An Analysis of Visual Responses in the Optic Tract and Tectum of the Crucian Carp[1)]

By

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(With 12 Text-figures)

The electrical activities of the tectal neurones of the teleostean fish have been recorded by many investigators (Jacobson and Gaze, 1963; Cronly-Dillon, 1964; Mark and Davidson, 1966; Sutterlin and Prosser, 1970). However, the exact functional role of the fish's optic tectum remains obscured, though the tectum is generally regarded as a higher order centre in the visual system.

In the teleostean fish, the whole set of axons from the retinal ganglion cells of one eye crosses over completely in the chiasma to the contralateral side before entering into the tectum, thus forming the optic tract. The tectum is laminated and, unlike the retina, it consists of several discrete layers, in which various neurones extend their dendrites and axons in horizontal as well as in vertical direction (Cajal, 1911; Witokovsky and Dowling, 1969; Leghissa, 1955; Schwassmann and Kruger, 1968; Ito, 1970).

The structural difference found between the retinal ganglion and the optic tectum could be reflected in the integrative properties of these two systems. Accordingly, it is natural to postulate that responses of the units recorded at the optic tectum should carry more integrated visual information than those recorded in the retinal ganglion.

To verify this postulation, the characteristics of neurones at each level of the visual system must be investigated. From this point of view, a preliminary analysis of single neuronal units has been performed in the previous paper (Niida and Sato, 1972).

The present paper deals with further descriptions of quantitative and qualitative analysis of characteristics of the neurones in both the optic tract and tectum.

1) Contribution No. 931 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

Material and Methods

Experiments were performed on the crucian carps (*Carassius carassius* Temminck et Schlegel). The fish was immobilzed by intraperitoneal injection of d-tubocurarine chloride (usually 6 mg/kg body weight). At this anaesthetic level, the eyes remained immobile. The skull was opened and then the optic tectum was exposed. The exposure of the tract was done by removing olfactory lobes. The exposed tectum and tract were covered with agar jelly or liquid paraffin to prevent from drying. Throughout the experiment the gill was perfused with tap water (12°C, 800 ml/min) through a tube inserted into the fish's mouth. In this manner, the fish could be kept in a suitable condition for detecting the neuronal activity for 30 hours or even more.

Recording: Single neurone activity from the tract and tectum was obtained using tungsten electrodes. The electrodes were sharpened electrolytically to 1–5 μ in the tip diameter and coated with polystyren up to their tips. Electrical signals of the single neurone activities were led to an ordinary AC amplifier and to one of the cathode-ray oscilloscope channels. With a phototransistor connected to the second channel of the oscilloscope the photic stimulus was monitored. The relevant data were photographed and the latency of response and impulse frequency were measured.

Optical stimulation: Visual stimuli were applied to the fish eye exposed in air, and the liquid paraffin was frequently applied to the eye. A tangential screen was positioned at a distance of 40 cm from the left fish eye, onto which stationary or moving spots were projected by an ordinary projector. As it was described in the previous paper (Niida and Sato, 1972) that tract and tectal neurones of crucian carps did not respond to photic stimulus of the ipsilateral eye, records in this experiment were usually obtained from the right optic tract and tectal neurones responding to the stimulation of the left eye only. A tungsten incandescent lamp was used as a light source for optical stimulation and the illumination intensity of projected image on the screen was controlled by interposing neutral density filters to change the intensity in steps of 0.3–0.4 log unit covering 5 log units. The stationary white spot was turned on or off by an electromagnetic shutter which was driven by an electric stimulator (MSE-3, NIHONKODEN). With this apparatus complete turning on or off of light was accomplished within 2 msec. A background illumination applied on the entire screen surface was generated also by the other projector and its intensity was controlled by the ND filters.

In order to indicate the receptive field of tract and tectal neurones, ordinate and abscissa (naso-temporal, dorso-ventral axes) were drawn on the screen so that the origin of these coordinates was faced to the centre of the eye ball. Thus, the positions of the receptive fields of all the neurones obtained were represented by a pair of angular coordinates measured from these axes. Moreover, axes of the receptive fields were also represented by subtended angles from the eye. Further experimental procedure will be described in later section.

Results

Part 1, Response of single neurone of the optic tract and tectum

In this experiment, 130 optic tract neurones of 156 studied and 345 tectal neurones of 367 studied were analyzed. From the response characteristics of neurones to the movement of a small black or white card across the receptive field, they could be classified into three easily recognizable groups. With a neurone of the first class, when a small white card moved on a dark background into the

centre of the receptive field of the neurone, the discharge frequency of neuronal impulses transiently increased. Removal of the card produced a transient suppression of impulse discharge. While, a black card moving on a bright background caused the neurone of this class to increase the discharge as it was withdrawn from the centre of the receptive field but it did not as it entered into the centre of the receptive field. Neurones belonged to the second class responded in the opposite manner: the movement of a white card from the receptive field produced a transient increment of impulse frequency and its movement into the receptive field a transient suppression of it, and with a black card, the response was vice versa. Neurones belonged to the third class responded with a strong sustained discharges to both the white and the black cards moved in one particular direction, either horizontal or vertical, but responded with a complete suppression of impulse discharge to those moved in the opposite direction. The response of the first class is to be expected from a neurone possessing a receptive field with an "on"-centre and that of the second one neurone possessing a receptive field with an "off"-centre. Neurones of the second class will be further divided into two subclasses by the details of responses obtained from the receptive field organization which will be described in the later section. On the other hand, the neurones of the third class seemed to consist of neurones having a directionally sensitive receptive field.

