudinalis could be more readily obtained than in the ipsilateral optic tectum. The recording sites of this region were shown in Figure 3A. The response types of the neurones recorded from this region were of type 3 and type 4 neurones. The receptive field of type 3 neurones was clearly demarcated, but the receptive field organization was not ascertained. The organization of the receptive field of type 4 was composed of excitatory centre with inhibitory surroundings so that the receptive field was clearly outlined. To determine the visual pathway to this region, the latency of type 4 neurones in this region and of the class 1 neurones in the contralateral optic tectum, which were the same as

type 4 neurones, was measured. The latency was measured just after 3 min light adaptation by varying light intensity covering 4 log units (Fig. 4). There is approximately 40 msec difference of the mean value between these two types of neurones throughout the light intensities used.

Visual responses from the neurones of ipsilateral valvula cerebelli

The recordings of the visual responses from this region were carried out after ablation of the whole ipsilateral optic tectum, making sure that recordings were made in valvula cerebelli. Histological preparation demonstrated that the optic tectum was successfully removed except a small area of the lateral portion (Figure 3B). According to the microscopical observation, valvula cerebelli contains a great number of the granule cells which were deeply stained by thionine. To detect reliably the recording sites, a large quantity of current was passed

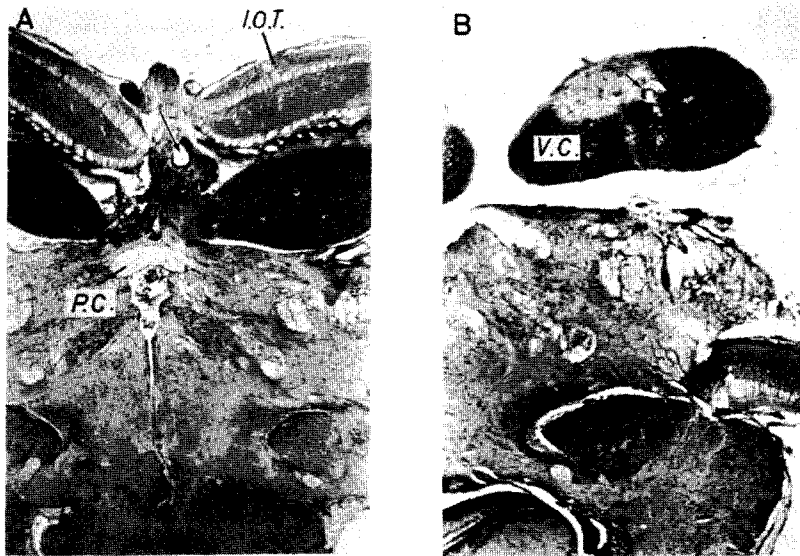


Fig. 3. The recording site in the ipsilateral torus longitudinalis and ipsilateral valvula cerebelli from which visual response was obtained. A: transverse section through the optic tectum. Under the tectal commissure section, the visual response can be recorded from ipsilateral torus longitudinalis. B: transverse section through the mesencephalon and the diencephalon. The visual response of valvula cerebelli is not abolished by the ablation of ipsilateral optic tectum and ipsilateral torus longitudinalis. Arrows show electrode lesions, which demonstrate the recording sites. Carbol-thionine stain. Abbreviation of this and subsequent figures: I.O.T., ipsilateral optic tectum; P.C., posterior commissure V.C., valvula cerebelli; T.C., tectal commissure; T.L., torus longitudinalis; L.O.T., lateral optic tract; P.C. (D), dorsal filament of posterior commissure; P.C. (V), ventral filament of posterior commissure; O.T., optic tectum.

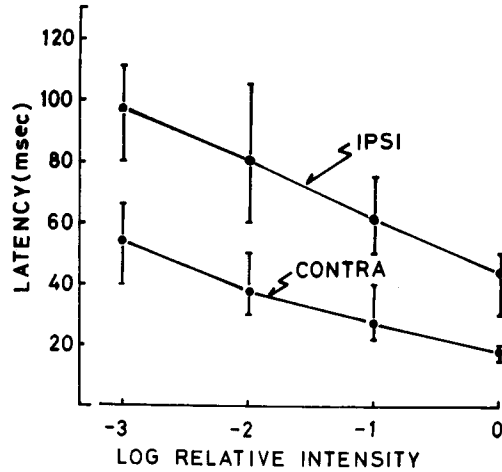


Fig. 4. Comparison of latency for the ipsilateral torus longitudinalis neurone and contralateral neurone. Each solid circle indicates the mean value of 5 neurones.

