J Comp Physiol (1982) 147:287–297

Journal
of Comparative
Physiology · A

Vision and Electroreception: Integration of Sensory Information in the Optic Tectum of the Weakly Electric Fish *Apteronotus albifrons*

Joseph Bastian
Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019, USA

Accepted March 17, 1982

Summary. The responses of single neurons to visual and electrosensory stimulation were studied in the optic tectum of the weakly electric fish *Apteronotus albifrons*. Most of the cells recorded in the region of the tectum studied, the anterior medial quadrant, were poorly responsive or completely insensitive to flashes of light or to bursts of AC electrical stimuli applied to the entire fish. However, these cells gave vigorous responses to moving visual or electrosensory stimuli. Most cells showed differences in their response contingent upon the direction of the stimulus movement and most received input from both the visual and electrosensory systems. Electrosensory responses to moving stimuli were depressed by jamming stimuli, 4 Hz amplitude modulation of the animal's electric organ discharge, presented simultaneously with the moving stimulus. However, the jamming signal presented alone typically evoked no response. Moving visual stimuli, presented simultaneously with the electrosensory, were usually able to restore the magnitude of a response toward its value in the unjammed situation. For most of the cells studied the receptive fields for vision and electroreception were in register. In some cases the visual and electrosensory components could be separated by presenting the two types of stimuli separately, or by presenting both simultaneously but with some amount of spatial separation, which causes the two to be misaligned relative to the fish. In other cases the individual responses could not be separated by spatial manipulations of the two stimuli and in these cases differences in the alignment of the two types of stimuli could cause changes in the intensity of the cells' responses.

Abbreviations: AM amplitude modulation; *EOD* electric organ discharge; *PLLL* posterior lateral line lobe

Introduction

The vertebrate optic tectum, mammalian superior colliculus, is known to be an important information processing center for various visual-motor behaviors (see Ingle and Sprague 1977 for review). The tectum is also known to receive input from a variety of non-visual sensory systems including the auditory, somatosensory and vestibular systems (Drager and Hubel 1976; Skarf and Jones 1981). The tectum has also been shown to receive input from the infrared sensory system of rattlesnakes (Hartline 1974; Newman and Hartline 1981) and anatomical (Carr et al. 1982) as well as physiological evidence (Bastian 1981c) shows that the tectum of weakly electric fish receives electrosensory information. A number of these studies show that the various sensory modalities are represented in a spatiotopic fashion within the tectum and that the various maps for the different modalities are, to a large extent, in register.

South American weakly electric fish possess an active electrosensory system consisting of either a muscular or neural electric organ which generates an electric field around the fish's body. Electroreceptors, modified lateral line elements scattered over the surface of the animal's body, are sensitive to the voltage developed across the animal's skin due to this discharge. Any alteration in this voltage, as might be caused by the presence of some object having a conductivity different from that of the water or due to the additional voltage from the discharge of another electric fish, alters the responses of these receptors and is thereby perceived by the fish. Any of the following recent reviews can be consulted for more complete information regarding the electric sense (Bullock 1982; Heiligenberg 1980, 1977; Scheich and Bullock 1974; Szabo and Fessard 1974).

0340-7594/82/0147/0287/$02.20

The eyes of these fish are relatively small, the animals are primarily nocturnal and blinded individuals do not behave noticeably differently compared to sighted animals. Vision is probably not the most important sense for these animals. Therefore, the processing of multiple types of sensory inputs by the tectum might be more easily understood in a tectum that is less dominated by the visual input. This report describes the responses of single tectal cells of the weakly electric fish *Apteronotus albifrons* to a variety of visual and electrosensory stimuli presented singly and simultaneously. Particular emphasis was placed upon experiments designed to reveal interactions between these two sensory modalities.

Materials and Methods

The weakly electric fish *Apteronotus albifrons* was used exclusively in these experiments. Surgical procedures and neurophysiological recording techniques were the same as described previously (Bastian 1976). The animals were suspended in the center of a black plexiglas tank measuring 45 cm long, 45 cm wide and 11 cm deep. Water conductivity was 10 kΩ·cm and temperature was between 23 and 25 °C. The experimental tank and recording and stimulation apparatus were housed in a darkroom and recording electrodes were advanced remotely from outside this darkroom.

Electrosensory Stimulation. Two types of electrical stimuli were used. Stationary stimuli consisted of sinusoidal or squarewave amplitude modulations (AM) of the fish's electric organ discharge (EOD). These were produced by recording the EOD via two electrodes placed near the animal's head and tail and multiplying this signal by a square or sinusoidal modulation signal. The output of the multiplier circuit was thus an amplitude modulated version of the animal's own waveform and this was applied through two large silver wire electrodes placed in the tank, 20 cm from either side of the fish.

Moving stimuli consisted of metal or plastic, conducting or non-conducting, rods 0.5 or 1 cm in diameter and 5 cm in length, oriented vertically and moved parallel to the long axis of the fish at a rate of 5 cm/s. The distance between the moving object's trajectory and the fish was usually 1 cm. The movement device has been previously described (Bastian 1981a).