Class 1 Neurones: Neurones detecting light objects moved into the centre of receptive field (CRF)

1) These neurones were found in both the tract and tectum, and in the tectum they were obtained from stratum pelxiforme et fibrosum externum, s. griseum externum, and s. plexiforme internum. These neurones are characterized by possessing the receptive field (RF) consisted of excitatory centre with inhibitory surrounding area.

2) When a part of area within the CRF was illuminated with a spot of light, the impulse frequency increased transiently just after a short latent period, reached to a maximum and then decreased to a low frequency level. This level maintained for several minutes, or even several hours and the impulse discharges disappeared imediately by the light-off. If simultaneous illuminations were applied to the CRF and also the surround of the RF (SRF), the activity of the CRF was depressed. At the light-off to the SRF, its depression was erased and the activity reappeared. These neurones responded to transient changes of background illumination, with discharges at the time of sudden light-on and with supression of discharge at the time of sudden light-off. After the sudden light-off, however, these activities recovered slowly in the dark.

3) These neurones responded with strong sustained discharges, when the small objects lighter than the background moved into the CRF and also when the darker ones moved out of the CRF. If the lighter objects were stopped in the CRF, the neurones gave maintained discharges. These responses to moving or

stopping objects did not depend on the shape or size of the objects, but did on the contrast of their luminosity against the background illumination.

Class 2 Neurones: Neurones detecting dark objects moved into the CRF

1) These neurones were found in both the tract and tectum, and in the tectum they were obtained from s. griseum externum and s. plexiforme internum. These neurones showed prolonged discharges in darkness and they were characterized by possessing the RF of an inhibitory centre with excitatory surrounding area.

2) When a part of area within the CRF was illuminated with a spot of light, the prolonged discharges were completely suppressed, followed by a long, probably infinite inhibitory period. When the light spot was turned off, these neurones exhibited an excitatory response which was the similar time course of impulse frequency to that of the class 1 neurones excited by light-on. If the SRF was illuminated with a light spot, impulse discharges were larger than those in the dark. These neurones responded to a change of background illumination, with discharges on sudden turning-off of light and with suppression on sudden turning on of light. After the sudden light-on, however, these activities slowly recovered.

3) These neurones responded to the moving objects in the opposite relation to those of class 1 neurone, that is, excitatory responses were induced by movement of small darker objects into, or lighter objects out of the CRF.

Class 3 Neurones: Neurones detecting the darkness of background illumination

1) These neurones were found in the tectum only and they were obtained from s. plexiforme et fibrosum externum and s. griseum externum. These neurones showed prolonged regular discharges in the dark and they were characterized by possessing the RF of an inhibitory area only.

2) When a part of area within the RF was illuminated with a light spot, a brief "on" response appeared, followed by a prolonged inhibitory period. At turning off of light these neurones exhibited the "off" response of the similar time course of discharge frequency to that found in the class 2 neurone. Transient changes of the background gave a brief "on" or "off" response, and then impulse discharges gradually increased after a short inhibitory period. Finally, the impulse frequency reached to a costant value (Fig. 1). This final value depended on the light intensity of the background, and decreased in increment of the intensity.

3) These neurones responded a little to the moving objects, and the excitatory responses were induced by movement of darker objects into or lighter objects out of the RF.

Class 4 Neurones: Neurones detecting moving-objects

1) These neurones were found in the tectum only and they were obtained from s. plexiforme et fibrosum externum and s. griseum externum. These neurones

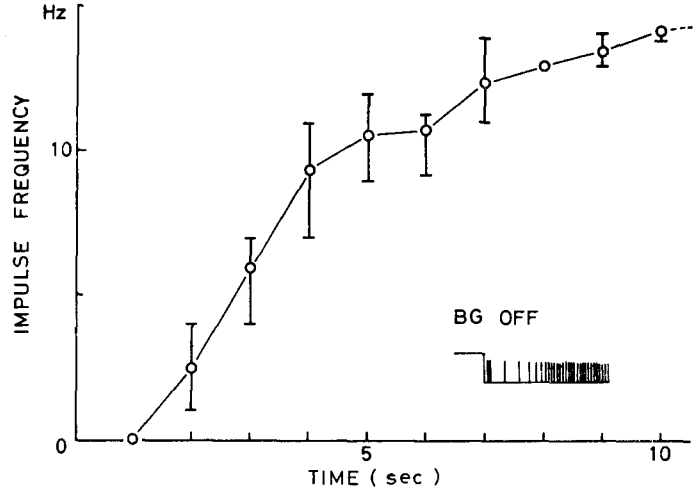

Fig. 1 Time course of impulse discharge of the class 3 neurone The preceeding illumination of the background (3 mL) was abruptly turned off (at origin time 0). Transient "Off" response is not shown in this figure. Values of impulse frequency were taken by counting impulse number within 1 sec. The data were obtained from three records of the same neurone and each vertical line indicates three samples and open circle indicates a mean value of them.

showed sustained discharges in both dark and light, and they were characterized by possessing the RF responding exclusively to the moving objects but not to the stationary stimuli.