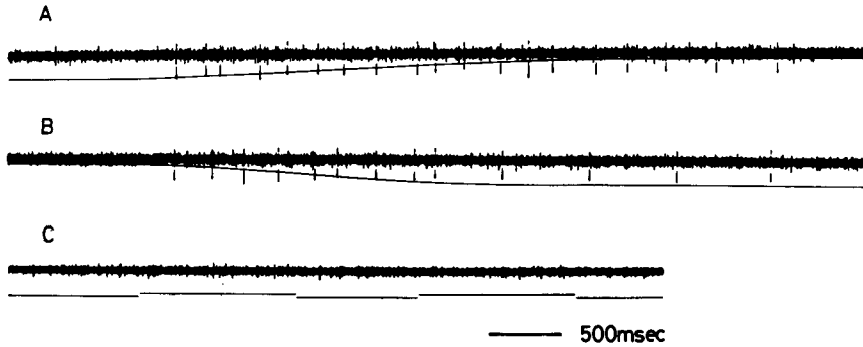


Fig. 5. Response from the type 8 neurone of the ipsilateral valvula cerebelli. A: response to moving spot of light from nasal to temporal. B: the same neurone as A, the response to the opposite direction (from temporal to nasal). Lower trace of the record indicates direction of movement of the spot of light. C: this neurone shows no response to the transient change in light intensity.

through recording electrode ($20 \mu\text{A}$ for 10 sec). Figure 3B shows the actual recording site of visual response from this region. In the valvula cerebelli, the type 3 and type 4 neurone were frequently detectable. The organization of receptive field of type 4 neurone was composed of excitatory centre with inhibitory surroundings. Besides these neurones, the neurones with the following characteristics were found to be present in this region.

Type 8 neurones: These neurones responded to moving spot of light (Fig. 5).

Unlike the type 5 neurones which showed 'habituation' to moving spot of light of a given direction, the neurones of this type did not show 'habituation' to the repetitive application of moving spot light ($15^\circ/\text{sec}$). However, its impulse frequency during the repetitive stimulation was considerably lower than that of the type 5 neurones. And this neurones did not respond to the transient change in light intensity (Fig. 5C).

Lesion of the tectal commissure and ipsilateral optic tectum and histological observation

To determine the visual pathway to ipsilateral hemisphere, several brain lesions were employed. Section of the tectal commissure was severed with fine iris scissors along the medial edge of the contralateral optic tectum, sparing the posterior commissure. The complete transection of the tectal commissure was