Visual Stimulation. Flash stimuli were delivered to the entire visual field by a Grass model PS22 photostimulator with the amplitude setting at 1. Moving visual stimuli were produced by two different methods. In one type of experiment, the electrosensory stimulus, conducting or insulating rods, contained a bundle of fiber optics fibers which could be illuminated by a remote light source. This light was visible through a 2 mm slit running the length of the rod. Therefore, this single object could provide an electrosensory or a visual and an electrosensory stimulus. In the second type of experiment where moving visual stimuli were to be presented alone or where spatial separation between a visual and electrosensory stimulus was required, the visual stimulus was a 2 mm diameter lucite rod illuminated via a fiber optics light guide. Both stimuli were carried on separate micromanipulators, which were attached to the movement device, so that they could be accurately aligned, the center of each on a line perpendicular to the long axis of the fish, or displaced relative to one-another. Displacements were always parallel to the long axis of the fish, i.e. in the plane of the movement.

The lucite rod is a non-conductor and therefore potentially detectable via the electrosensory system. When it was used, control experiments were run in darkness with the rod moving close to the animal to determine if the cell under study could detect this non-conductor. The cells normally did respond to this stimulus, therefore the distance between the moving object's trajectory and the fish was increased until no response was evoked. The visual and electrosensory stimuli were then presented at this distance from the fish. The visual stimulus was placed just in front of, closer to the fish, than the metal or plastic objects which were covered with black fabric to reduce their visibility.

The moving visual stimuli were not bright so that shadows and reflections within the apparatus were minimal. The illuminance of the lucite rod was approximately 0.05 lux and that of the light source within the metal and plastic rods was about 0.09 lux.

Results

Two distinctly different single unit categories were seen in the region of the optic tectum studied. Units having low frequency spontaneous activity (< 10 Hz) were usually encountered from just below the tectal surface to approximately 150 μm in depth. The spikes produced by these cells were of long duration and an individual unit could be observed over long distances of electrode travel. These units were usually weakly responsive to strobe flashes and to moving objects but rarely responsive to tone bursts of electrical stimuli. Responses consisted of increases and/or decreases in activity and in the case of the moving object stimulus, responses sometimes differed dependent upon object illumination. The large spike size and the long distance of electrode travel over which these could be recorded suggests that these recordings were from the large dendrites of the pyramidal neurons found in the stratum opticum and stratum fibrosum et griseum superficiale (Schroeder and Vanegas 1977).

The second, more thoroughly studied cell category, was routinely found in deeper layers of the tectum, 200 to 450 μm, and marks left by iontophoresis of the dye alcian blue from recording electrodes showed that these recording sites were usually in the stratum griseum centrale or the stratum album centrale. Both of these regions receive input from the torus semicircularis, a major electrosensory processing area in these fish (Carr et al. 1982). Units of this second category usually lacked spontaneous activity and were usually completely insensitive to flashes of light or to bursts of electrical stimuli. It was necessary to constantly stimulate the fish with moving electrical or visual stimuli while searching for this type of cell.

In addition to these major categories, occasionally spontaneously active cells which responded to both moving and flashed visual stimuli were recorded from superficial regions and spontaneously active cells responsive to stationary electrical stimuli were found in deeper regions. These units had small, very fast

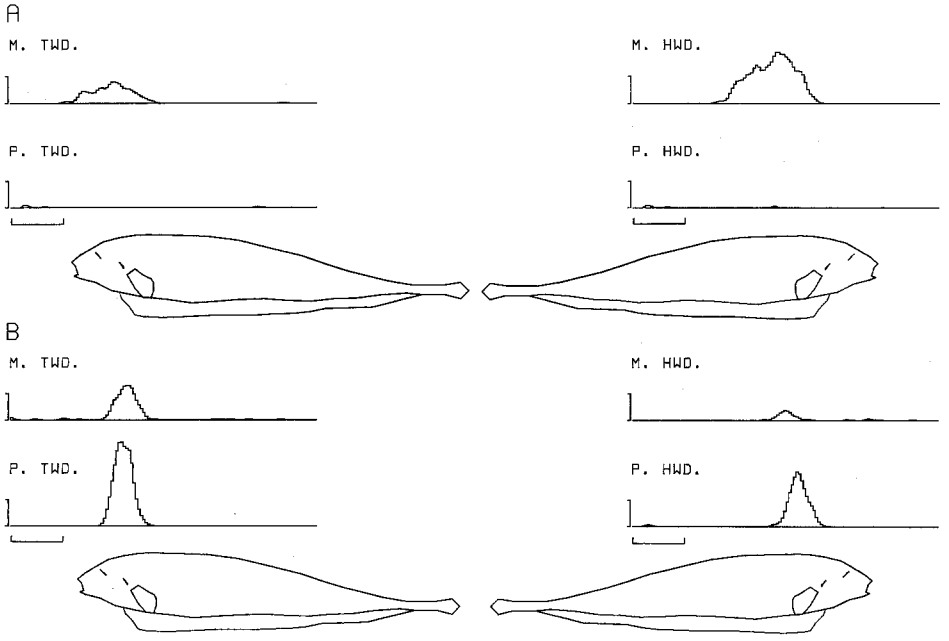

Fig. 1A, B. Responses of deep tectal cells to moving electrosensory stimuli in darkness. In all figures of this type *M* indicates metal object, *P* plastic object. Outlines of the fish are scaled to the length of the histograms so that position and duration of the responses indicates the size and position of the cell's receptive field. Unless indicated otherwise the vertical and horizontal tic marks correspond to 10 spikes/bin and 2.5 cm and 0.5 s respectively. Movement direction is always from left to right and *TWD* and *HWD* indicate tailward and headward movements. The histograms in **A** summarize the responses to 15 replicates of the movement and those in **B** are based on 10 replicates

spikes and might correspond to the activity of the afferent visual and electrosensory fibers respectively.