2) Transient changes of illumination given to the RF or to the background did not change the impulse frequency of these neurones, but sometimes gave a brief "on" or "off" response. Moreover, the impulse frequency of these neurones was independent of the changes in light intensity and illuminated area.

3) These neurones were directionally sensitive to the moving objects, and they responded to both light or dark objects moved in one direction (excitatory direction) and showed an inhibition of response to movement in the opposite direction (inhibitory direction). The excitatory directions of these neurones approximately coincided with the vertical and horizontal axes of the fish's eye. Moreover, their response to movement along the excitatory direction depended on the velocity of movement, and the maximal response was elicited with the movement of about 20°/sec.

Part 2, Visual projection upon the optic tectum

A question is raised whether neurones classified into each of the classes in the Part 1 are localized in a given area of the tectal surface or not. The answer

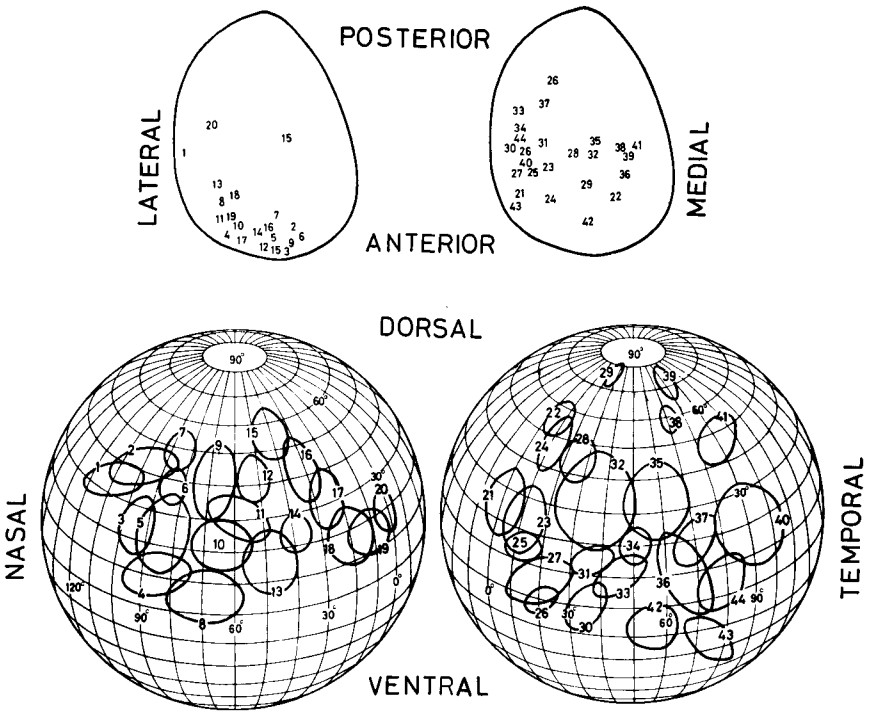

Fig. 2 Projection of the centres of receptive field of the left eye onto the right optic tectum in the class 1 neurones. Left side figure indicates the projection of the nasal area, right side the temporal area, respectively. Corresponding electrode positions in the dorsal view of the tectum (upper figures) and centre of the receptive fields (lower figures) are related with the same numbers.

will be given by the test done on the receptive field projection of sigle neurones upon the optic tectun. The RFs of the neurones recorded from the tectal surface as well as from the tract, have been determined by the following procedures. When the impulses of a single neurone of the tract or tectum were clearly isolated in these amplitude from the noise level, the response class of the neurone was determined by the results described in Part 1. Then, the RF was explored with a spot of light (5° in subtending angle and 3 mL in luminous intensity) moved horizontally or vertically across the RF against the dark background. We could easily recognize the boundary of the CRF of the class 1 and the class 2 neurones, as these neurones responded to the moving light spot with a strong burst of impulses. However, the outer circumference of the SRF of the neurones could not be defined by this method, so that the only CRF was outlined in the class 1 and the class 2 neurones. The position of the frontal edge of the spot, moved from the centre toward the external boundary of the RF in the class 1 neurone (the reverse in the class 2 and 3 neurones),

