Visual Responses from Ipsilateral Optic Tectum of Crucian Carp

By

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(With 3 Text-figures)

Many investigators failed to record electrical activities of the ipsilateral and binocular neurone from diencephalon and mesencephalic optic tectum of the fish (Jacobson and Gaze, 1963; Sutterlin and Prosser, 1970; Page and Sutterlin, 1970; Niida and Sato. 1972). Only Mark and Davidson (1966) recorded comissural responses from the tectal commissure, which connects the tectal halves.

According to behavioural experiments (Sperry and Clark, 1949; McCleary, 1960; Ingle, 1965; Mark, 1966), it is known that there is a phenomenon of the interocular transfer in fish. The fish learned to discriminate colours or patterns in only one eye can discriminate them using opposite eye alone.

The visual information in fish is transferred to the contralateral optic tectum because of the complete optic nerve crossing. Therefore, the presumable optic pathway which would take part in the interocular trasfer is regarded as commissural fibres between two halves of the brain.

The electrical activities of ipsilateral hemisphere are of special interest on the ground that it may give the clue of the mechanism of interocular transfer as well as the pathway of ipsilateral visual information.

In this experiment the author successfully obtained the responses of single neurones in the ipsilateral tectum. The present paper will give a preliminary description of response types of these single neurones and the recording sites in the tectum.

Material and Methods

Animals

Experiments were performed on the crucian carps (*Carassius auratus langsdorfii* Temminck et Schlegel). The fish was initially anaesthetized in MS–222 and then the

Jour. Fac. Sci. Hokkaido Univ., Ser. VI, Zool. 19 (1), 1973.

medulla was cut with iris scissors at the level of the vagal lobe, thus the fish was immobilized. The fish was secured in a U-shaped holder. The optic tectum was exposed by opening the cranial bone and removal of menings covering the tectum. Simultaneously, the contralateral eye was removed. The movement of ipsilateral eye ball was fixed by applying the adhesive for surgical operation, Alkyl-α-cyanoacrylate (Aron alpha A "Sankyo"). Throughout the experiment the gill was perfused with aerated water (at 15°C–17°C) through a tube inserted in the fish mouth.

Recording and visual stimulation

Tungsten micro-electrodes and conventional recording techniques were used. Detailed account was given elsewhere (Niida and Sato, 1972).

Visual stimuli were performed with the fish in air, in some cases in water, and liquid paraffin was applied to prevent drying of cornea. Stationary photic stimuli through the light guide of the glass fibre optics, the aperture of which was 2 mm, was applied at the distance of 10 cm from the left eye and the light intensity was 240 mL. As a light source, a tungsten incandescent lamp was used. The stationary light was turned on and off by the electromagnetic shutter. Besides the stationary photic stimuli, movement stimuli were employed. In this case, a hemisphere of acryl plastic (60 cm in diameter) was supported vertically and the stimulus light through the light guide was moved on the outer surface of the hemisphere.

Lesion

In order to determine the recording site, electrolytic lesion was made in the tectum by passing current through recording micro-electrode (5 μA, for 10 sec). After this procedure, the brain was fixed in 80% alcohol, embedded in paraffin, serially sectioned at 15 μm and stained with carbol-thionin.

Results

32 single neurones of the ipsilateral tectum were studied and the response types were classified into 6 ones. Ipsilateral neurones were different from contralateral neurones with respect to the organization of receptive field (RF) and the behaviour of neurone to photic stimuli.

In a previous paper (Niida and Sato, 1972) the tectal neurones were classified as follows:

Class 1 neurone (neurone detecting light object)
Class 2 neurone (neurone detecting dark object)
Class 3 neurone (neurone detecting darkness of background illumination)
Class 4 neurone (neurone detecting moving object)

As for the organization of the RF, for example, the class 1 neurone consisted of excitatory centre with inhibitory surrounding area and the class 2 and vice versa. The RFs of these neurones were clearly defined in boundary between centre and surrounding area.

Response type

Type 1 neurones. These neurones showed spontaneous discharges in the dark and responded to off of light with decrease in the rate of discharge. At light-off, off-activation was not observed (Fig. 1A). The RF of this type consisted of inhibitory area only. The contour of the RF was not clearly outlined.