Recordings were limited to the anterior medial quadrant of the tectum, a region whose cells have receptive fields over the anterior half of the body. Responses of the neurons in the remaining regions of the tectum will be described in a subsequent report.

Electrosensory Responses in the Absence of Light

Responses to Metal and Plastic. Cells suspected of being electrosensory are typically stimulated with identically shaped metal and plastic moving objects. Since these objects have markedly different conductivities but produce similar patterns of turbulence when moved through the water, cells receiving an electrosensory input produce different responses, and those receiving a mechanoreceptive input produce similar responses to these objects (Enger and Szabo 1965; Hagiwara et al. 1965; Scheich and Bullock 1974; Scheich 1977; Bastian 1976, 1981a, b).

Responses of tectal cells to moving objects varied widely. A number of cells were encountered that responded well to the metal object but were virtually unresponsive to the plastic (Fig. 1A). The reverse was also seen but much less often. Usually either type of object would evoke responses but either the magnitude of the response, number of spikes evoked, or the shape of the response histogram varied with objects of opposite conductivity (Fig. 1B). A third type (Fig. 2A) gave very similar responses to the objects of opposite conductivity. The responses of this latter type usually showed small but statistically significant shifts in the position of the response relative to the fish, dependent upon object conductivity. In the case shown, the responses to the non-conductor peaked approximately 5 mm more anterior than did the responses to the metal object. Such a small difference in the responses, due to the conductivity of objects, is not a convincing indication of an electrosensory input. However, the alterations in the responses of these types of cells to moving objects in the presence of 'jamming' electric fields verifies that they receive an electrosensory input.

The Effects of Jamming Stimuli. A well described phenomenon associated with electrolocation systems is their susceptibility to what have come to be called 'jamming stimuli'. Objects moving near to the animal cause amplitude modulations (AM's) of the voltage across the skin and electroreceptors. Foreign signals, EOD's of other fish, sum with the EOD of a given fish resulting in a beat waveform. This beat results in an amplitude modulation of the voltage sensed by the electroreceptors and if the frequency of the beat is between approximately 1 and 10 Hz, electrolo-

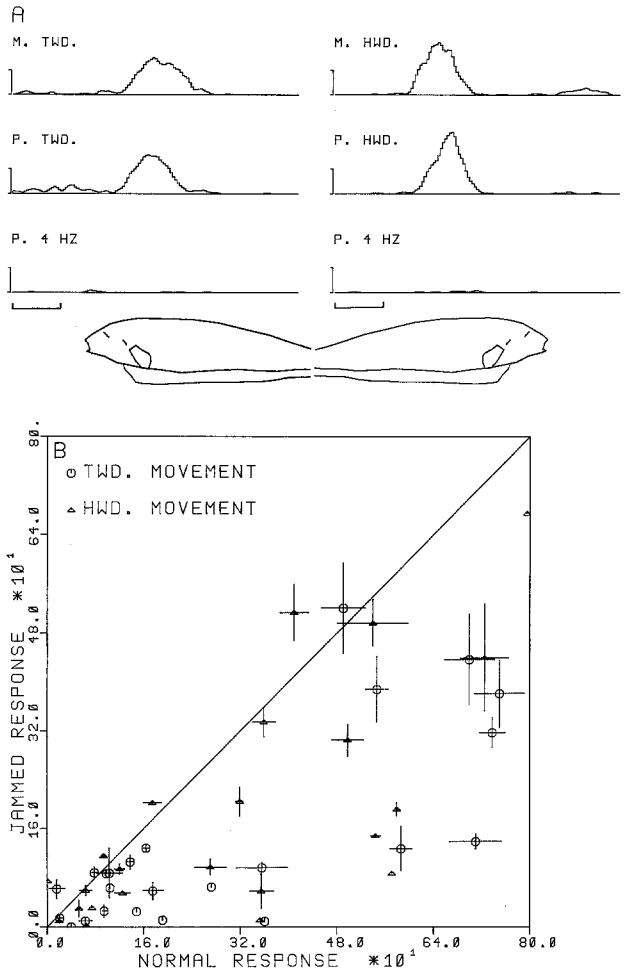

Fig. 2. A First and second sets of histograms show responses to metal and plastic moving objects in darkness. Third traces, the effects of a 4 Hz jamming stimulus presented simultaneously with a moving metal stimulus. Histograms based on 10 replicates of the stimulus movement. **B** Summary of effects of jamming on tectal cell responses to moving objects. Response is the total number of spikes evoked by 10 or 15 passes of the stimulus. *Bars:* ±1 s.e. of the mean