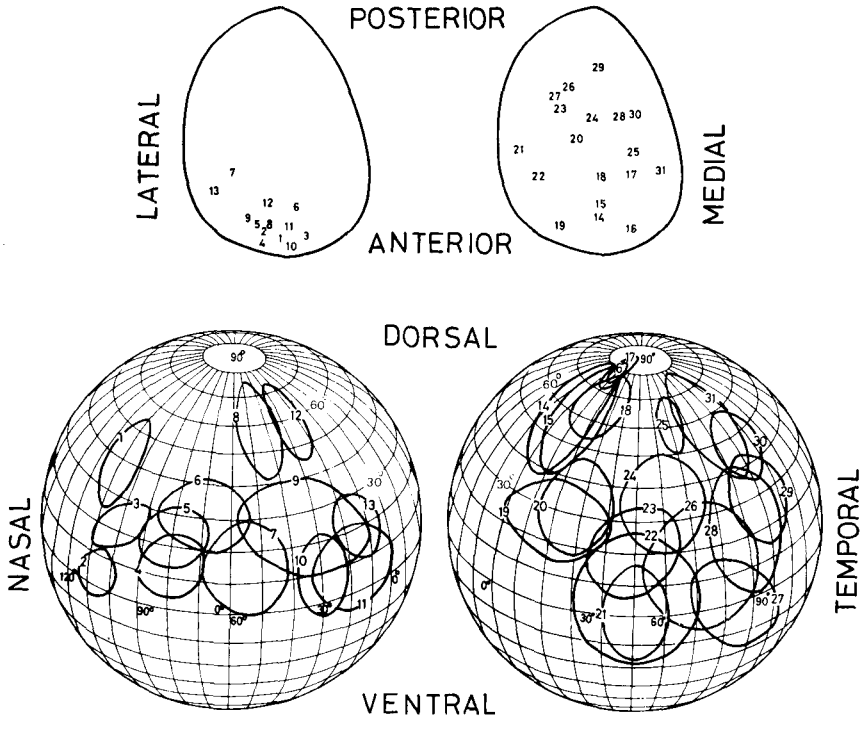

Fig. 3 Topographical arrangement of the centres of receptive fields and corresponding electrode positions of the class 2 neurones. All the expressions are the same to those of Fig. 2.

was marked on the screen, and regarded as the outline of CRF. In the class 4 neurone which showed sustained discharges of impulses in the dark and which had immensely large receptive field, an approximate estimation of the boundary was obtained by the repetitive movements of the spot along the excitatory and inhibitory directions spanning a short distance in a different area of the screen. In each unit analysis, one field required 3–5 min in mapping. After this, angular coordinates representing the position and subtending angular size of the RF were measured and recorded. Simultaneously, the electrode position was designated on the profile of dorsal view of the tectal surface. Then another neurone was obtained and the procedure repeated. All the classes of neurones were studied in this manner.

The results were generally similar to those of previous investigators (Jacobson and Gaze, 1964; Shwassmann and Kruger, 1965). In common with all classes of neurones, the RFs of the upper half of the left eye were projected onto dorsal

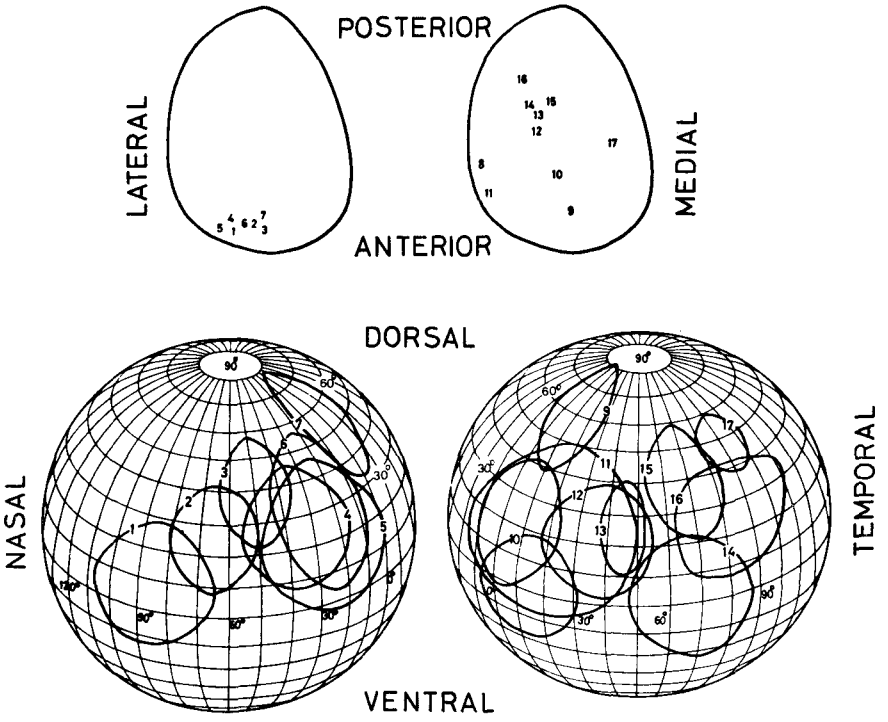

Fig. 4 Topographical arrangement of the receptive fields and corresponding electrode positions of the class 3 neurones.