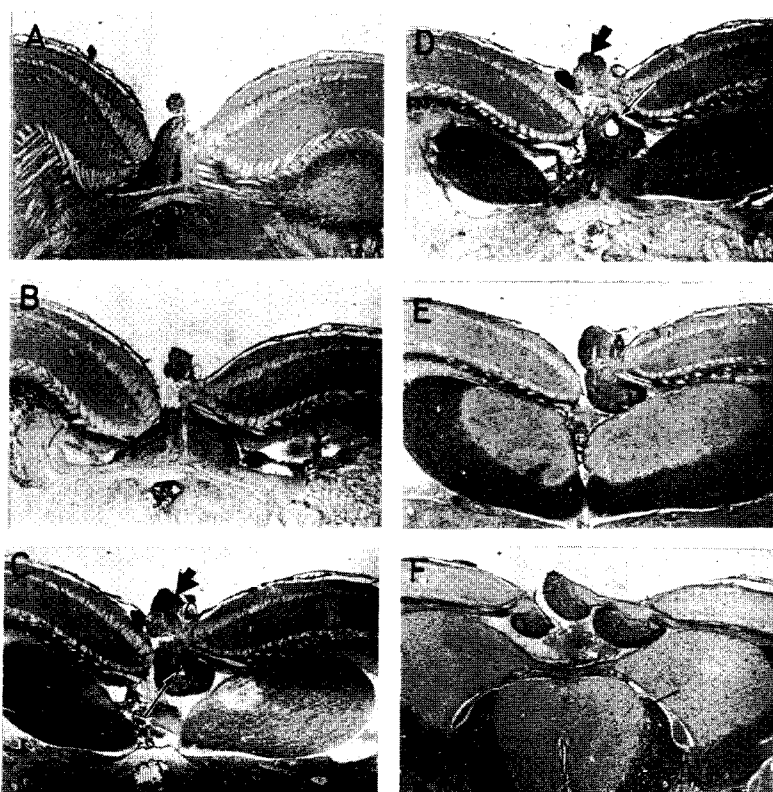


Fig. 6. Transverse section through the optic tectum. Sections are shown anteroposteriorly (A to F). Tectal commissure is completely sectioned and posterior commissure is intact. Thin arrows of C and D indicate the electrode lesion. Carbol-thionine stain.

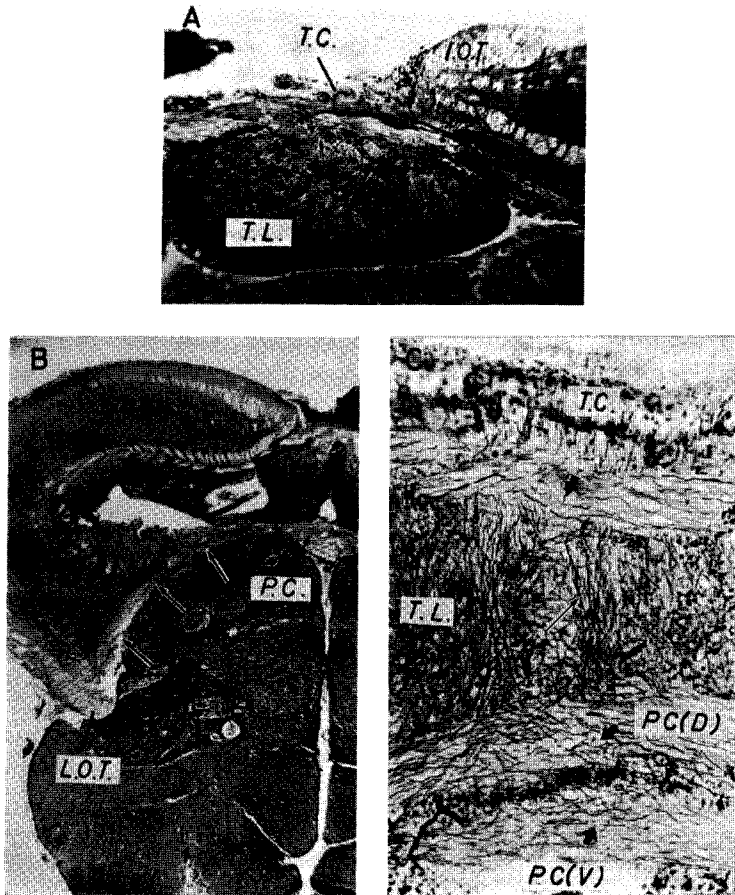


Fig. 7. Transverse section through the anteroposterior portion of the optic tectum. Modified Bodian stain. A: relations of tectal commissure and neighbouring optic tectum. Tectal commissural fibre runs towards the stratum fibrosum profundum of the ipsilateral optic tectum. B: section at more posterior portion than at the level of lateral geniculate nuclei. One filament of posterior commissure (arrows) runs down to the lateral optic tract. C: higher magnification of torus longitudinalis portion. Thick arrows indicate T.C., P.C.(D), and P.C.(V), respectively.

found through anterior to posterior part of the tectum (Fig. 6). The thick arrows of Figure 6C, D indicate contralateral torus longitudinalis isolated by the procedure mentioned above. The ipsilateral torus longitudinalis lies beneath the part indicated by the thick arrow. This procedure did not abolish the visual responses of the ipsilateral torus longitudinalis as stated in the preceding part. The tectal commissural fibres connect each other two halves of the optic tectum. Some of