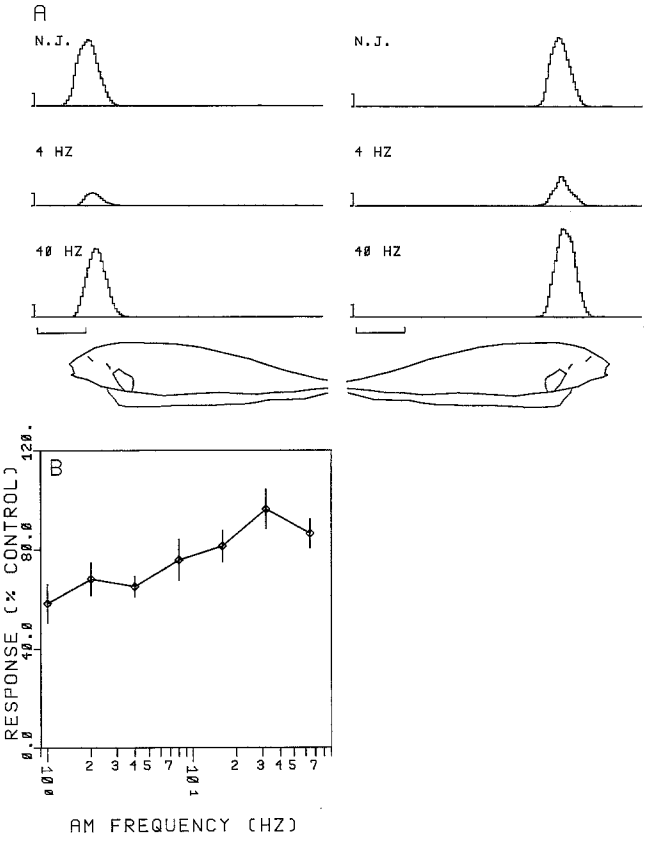

Fig. 3. A Effects of jamming stimuli of 4 and 40 Hz on the magnitude of a cell's responses to a moving object. *N.J.* no jamming stimulus. 15 replicates of the movement cycle per histogram. **B** Effect of jamming frequency on the magnitude of the responses of 7 tectal cells to moving object stimuli. *Bars:* equal ±1 s.e.

cation deteriorates (see reviews by Bullock 1982; Scheich and Bullock 1974; Heiligenberg 1980).

Jamming stimuli are potentially useful in demonstrating an electrosensory input to various central neurons. An alteration in a cell's responses to a moving object stimulus due to a jamming stimulus is clear evidence of such an input. However, a lack of a change in response during jamming does not necessarily rule out such an input since neural mechanisms have been discovered which can greatly reduce an animal's sensitivity to jamming stimuli (Matsubara 1981).

Figure 2A shows the effects of jamming on a tectal neuron which gave very similar responses to the plastic and metal object. Application of a 4 Hz, 6.3 mV/cm jamming stimulus virtually removed the cell's responses to the moving object. The cell showed no responses to bursts of electrical stimuli or to the jamming stimulus alone. Less often, a cell's response to a moving object would be augmented by a jamming stimulus and rarely the AM stimuli would induce steady activity in a cell without a moving object.

Figure 2B summarizes the results of 24 experiments in which a cell's responses to a moving object were compared, with and without the presence of a jamming stimulus. The size of the response without jamming, total number of spikes evoked by 10 or 15 passes of the moving object, is plotted against this same measure during jamming. In the majority of cases jamming reduced the size of the response. In cases where multiple replicates of the experiment were performed on a given cell, means and bars indicating plus and minus 1 standard error are plotted.

As mentioned earlier, the effect of a jamming stimulus depends upon its beat frequency, and a beat of 4 Hz does the most damage to the animal's electrolocation abilities (Heiligenberg et al. 1978), while frequencies in excess of 10 Hz are much less damaging at reasonable stimulus intensities. Figure 3A shows the effects of a 10-fold increase in AM frequency on the responses of a tectal cell. The deleterious effects

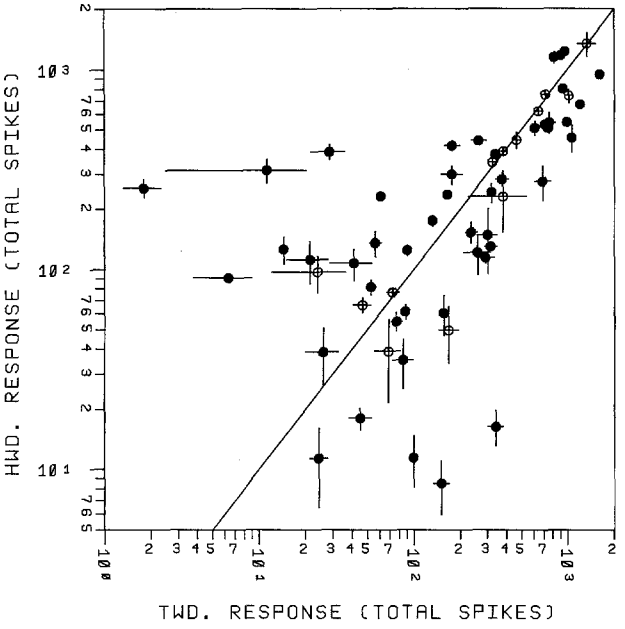

Fig. 4. Comparison of tailward and headward response sizes. *Bars:* equal ± 1 s.e.; *filled symbols:* responses significantly different for opposite directions of movement. Responses plotted above and below the diagonal line correspond to responses greater for headward or tailward movement respectively