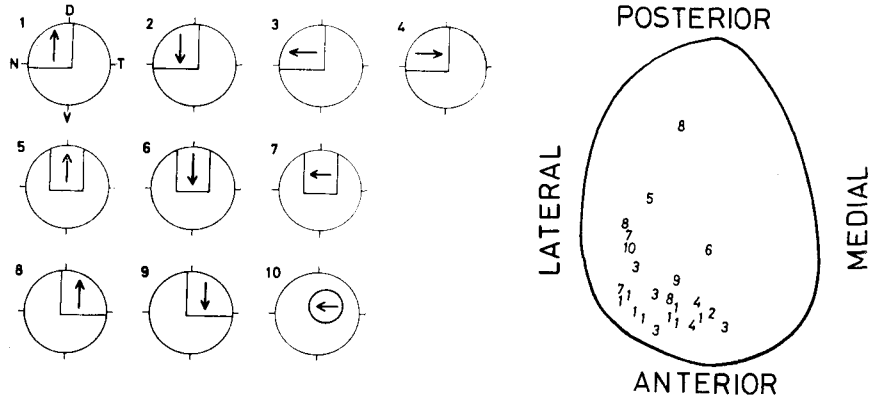

Fig. 5 The receptive fields of the left eye (left figures) and corresponding electrode positions of the right optic tectum (right figure) of the class 4 neurones. The circle of each figure of the left hand indicates the whole receptive field of the eye and the arrow indicates an excitatory direction. Neurones having the same receptive field and excitatory directions belong to the same number.

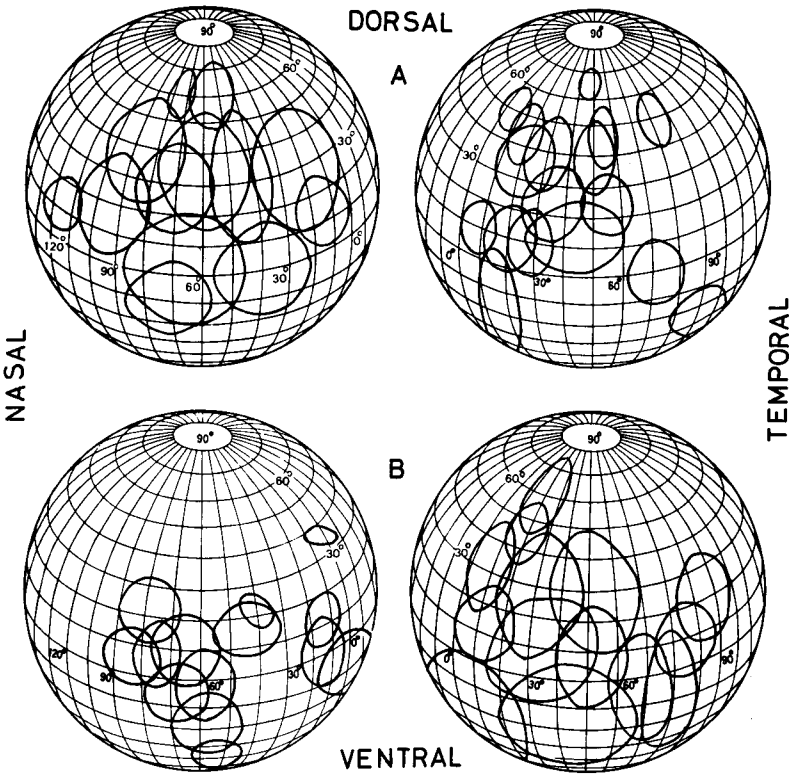

Fig. 6 Topographical arrangement of receptive fields of tract neurones particularly ventral area of the eye. The position of electrode in the tract was not recorded in this experiment. A: the class 1 neurones B: the class 2 neurones.

surface of the right optic tectum. Nasal areas of the eye were projected to the anterior portion and temporal areas were projected to the posterior middle dorsal surface of the tectum (Fig. 2, 3, 4, 5). As for lateral surface of the tectum, the projections from the lower half of one eye were not found except in a small part. This was because of difficulty of driving the electrode to the lateral surface of the tectum. But there certainly existed projections from that part to the lateral surface, since the units recorded at the tract contained the ones related to the lower half as well as the ones related to the other portions of the visual field (Fig. 6). As stated above, the RFs of all neurones registered in this experiment were equally distributed on the surface of the tectum, they were not localized in a given area. Thus, it was concluded that the neurones were distributed in reference to the visual field rather than the functional specialization, and one particular class of neurones was not restricted in a particular area of the tectum.

As for the shape and dimension of the RF, we discussed in the previous paper (Niida and Sato, 1972)

Part 3, Time course of impulse discharge of class 1 and class 2 neurone

As was described in previous part, among the four response classes, the class 1 and the class 2 neurones clearly displayed an initial transient increase in impulse discharge frequency which decayed to a lower constant frequency by transient change of illumination. A general feature of the change of impulse discharge of these neurones with change of illumination is illustrated in Fig. 7. As is seen in this figure, the time course of the impulse discharge can be classified into three periods, namely 1) latent period, 2) dynamic period, and 3) static period.