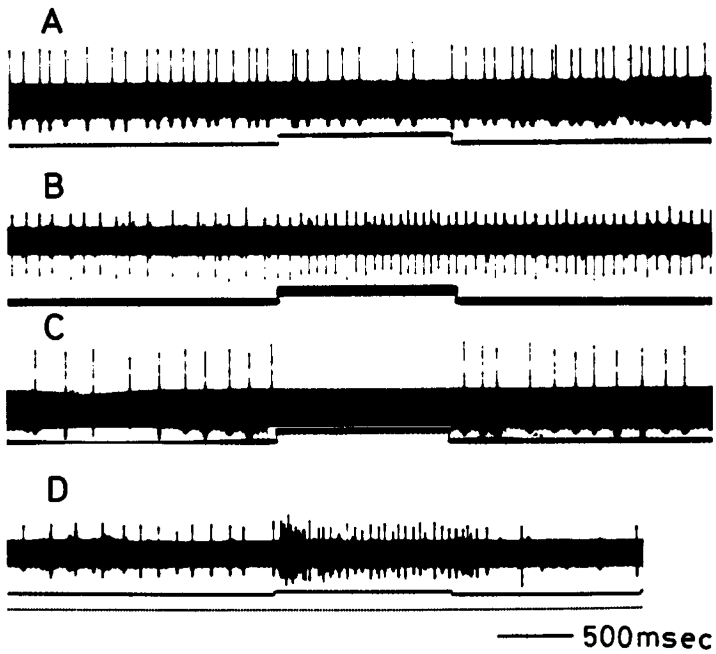

Fig. 1. Typical responses from ipsilateral optic tectum. A: type 1 neurone; B: type 2 neurone; C: type 3 neurone; D: type 4 neurone. Lower trace of each record shows stimulation signalled by the response of a phototransistor; upward: light-on, downward: light-off.

Type 2 neurones. The neurones of this type behaved in opposite way to the type 1 neurones, that is, in the dark spontaneous discharges were similarly observed but at light-on, impulse discharges were increased to a some extent. At light-on, they did not increase transiently (Fig. 1B). The RF of this type possessed excitatory centre only and the RF was not exactly demarcated.

Type 3 neurones. The spontaneous dark discharges were completely supressed by illumination (Fig. 1C). In this respect, the type 3 neurones were similar to the dark detector neurone. But at light-off, no off-activation was elicited, and the spontaneous dark discharges were at a low frequency level in comparison to the dark detector neurone. Furthermore, if repetitative stimuli were applied to these neurones, they showed the tendency of habituation. The circumference between centre and surrounding area could not be exactly defined.

Type 4 neurones. These neurones also exhibited spontaneous discharges in the dark. The spontaneous discharges disappeared just after illumination. Unlike the type 2 neurones, at light-on, the impulse frequency increased transiently (Fig. 1D). The general feature of this response resembles to light objec detector neurone during illumination. Among these neurones the RF was outlined clearly. The organization between centre and surrounding area of the RFs were not ascertained here, but in view of a well defined RF, it is expected that the RF consists of excitatory centre with inhibitory surrounding area.

Type 5 neurones. The neurones of this type responded to moving spot light in all directions (Fig. 2A, B). These neurones responded to light-on with a brief