of jamming were completely removed when the AM frequency was increased to 40 Hz. Figure 3B summarizes the effects of a series of different AM frequencies on the responses of 7 tectal cells to moving metal objects. The deleterious effect of the jamming decreases linearily with the logarithm of the AM frequency. A somewhat similar effect of the beat frequency upon the magnitude of the jamming effect has been found in cerebellar neurons of these same fish (Behrend 1977).

The jamming stimulus that was used in these experiments is not exactly the same as the animal would experience in a natural situation. When two EODs sum, the amplitude of the resultant beat signal is modulated as well as the phase of the resultant signal, relative to either of the component signals. Both the amplitude and the phase modulations are needed if an animal is to perform a correct jamming avoidance response (Heiligenberg et al. 1978), however, it is the AM portion of the beat signal that is most detrimental to the electrolocation function and the jamming stimulus used here was a pure AM.

Directional Responses. As shown in Fig. 1, responses to moving objects frequently depend upon the direction of the stimulus movement. Most often histogram shape remained similar for opposite directions of movement but the size of the response, number of spikes evoked per movement cycle, changed. In a few extreme cases, one direction of movement evoked a vigorous response while the opposite produced no response. The responses of 61 cells to headward and tailward movements are shown in Fig. 4. The number of spikes produced during 10 or 15 passes of the stimulus in the tailward direction is plotted against the same measure for headward movement. Logarithmic axes were chosen because of the wide range of response sizes seen. Typically several replicates of the experiment were performed for each cell so that a statistical test of differences, Wilcoxon's signed rank test, could be used. In 80% of the cases (filled symbols) the responses differed significantly depending upon movement direction; however, approximately equal numbers of cells favored movements in either the headward or tailward direction. Studies of the retinal afferents to the tectum of other fish showed that movement in the headward direction was preferred by the majority of the units recorded (O'Benar 1975; Wartzok and Marks 1973). The electrosensory units in the tectum do not show this generalized directional preference.

Interaction of Vision and Electroreception

Effects of Light on Normal Electrosensory Responses. The majority of cells responding to moving electrosensory stimuli showed altered responses when the object was made visible via its internal light source. These responses to the addition of light fell into two very general categories. The most common response alteration, typified by Fig. 5A, consisted of increases or decreases in the height and the width of the response profile. This type of visual effect was typical of the deeper, non-spontaneously active cells and it suggests that the receptive fields for vision and electroreception are superimposed or in register.

The second response type (Fig. 5B) was most often recorded from the superficial cell types and consisted of the appearance or disappearance of a feature, a peak or valley, of the response. The responses of these superficial cell types were always relatively weak and more variable so that each experimental variation had to be repeated several times to insure reproducibility. The histograms shown are the sums of 4 replicates of 10 movement cycles. Each replicate of 10 showed the same features. An extreme case of the effects of adding the visual stimulus to the electrosensory is shown in Fig. 7B. This cell was virtually unresponsive to metal (upper traces of Fig. 7B) and weakly responsive to plastic. Illumination of the visual stimulus within the metal object resulted in a two peaked response, and as will be discussed later, only one of these peaks was due to electroreceptive input. The receptive fields for electrosensory and visual inputs are not superimposed in this case.

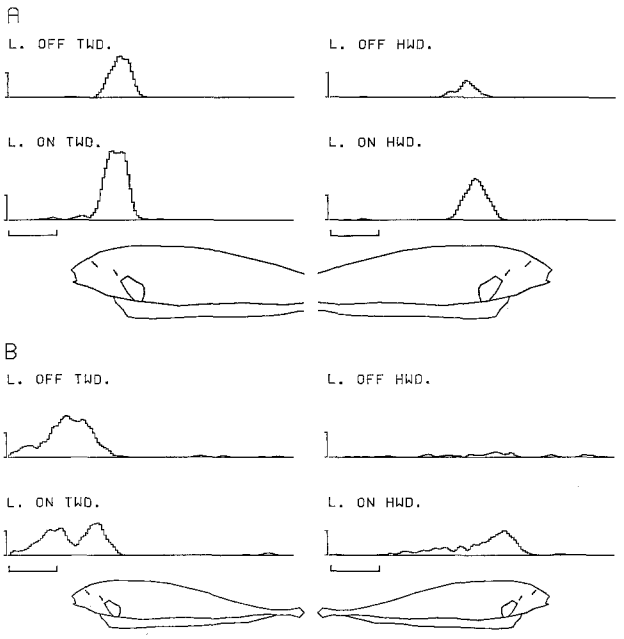

Fig. 5. Effect of object illumination on the responses of a deep tectal cell (**A**) and of a superficial tectal cell (**B**). 10 stimulus replicates per histogram in **A**. Histograms of **B** are averages of 4 repetitions of 10 replicates each