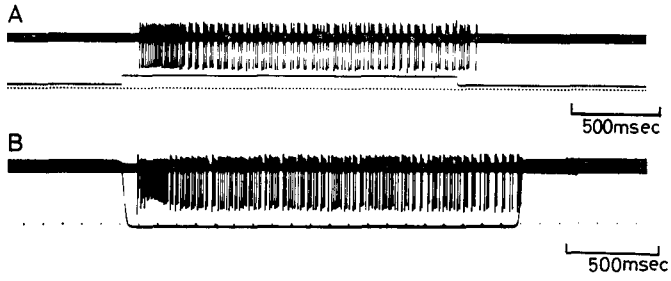

Fig. 7 Typical responses of the class 1 (A) and class 2 (B) neruones of the tract to changes of illumination of the light spot within the centre of the receptive field. Light – on (upward deflection one) and – off (downward) are indicated by the second line of each record.

(1) Duration of latent period (latency): Latency of "on" response in the class 1 neurone had a linear relation to light intensity, and shortened with an increase of intensity (Fig. 8). Though the value of latency varied from neurones to neurones, at the strongest light intensity employed (3 mL) the latency was from 32 to 68 msec. Fig. 9A clearly shows that the point of first spike onset becomes increasingly later with decrease of light intensity. On the other hand, the latency of "off" response in the class 2 neurone which was obtained by the same procedure slightly shortened with decrease of light intensity. However, Fig. 9B shows that the time of first spike onset after light – off was nearly constant, and independent of light intensity. In addition, Fig. 10A also shows a constant latent period between 40 msec and 50 msec with changes of light intensity, where stimulus duration was 1 min. When a stimulus of short duration was applied, the latency was shorter as a function of the duration (Fig. 10 B). Thus, the parameters which determine the latency of the class 2 neurone were stimulus intensity, stimulus duration and probably stimulus area.

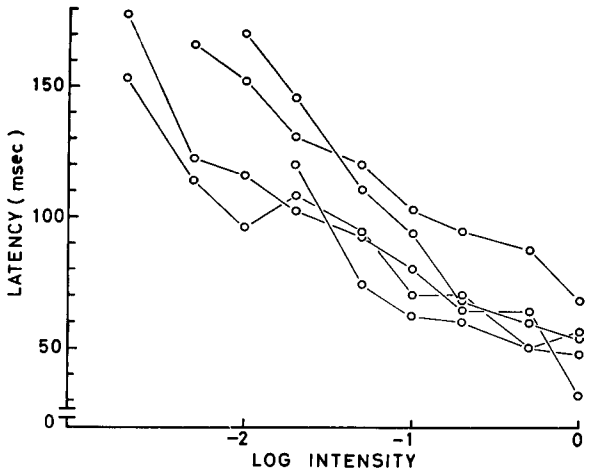

Fig. 8 Latent period of 5 neurones of the class 1 neurone plotted on a logarithmic scale of light intensity. The maximal light intensity (log I=0) employed was 3mL and size of the spot was 5°.

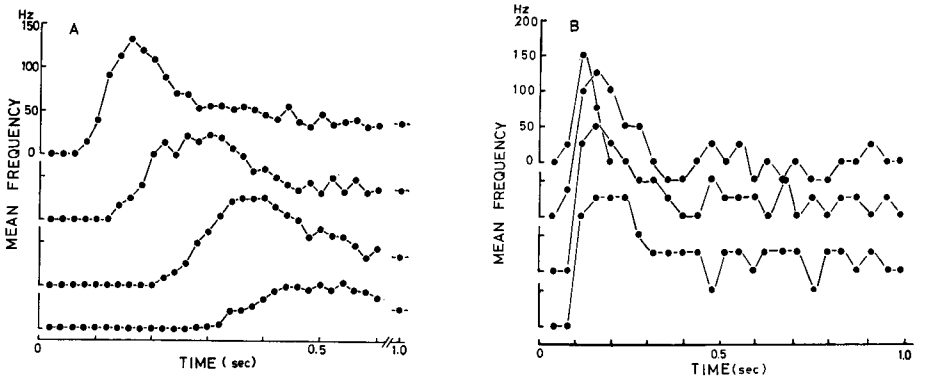

Fig. 9 Discharge frequency of tectal neurones after the transient change of illumination (at the time 0). Frequency values were obtained by counting impulse number within 20 msec in A, and 40 msec in B. A: the class 1 neurone. Stimulus intensity of the uppermost curve is 3 mL. Subsequent curves represent the response to the intensities of one decade steps and 1/10, 1/100, 1/1000 of 3 mL, respectively. Interstimulus interval is 9 sec, and stimulus duration 1 sec. B: the class 2 neurone. The uppermost curve is 1/2 of maximal intensity (3 mL), subsequent curves represent 1/20, 1/200 of it respectively and the lowermost curve is of complete darkness. Duration of preceding illumination was between 170 msec and 290 msec.