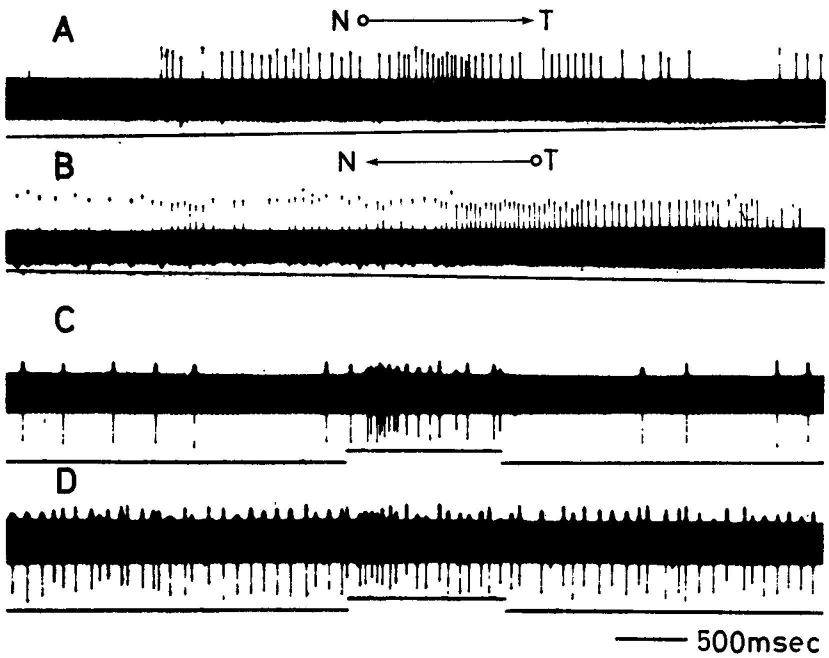

Fig. 2. Typical responses from the ipsilateral optic tectum. A and B: type 5 neurone. This neurone responds to moving light stimulus anywhere within RF. A: response to moving light stimulus from nasal (N) to temporal (T). B: the same neurone as A, response to the opposite direction. Lower trace shows direction of moving light stimulus. C and D: type 6 neurone. This neurone responds to both the sound of clapping hands of the investigator and visual stimulation. C: response to pure visual stimulation. Spontaneous discharges are normally observed. D: the same neurone as C. An increase in the rate of spontaneous discharge occurs by clapping hands. Simultaneously visual stimulation is applied.

burst but did not to light-off. This brisk on-response instantly showed habituation. But at another part within the RF, the brisk on-response reappeared. The RF of this type neurone was very large like the class 4 neurone (3 times the size of the RF of the class 4 neurone) but it was not outlined clearly.

Type 6 neurones. Besides the 5 type neurones above mentioned, multisensory neurones were found. These neurones responded to both sound of low frequency and photic stimuli. In these neurones spontaneous discharges were normally shown. Light-on gave sustained discharges (Fig. 2C). The spontaneous discharges were increased by clapping of the investigater's hands in air over the fish (Fig. 2D). When the fish was submerged in water and turbulence of the water surrounding the fish was made, the neurone of such a type responded with more increment of spontaneous discharges than in clapping of hands. This fact implies the existence of neurones with visual and lateral line convergence on the optic tectum. The RFs of these neurones were not also well defined.

Recording site

Electrical activities of ipsilateral neurones were frequently recorded at anter-

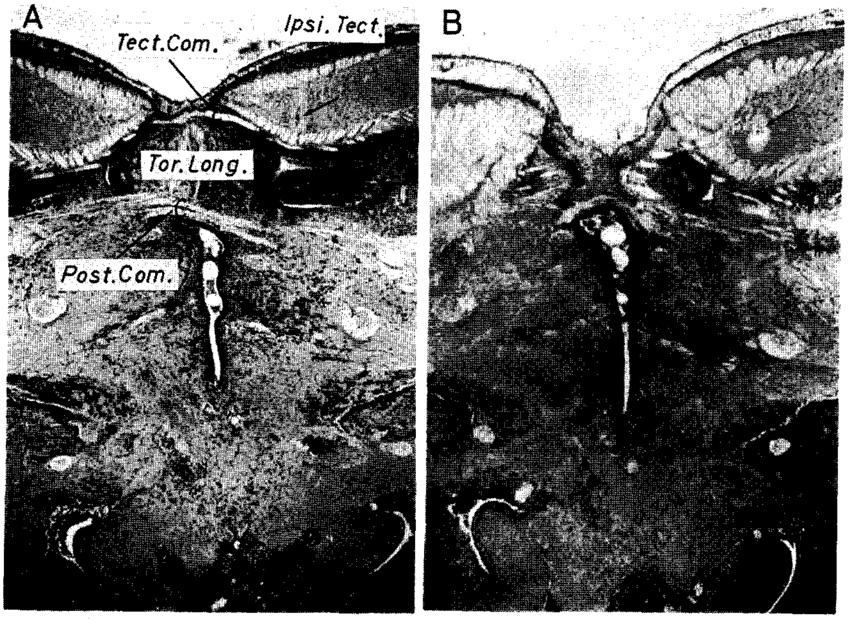

Fig. 3. A and B show cross sections through the optic tectum in different fishes, stained with carbol-thionin. Arrows indicate the lesion of the ipsilateral optic tectum. In each photograph the bar represents 200 μm. Recording sites are described in the text. Ipsi. Tect.: ipsilateral tectum; Tect. Com.: tectal commissure; Tor. Long.: torus longitudinalis; Post. Com.: posterior commissure.