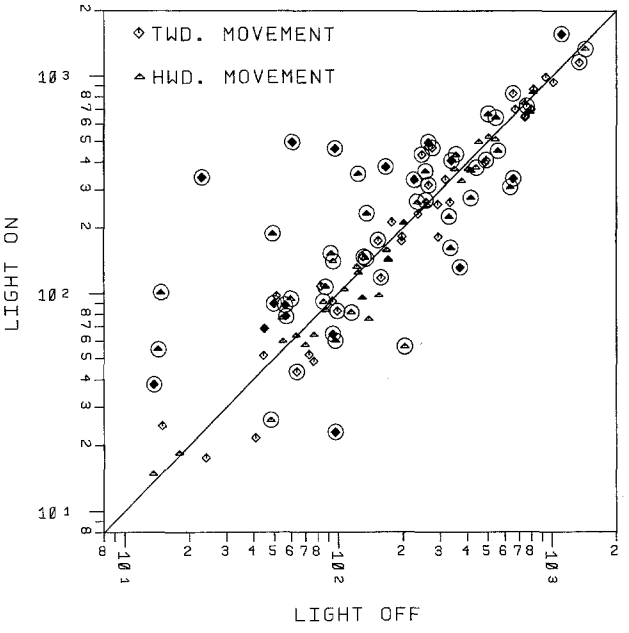

Fig. 6. Summary of the effect of adding illumination to the moving electrosensory stimulus. Total number of spikes evoked by the electrosensory stimulus with the light on is plotted against the same measure with the light off. *Filled symbols:* responses significantly different in response size. *Circled symbols:* responses differing significantly with regard to response shape

Figure 6 summarizes the effects of illumination of the moving metal cylinder. A given cell's response size in darkness is plotted against its response with the object visible. In about 30% of the cases the addition of the visual stimulus caused a significant change in the response size. Each point represents the mean of at least two replicates of the experiment and filled symbols indicate that the mean responses with light on and off were significantly different at the 5% level as judged by a *t*-test.

Simply computing the number of spikes evoked for some number of stimulus movement cycles is a rather insensitive method of gauging a cells sensitivity to the added visual input since large changes in histogram shape, or complexity, are possible without altering the total number of spikes. Therefore a method was developed to test for differences in histogram shape. First, a correlation coefficient was calculated for the data of two replicates of the experiment in the absence of illumination. The contents of the same bins in each of the two histograms formed the paired data for the correlation analysis. The correlation between these control histograms was generally greater than 0.9. Secondly, a correlation coefficient was calculated for the data of one of the control experiments paired against a set of data in which the object was illuminated. The two correlation coefficients were then tested for significant differences according to the method described by Simpson et al. (1960). Responses were judged to be significantly different only if the correlation coefficient for the control data sets was significantly larger ($P<0.05$) than that for the control and experimental data sets. Sufficient data was available in most cases to allow two tests to be performed as described as well as two replicates of the reciprocal test, paired experimental data sets compared with an experimental-control pair. Circled data points of Fig. 6 indicate responses that differed significantly in shape and in most cases responses that were different in spike count were also different according to this test for shape. An additional 26 responses which did not differ with regards to spike count, did differ in response shape.

Effects of Light on Jammed Responses. Although jamming stimuli usually reduced the responses to electrosensory stimulation, jamming did not usually reduce the responses to visual stimulation. Therefore making an object visible could partially alleviate the deleterious effects of a jamming stimulus. Furthermore, as is shown in Fig. 7A, visual input frequently augmented a jammed electrosensory response far more than it enhanced the cells' electrosensory response in the absence of jamming. Light increased the responses to the metal rod by 18 and 23% for tailward and headward movements respectively (Fig. 7A, top two sets of traces). However, when jammed, the addition of the visual stimulus increased the responses by 297

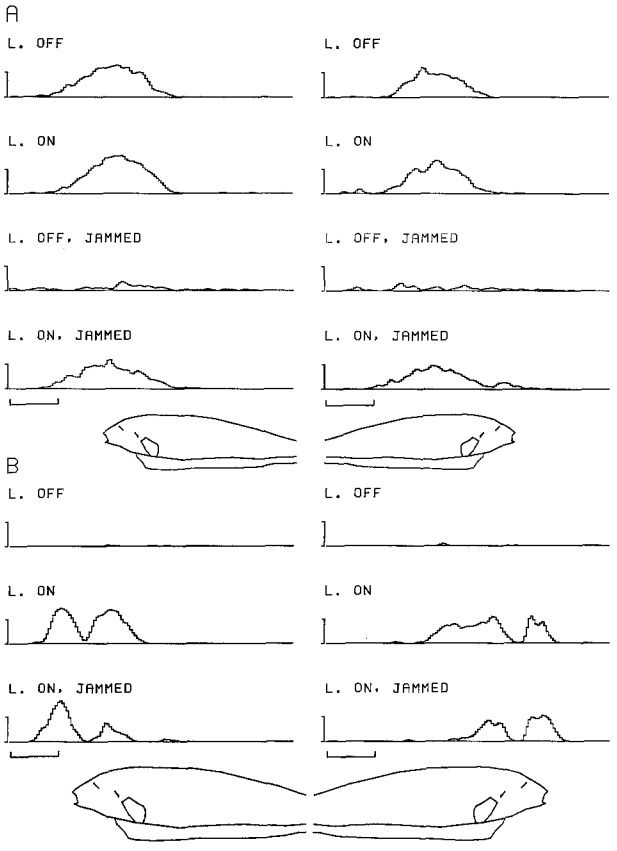

Fig. 7A, B. Effects of illumination on normal and jammed electrosensory responses to moving metal objects. 15 replicates per histogram in **A**, 10 per histogram in **B**