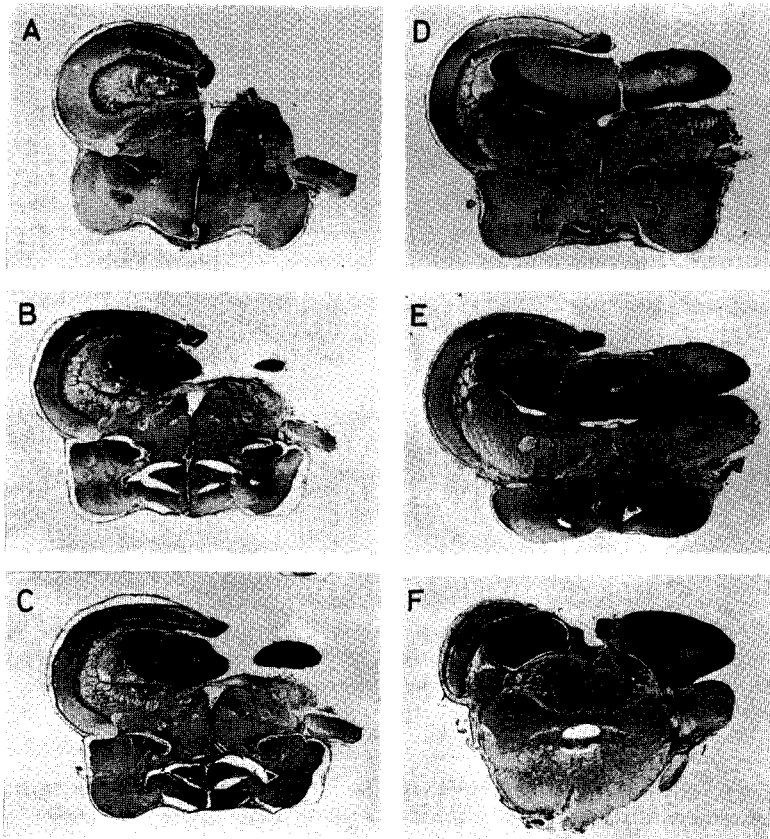


Fig. 8. Transverse section through the whole brain. Sections are shown anteroposteriorly (A to F). Ipsilateral torus longitudinalis and ipsilateral tectum are removed. Carbol-thionine stain.

them enter the torus longitudinalis (the thin arrow in Fig. 7A). The anterior part of the torus longitudinalis is fused with posterior commissure (Fig. 7B). At its anterior part, the branch of posterior commissural fibre was seen to pass in the torus longitudinalis (the thin arrow in Fig. 7C). The posterior commissural fibre curves down to the lateral optic tract which is indicated by the thin arrows in Figure 7B.

Removal of ipsilateral optic tectum

In two fish, complete ablation of the ipsilateral tectum was made (Fig. 8, in this figure the sections were arranged anteroposteriorly). Even after the ablation of the ipsilateral tectum, the ipsilateral visual responses of the valvula