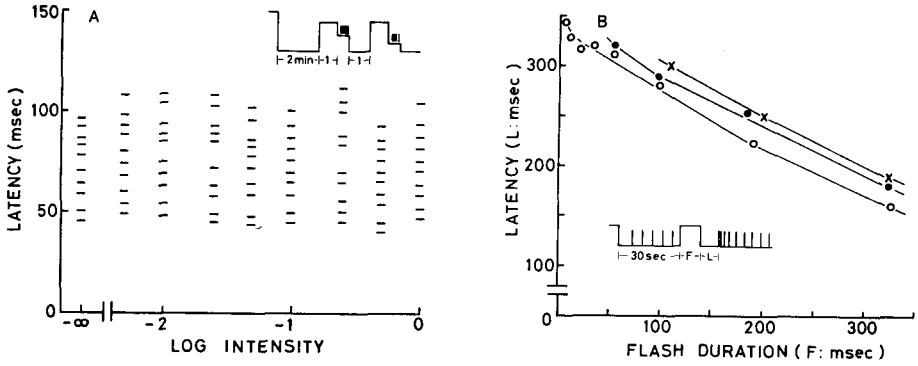

Fig. 10 Latent period of the class 2 neurones to transient decrements (A) and different durations of the preceding illumination (B). A: the fixed duration of preceding illumination was 1 min, and interstimulus interval was 2 min. B: interstimulus interval was 30 sec. and stimulus intensity of the lower curve was the maximal intensity (3 mL), the middle curve and upper curve are 1/10 and 1/100 of the maximal intensity, respectively.

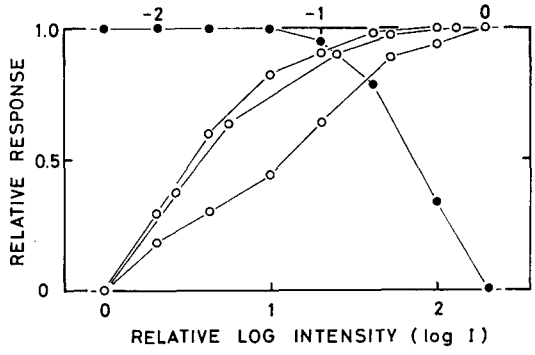

Fig. 11 Peak frequency of the dynamic response with different photic stimuli. The size of light spot was 5°. The origin of abscissa indicates the intensity of just above the threshold in each neurone. The intensity of the spot was abruptly increased from a complete dark level to the test light level in the class 1 neurones (lower scale) and decreased from the conditioned level (the intensity of subthreshold) to the test light level in the class 2 neurone (upper scale). Open circles: the class 1 neurones, solid circles: the class 2 neurone The response magnitude was expressed in term of relative response R/Rmax, where the R, peak frequency, was obtained by counting the impulse number for 100 msec starting from the first impulse and Rmax represents the maximal peak frequency of a response to a stationary stiumlus (at least 3 log units above the threshold).

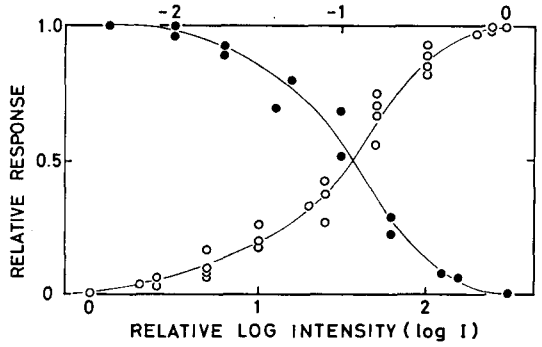

Fig. 12 Relation between the light intensity and impulse frequency of static response of the class 1 neurones (open circles) and the class 2 neurones (solid circles). The expressions are same to those of Fig. 11. Static frequency was obtained from the impulse number during 1 sec after 1 sec from the light stimulation onset or cessation.

(2) Dynamic period: After a given latent period, these neurones exhibited a transient increase in impulse frequency, which reached to a peak and decreased into a constant level. This dynamic impulse discharge lasted for 150–200 msec in the class 1 neurone and 200–300 msec in the class 2 neurone. In the former neurone, the peak frequency increased linearly with increase of light intensity. However, these impulse frequency reached to the maximum (110 imp/sec) by changing intensity over 100 times of the threshold. In the latter neurone the peak reached to 135 imp/sec, but the maximal response was found in light intensity change of approximately 10 times the threshold (Fig. 11).

(3) Static period: At a constant light intensity, these neurones exhibited a steady discharge. The relation between frequency of steady response and light intensity is graphically shown in Fig. 12. As is seen from Fig. 12, as a whole, the contour of these curves is sigmoidal and also linear at the optimum light intensity.