ior portions and the medial edges of the ipsilateral optic tectum. At another portions no record from ipsilateral neurones has been obtained yet. Fig. 3A and B indicate two examples of the recording sites recorded from the type 1 neurone and the type 4 neurone respectively, and the recording sites were both *strutum griseum internum.*

Discussion

Recording from the ipsilateral tectum

It is very difficult to record from single neurone of the ipsilateral tectum. In the previous paper (Niida and Sato, 1972), a unit analysis of the contralateral tectum was carried out but no ipsilateral neurone was found. The reason why the recording from the ipsilateral tectum was successfully obtained was emphasized in following points. First, one eye was removed. When the contralateral eye is alive or covered with black cap, the diffused faint light from the stimulating light applied to the ipsilateral eye induces the contralateral responses. On the contrary, in the case of removal of one eye, there is no visual input from the contralateral eye. Therefore, it is easy to isolate the ipsilateral neurones and the units recorded in the ipsilateral tectum are able to be identified as the ipsilateral neurones. Secondly, the medulla was cut. In this case the inhibition from the periphery to the tectum was eliminated so that the neuronal activity of ipsilateral tectum may be enhanced. Whether or not a disinhibition of the ipsilateral tectum by means of cutting medulla occurs has not been ascertained systematically. However, cutting medulla generally seems to raise the neuronal activity of the ipsilateral tectum.

Neurone of ipsilateral tectum

The paired optic tecta are connected by two commissures, the tectal and posterior commissure. Mark and Davidson (1966) recorded responses from fibres of the tectal commissure, these commissural fibres are rhythmically active for prolonged periods in the dark and respond to light by a decrease in the rate of discharge. The responses of the type 1 neurones are similar to that of the tectal commissure, but there is no rebound acceralation in the type 1 neurones unlike responses from the commissural fibres. All the responses from the commissural fibres were of this type. On the other hand, the ipsilateral neurones were classified into various types. Since the tectal commissure terminates in the ipsilateral tectum, various response types should be obtained from the commissural fibres. A question is raised here. Why does occur the difference between neuronal responses of commissural fibre and those of the ipsilateral tectum? There are two answers. One of them is given by cut medulla. This procedure eliminates the inhibition to the tectum from the periphery. As a rsult, various response types may be produced. The second is given by the existence of termination to the ipsilateral tectum via another visual route, for example the posterior commissure.

With exception of the type 6 neurones, the ipsilateral neurones of 5 types are purely visual. But these neurones also have possibility to be multisensory neurones. Because the cutting medulla may shut out the input from another sensory, somatic and acoustico-lateral line. From this point of view, responses as seen from Fig. 2C and D will be due to imperfectly cut medulla. As to this multisensory type in the tectum, Callens *et al.* (1967) have reported the existence of neurones with retinal and lateral line convergence on the optic tectum of goldfish. Present results conformed their findings.

During the present studies activities of the neurone binocularly driven have not yet been able to be recorded satisfactorily. The responses of contralateral units were more sensitive than those of ipsilateral ones. Accordingly, if the two eyes are alive, it is very difficult to isolate binocular unit. Among the units ipsilaterally driven binocular neurones may be involved.

Interocular transfer and ipsilateral neurone

Present results indicate that visual information from one eye is immediately transferred to the ipsilateral tectum via the commissural fibres.

It is not apparent whether all visual informations by way of the commissural fibres are related to interocular transfer or not. But at least it may be said that some visual informations from one eye will concern with interocular transfer. Interocular transfer of learning with the behavioural experiment was carried out regarding to visual discrimination of pattern (Mark, 1966). As long as a fine pattern discrimination is performed, it is required to possess a well defined RF. Accordingly, the neurones with a well defined RF (e.g. the type 5 neurones) may be involved in interocular transfer of learning with pattern discrimination.

Summary

1. Visual responses were obtained from the ipsilateral optic tectum of the crucian carp by cutting medulla and they were classified into 6 types.

2. Among these response types the neurone with visual and lateral line convergence was found in the ipsilateral tectum.

3. The RF of ipsilateral unit, except the type 5 neurone, was not clearly demarcated.

4. Ipsilateral units were recorded at anterior portions and medial edge of the ipsilateral optic tectum. Two examples of recording site were shown.

5. Whether visual information via the commissural fibre relates to interocular transfer or not was discussed.

Acknowledgement: The author wishes to express his gratitude to Professor Mituo Tamasige, Zoological Institute, Hokkaido University for his expert guidance throughout the course of these experiments and for his kindness in reading the manuscript.

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