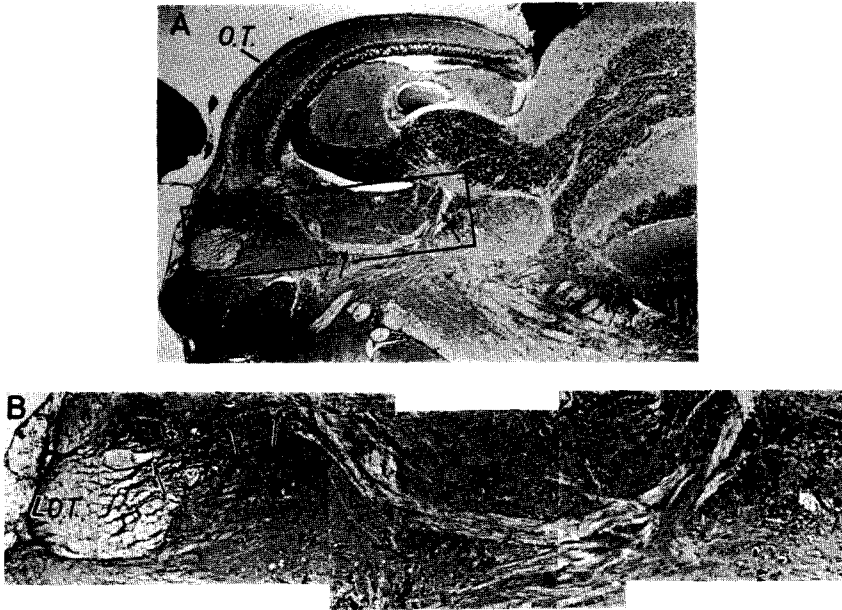


Fig. 9. A: sagittal section through whole brain. Arrows indicate tractus mesencephalo cerebellaris anterior (possibly). B: inset at higher magnification. Arrows indicate the branch of optic tract joining to the tractus mesencephalo cerebellaris anterior. Modified Bodian stain.

cerebelli were found remained. According to serially sectioned histological observation, the anterior part of the valvula cerebelli caudally fused with basal part of mesencephalon, where the fibres from the basal part of tectum were seen to course (the arrows in Fig. 9A) and the branch of the lateral optic tract can be also traced (Fig. 9B).

Discussion

Visual pathway to ipsilateral brain halves

It is commissural system that plays a role to transfer the contralateral visual information to the ipsilateral brain halves. This commissural system involves the tectal commissure, the posterior commissure, and another subtectal commissure (e.g. the post optic commissure) which can be accounted for as possible pathways connecting each other both halves of brains.

1) Possible visual pathways to ipsilateral optic tectum

Tectal commissure: Mark *et al.* (1973) describes that the tectal commissural

fibres terminate mainly in the fibrous marginal layer of the opposite tectum forming spine synapses on the large superficial pyramidal cells and that some cell originated from the tectal commissure is probably the tectal interneurone.

The ipsilateral tectal neurones in the present experiment are characterized by the ambiguity of centre-surroundings organization of the receptive field and the lack of sharp responsiveness to the photic stimuli (e.g. the type 1, 2 and 7 neurones). This may infer that the contralateral visual informations are relayed to the ipsilateral tectal neurone via at least several interneurons in the contralateral optic tectum. On the contrary, type 4 neurones show "on" — discharge during illumination and possess well defined organization of the receptive field. Accordingly, it is supposed that the neurone of this type receives the visual information relayed by fewer interneurone than that of the type 1, 2 and 7 neurones. However, besides tectal commissure the following visual pathway to ipsilateral optic tectum is also available.

Axons of the neurones in the torus longitudinalis: P. Ramon (1899) showed that the axon of the neurone in the torus enter the stratum opticum of the ipsilateral optic tectum. Such connection could be actually traced in the present experiment. This fibre connection between ipsilateral torus longitudinalis and stratum fibrosum marginale in the ipsilateral tectal layer can be seen (arrows in Fig. 10). Furthermore, when the tectal commissure was severed, the visual responses still could be obtained from the neurones of ipsilateral torus longitudinalis. Thus, it is inferred that contralateral visual information may reach the ipsilateral optic tectum via the torus longitudinalis.

Posterior commissure and another subtectal commissure: A part of posterior

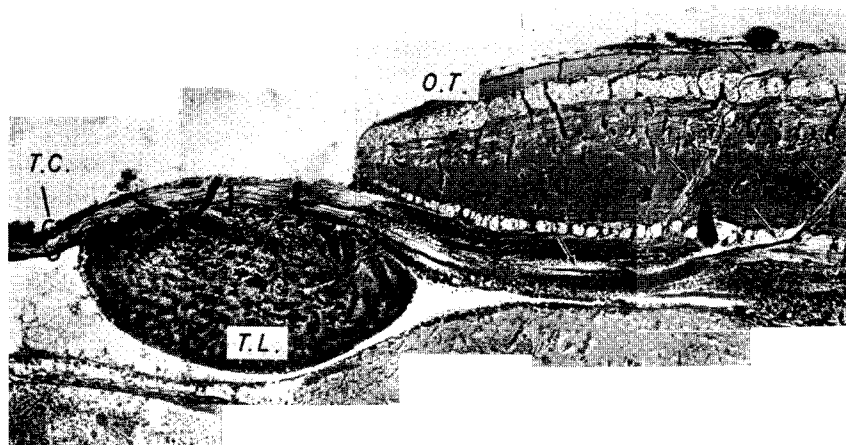


Fig. 10. Transverse section through further caudal portion of the optic tectum. Oblique bundles of fibres from torus longitudinalis can be seen to stream into stratum fibrosum marginale (arrows).