Discussion

Jacobson and Gaze (1964) classified the tectal neurones in the gold fish as follows: "On"-centre units with inhibitory surround, "on-off" unit, "on" unit and "off" unit. In some respect, their "on"-centre unit with inhibitory surround is not consistent with the class 1 neurones particulaly in respect to the response in the inhibitory area. They described that some of the units show the responses to movement of light spot or black disk in one direction through the receptive field but not to that in the opposite direction. From the present experiment, the RF of the class 1 neurone has a gradient of response degree to light stimuli. Eventually the movement of light spot from the periphery to the centre of the RF gave a prominent response against the opposite movement. However, this neurone highly

depends upon the light intensity, therefore the neurone does not match with the defined characteristics of the movement detector.

The behaviour of "on-off" unit observed by Jacobson and Gaze is similar to the class 2 neurone found in this study. The neurones of this class were as widely distributed and commonly found as the class 1 neurones in both the tectum and tract. Its RF consists of "off"-centre with excitatory surround and was of circular or oval shape. The side by side arrangement of "on-off" zone which Jacobson and Gaze has shown in their figure is in fact identical to the oval receptive field of the class 2 neurone. They state that this "on-off" unit also shows directional selectivity. In this experiment, the class 2 neurone was found to respond to a light spot moving radially from the centre to any direction but produced no response to the spot moving toward the centre. Thus, it is probable that they observed only a part of these responses.

Directional selective unit of Barlow et al (1964) and Michael (1968) does not depend on light intensity. Accordingly, the term of directional selectivity which Jacobson and Gaze employed is a misnomer. In one way or another, all the neurones registered in the present experiment respond to movement stimuli, but it is not appropriate to call of them as the movement detector.

"On" unit by Jacobson and Gaze seems to be identical to the "on"-centre unit with inhibitory surround. It is likely that they overlooked inhibitory effect because of its weak influence. The "off" unit by Jacobson and Gaze can be interpreted also in the similar way. This is identical to the class 2 neurones of the present study but they overlooked the effect of excitatory area because of its weak influence. The neurones found as the class 1 and the class 2 units are of prototype units (Kuffler, 1953; Wagner et al, 1963), i.e. "on"-centre unit with inhibitory surround, or reverse. As pointed out by Wagner and others, the balance between the two areas determines the firing patterns of a given ganglion cell. Thus, inconsistency between neurones of this experiment and those of Jacobson and Gaze may be due to the difference in dominancy of each zone, which is perhaps variable by light intensity level. This relation also exists spatially. For example, the boundary between "on" and "off" areas can produce an "on-off" response. Extending this view point, the class 3 neurone of this experiment may be said to be of the same category of the class 2 neurone. In the optic tectum, the class 3 and the class 4 neurones were found besides the class 1 and the class 2 neurones. The findings of the class 3 and the class 4 neurones only in the optic tectum indicate that output from retinal ganglion is further modified through laminal structure of the optic tectum.

The functional roles of the class 1 and the class 2 neurones may be interpreted as follows: Firstly these neurones, detect the information of brightness and darkness of light. As is seen from Fig. 7A, 7B, 9A and 9B, the dynamic and static phase of these neurones coincide with dynamic and static circumstances of photic stimulus. That is, the dynamic phase concerns with dI/dt (I: stimulus intensity, t: time), and the statci phase with degree of brightness or darkness.

For example, as to the class 2 neurone, the highest curve of Fig. 9B represents only the dynamic phase and does not show the static phase. In this case, the light intensity is one-half of the strongest intensity (3 mL). Thus at the level of this light intensity the static phase is supressed. On the other hand, in the tectum, there exist the class 3 and the class 4 neurones. The class 3 neurone shows a gradual increase of impulse frequency (Fig. 1). This may indicate that this type of neurone is suitable for the abstraction of gradual change of light. The class 4 neurone responds to movement stimulus with directional selectiveness and strongly to optimal speed. Accordingly, at the level of optic tract of crucian carp, the neurone concerning abstraction of darkness and brightness and orientation of light is formed. Whilst, in the tectum there exist detecting neurones of gradual change of brightness or darkness, and direction and speed of moving stimulus.

Moreover, it is presumable that the functional difference of tract and tectum should appear in the shape and dimension of the RF. But the present experiments were all performed on the fish in air. The further experiment with the fish placed in water is necessary to determine the receptive field properties.

Summary

(1) Distinct classes of response patterns were found by single neurone analysis in the optic tract and tectum of the crucian carp as follows: 1) the class 1, and 2) the class 2 neurones in the tract, whilst 1) the class 1, 2) the class 2, 3) the class 3, and 4) the class 4 neurones in the tectum. And the class 3 neurone was newly registered, which had not been reported in the fish by previous investigators.

(2) The visual projection to the tectum was investigated electrophysiologically by the single unit response.

(3) Topographical arrangement of receptive field of the tectal neurone was roughly represented on the tectum. In common with each class of neurone registered, nasal areas of the eye were projected to the anterior portions, and temporal areas to the posterior middle dorsal surface of the tectum.

(4) All neurones registered were not localized in a given area of the tectal surface.

(5) On the basis of the single neurone analysis, the difference in neuronal response between the observation of Jacobson and Gaze and that of us was discussed.

(6) The functional roles of the tectum in the visual system were given.

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