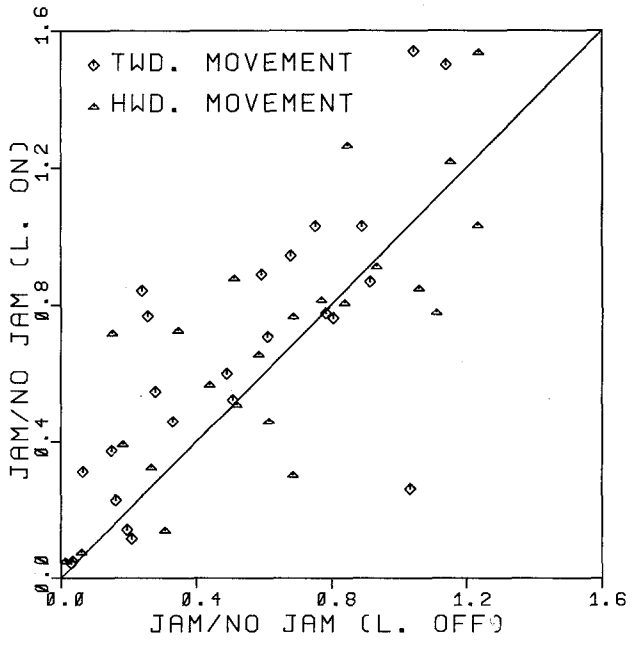

Fig. 8. Summary of the effects of an added visual input on normal and jammed electrosensory responses. Ratio of the responses in the jammed and unjammed situation with the light on are plotted against the same ratio for experiments with the light off

and 271% respectively (bottom two sets of traces, Fig. 7A).

Further support for the idea that the jamming stimulus effects the electrosensory alone is given in Fig. 7B. In this case, only when the object was visible did the cell produce a two peaked response. Only one of these peaks, the more caudal, was sensitive to jamming (third set of traces).

Figure 8 summarizes the effects of object illumination on jammed electrosensory responses. For each cell the ratio of the mean responses in the jammed and unjammed situation, with the light off, are plotted against this same measure with the light on. Responses of cells for which the presence of light makes no difference should fall along the diagonal line, while those that have the jammed response improved by light will fall above this line. Twenty seven of the 47 responses were improved by the illumination while 13 responses were further reduced by the light. The remaining 7 were essentially unchanged.

The Effects of Spatially Separated Visual and Electrosensory Stimuli

Separate moving visual and electrically detectable objects were used in order to study the responses to each stimulus modality presented alone. These two stimuli could also be presented simultaneously with various degrees of separation in the antero-posterior direction. The distance between the movement trajectory of this visual stimulus (lucite rod) and the side of the fish was adjusted so that the rod was below threshold as an electrosensory stimulus for the cell under study, as described in the Methods.

Figure 9A shows the responses of a non-spontaneous tectal cell to the moving metal object without a visual stimulus, top traces, and the responses to the moving visual stimulus without an electrosensory stimulus (second traces). The electrosensory responses were similar for both directions of movement but the visual responses were directionally sensitive, tailward movement being more effective. The positions of the responses to the two types of stimuli were also different, despite the fact that the two stimuli were accurately aligned (see Methods). The responses of this cell to both types of stimuli presented simultaneously are shown in the third traces. In the case of tailward movement the shape and the magnitude of the response is nearly what would be expected assuming that the two response types simply sum. However, in the case of headward movement, the addition of light caused a slight reduction in the response.

The third through the fifth traces of Fig. 9A illustrate the effects of displacing the visual stimulus

1.5 cm toward the animal's head or tail relative to the metal object. In the case of tailward movement, the displacement of the light toward the tail (4th set of traces) means that the visual stimulus leads the electrosensory stimulus and this broadens the response by 1 cm, compared to the case where the two stimuli are centered, and two separate peaks become evident.

The responses of this cell were variable in terms of the total number of spikes evoked per set of stimulus movements, therefore each experiment in which the light was displaced was preceded by a control in which the two stimuli were centered. The results of each pair of experiments are then expressed as the ratio of the responses with the light displaced to the responses in the control situation. This ratio averaged 1.04 for three replicates of the 1.5 cm tailward displacement when the stimuli were moved in the tailward direction, indicating that although the response increased in duration it did not increase in the total number of spikes evoked. When the stimuli were moved in the headward direction the tailward displacement of the visual stimulus did not significantly change the duration of the response but it did cause a shift in the position of a small secondary peak near the animal's head. The size of the main response was, however, significantly increased. The ratio of the number of spikes evoked due to the displaced stimuli, to the number evoked by the centered stimuli averaged 2.48, the response was more than doubled by this treatment.