commissural fibres passes to the ipsilateral torus longitudinalis and its stem fibres run caudally down to the ipsilateral hemisphere. Possibly there, contralateral visual informations are relayed to another pathway and travel up along the lateral wall of the ipsilateral brain halves to the ipsilateral optic tectum.

In the frog, Keating and Gaze (1970) demonstrated that ipsilateral optic tectum also receive the visual information of the contralateral optic tectum via the post optic commissure. In the present experiment, the simultaneous sections of tectal and posterior commissure were not attempted. However, the possibility of this visual pathway in fish would not be neglected.

2) Possible visual pathway to ipsilateral torus longitudinalis

As is seen in Figure 7B, torus longitudinalis rostrally fused with the posterior commissure and between them fibre connections can be seen (Fig. 7C). As far as the present histological observation, it is not evident whether these fibres pass in or pass out of the ipsilateral torus longitudinalis. To elucidate this respect, after the section of tectal commissure, photic stimuli were applied to the ipsilateral eye. As the result, visual responses could be obtained from the torus longitudinalis. This implies that a part of commissural fibre enter this region and the posterior commissure carries informations of ipsilateral eye.

Posterior commissure consists of two filaments, dorsal and ventral ones (Ariens Kappers *et al.*, 1935; Mark *et al.*, 1973). Mark *et al.* (1973) describes that dorsal filament goes towards the lateral geniculate nuclei and ventral one towards the midbrain tegmentum. Which of these two filaments would carry the visual information to the ipsilateral torus longitudinalis? The dorsal filament appears to be the better candidate. One of reasons is that the visually driven neurones in the torus longitudinalis show no "adaptation" or no "habituation". Furthermore, the filament to the lateral optic tract (Fig. 7B) probably makes synaptic contact with the cell of the lateral geniculate nuclei, because there is a difference of 40 msec between the latency of type 4 neurones of the ipsilateral torus longitudinalis and that of class 1 neurones in the contralateral tectum. In this case, visual responses from class 1 neurones were obtained in the stratum plexiforme et fibrosum externum which contains optic fibres. If the filament of the lateral optic tract is a collateral of the optic tract, such difference in latency would not occur. The ventral filament running to the tegmentum would not be connected to the torus longitudinalis, because in the midbrain tegmentum there are visual units showing exclusively rapid "adaptation" to the repetitive visual stimuli (Page and Sutterlin, 1970).

3) Possible visual pathway to the valvula cerebelli

After the ablation of paired torus longitudinalis and ipsilateral optic tectum, the activity of neurones visually driven can still be recorded in the valvula cerebelli. The valvula cerebelli is separated from the midbrain basal part at its anterior

part, but it is fused with it at the posterior part (Fig. 9A), where the tract from the basal part of the tectum is seen to course (perhaps tractus mesencephalo cerebellaris anterior), and furthermore, the branch of lateral optic tract joins to this tract (Fig. 9B). According to Leghissa (1955), on the tractus mesencephalo cerebellaris anterior the dorsal filament of posterior commissure is terminating. Which of the two filaments in posterior commissure would terminate there? Dorsal filament connects the tegmentum bilaterally where the activities of visual tegmental neurones were recorded. These neurones show "adaptation" (Page and Sutterlin, 1970) so that dorsal filament originated from tegmentum would carry visual impulses with "adaptation" to the tractus mesencephalo cerebellaris anterior. However, in the present experiment the neurone activated visually in the valvula cerebelli does not show both "adaptation" and "habituation". Consequently, the ventral filament running down to the lateral optic tract would convey the visual information to the ipsilateral tractus mesencephalo cerebellaris anterior. Based on the reasons described above, the visual pathway to the valvula cerebelli was concluded as follow: First, the visual information from the ipsilateral eye is carried via the dorsal filament to the tractus mesencephalo cerebellaris anterior. Secondly, the visual information travels along the tractus mesencephalo cerebellaris anterior to the valvula cerebelli and turns back to the anterior part of the valvula cerebelli. In Figure 11 the possible visual pathways

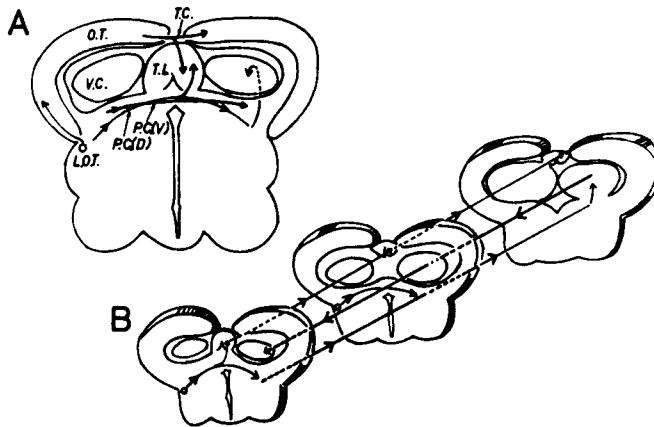


Fig. 11. Schematic representation of possible visual pathways to the ipsilateral optic tectum, torus longitudinalis and valvula cerebelli (A and B).

to the ipsilateral brain halves are schematically summarized. In A of this figure, the tectal commissural fibre entering the ipsilateral optic tectum is localized at the mediodorsal edge. This is determined by the distribution of the recording sites which are illustrated in Figure 1A.

Interocular transfer and ipsilateral visual pathway

Severance of the tectal commissure abolished the interocular transfer of the pattern or colour discrimination (Mark, 1964; Mark *et al.*, 1973). This result suggests that the visual pathway concerning with interocular transfer of visual learning is likely the tectal commissure. Here, a question arises: whether or not the posterior commissure or another subtectal commissure plays a role in relation to the interocular transfer of learning. The present results indicate that at least the posterior commissure can transfer the contralateral visual information to the ipsilateral brain halves as well as the tectal commissure can do. Ingle (1965) described that in goldfish the interocular transfer of a conditioned escape response was blocked if the posterior commissure was cut before monocular training. The experiments of the interocular transfer so far were carried out with respect to the stationary visual cues, e.g. shapes or colours (Sperry and Clark, 1949; MacCleary, 1960; Ingle, 1965; Mark, 1966; Mark *et al.*, 1973). The interocular transfer of information for discrimination by moving visual cues (e.g. the direction of moving spot of light) has not been studied yet. If this experiment is accomplished. The functional roles of the posterior or another subtectal commissure in the interocular transfer may be found out.

Summary

1. Visual responses to light stimuli of the fish eye were recorded from some regions of the ipsilateral brain halves (optic tectum, torus longitudinalis and valvula cerebelli). Recording sites in these regions were determined by electrolytic lesion made through the recording electrode.
2. In the ipsilateral optic tectum, the activities of neurones (type 7) responding to flicker light were recorded. They did not respond to the transient change in a spot of light.
3. Even after severance of the tectal commissure, the activities of visual neurones were recorded in the ipsilateral torus longitudinalis. They were type 3 and 4 neurones.
4. Under ablation of the ipsilateral optic tectum, the activities of visual neurones were recorded from the ipsilateral valvula cerebelli. They were type 3 and 4 neurones. Besides these types of neurones, the activities of neurones responding to a moving spot of light were recorded. They showed no "adaptation" or no "habituation".
5. Type 4 neurone was found from all the regions of ipsilateral brain halves mentioned above. The receptive field of this neurone was composed of an excitatory centre with inhibitory surroundings.
6. Based on the characteristics of the neurone and the brain lesion, possible pathway of the visual information from the eye to the ipsilateral brain halves was proposed.

Acknowledgement: I wish to express my gratitude to Professor Mituo Tamasige, Dr. Mituhiko Hisada, Zoological Institute, Hokkaido University, and Dr. Yoshiaki Sato, St. Marianna University, School of Medicine for their much expert guidance through the course of this work and also for their kindness reading the manuscript.

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