Shifting the visual stimulus 1.5 cm towards the animal's head (Fig. 9A, 5th traces) resulted in a compression of the response to tailward movement so that its duration was about the same as that due to the metal object without any visual stimulus and also caused a slight decrease in the size of the response. The average ratio of the experimental to control responses was 0.88. This same displacement caused no change in the duration of the response to headward movement but again resulted in a small decrease in the average size of the responses. The experimental to control response ratio was 0.79.

Figure 9B and C summarizes the effects of different amounts of light displacement, relative to the metal object, on the width or duration of the cell's responses. Response duration was measured between the positions, relative to the fish's snout, where the response was equal to 50% of its maximum amplitude. The triangles indicate the position of the headward boundary, circles indicate the position of the tailward boundary and the squares show the position of the peak of the response. With tailward stimuli movement, the headward boundary shifts as a linear function of light displacement, but the peak and the

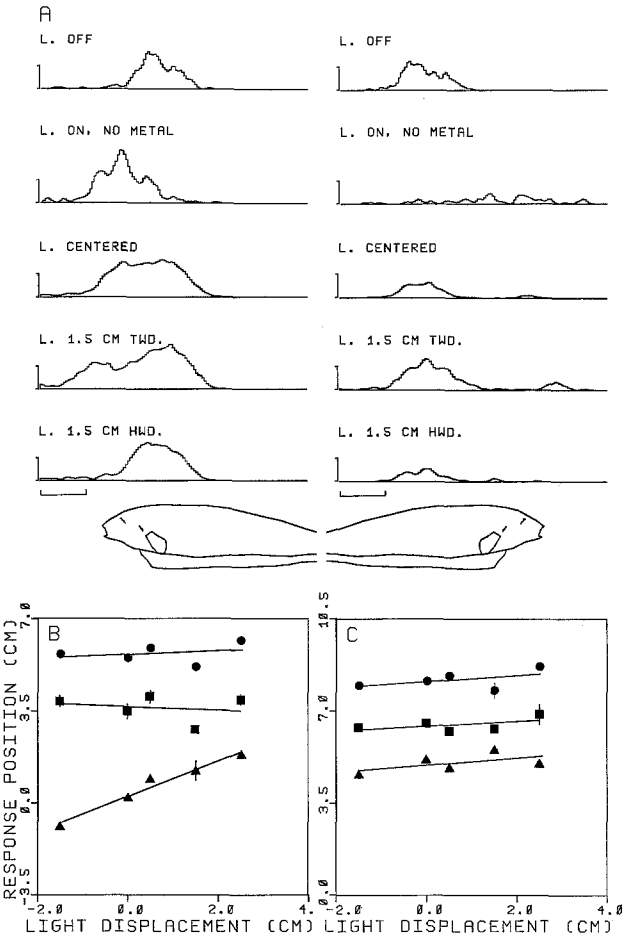

Fig. 9. A Responses of a deep tectal cell to 10 replicates of a electrosensory stimulus alone (1st set of histograms) and to a visual stimulus alone (2nd set). The 3rd set, averages of 6 experiments consisting of 10 replicates of stimulus movement with the visual and electrosensory stimuli centered. 4th and 5th sets of histograms, averages of 3 repetitions of 10 replicates each when the light was displaced 1.5 cm tailward and headward respectively. Vertical tic marks indicate 5 spikes/bin. **B, C** Position of the headward boundary (*triangles*), the center (*squares*), and the tailward boundary (*circles*) as a function of the displacement of the visual stimulus relative to the metal object. Response position of 0. corresponds to the tip of the animal's snout, negative positions are in front of the animal. Displacement of 0. corresponds to centered stimuli, negative displacements indicates the visual stimulus is positioned toward the animal's tail relative to the metal rod. **B, C** tailward and headward movement of the stimuli

tailward boundary do not shift (Fig. 9C). This results in a compression of the response from 6.5 cm to 4.4 cm over the range of displacements used. Headward stimulus movement however, resulted in no significant shifts in any of the measures of response duration or the position of the major peak. Width is constant despite the fact that the magnitude of the response more than doubles when the light was displaced in the tailward direction by −1.5 cm (4th traces of Fig. 9A).

Tectal cells generally responded to the spatial separation of the two types of stimuli with some alteration in the width of the composite receptive field, and measures of the width were very reproducible despite the fact that the total number of spikes generated in any single replicate could vary by more than a factor of two. Reproducible changes in the numbers of spikes evoked without concomitant changes in the width of the response, such as is shown for headward movement in Fig. 9, were seen less often.

Experiments were also performed in which the visual and electroreceptive stimuli remained centered but the animal's eye was mechanically rotated. This treatment also generates a shift in the times when the electroreceptive and visual receptive fields are stimulated and similar results were obtained. However, this latter method is less desirable than separating the stimulus sources because rotation of the eye could alter the optics or perhaps the responsiveness of the visual system.

Discussion

This preliminary study shows that the optic tectum of gymnotoid fish is a major electrosensory processing area and that, despite the subjective impression that the animal's visual system is poorly developed, light stimuli cannot only evoke responses in most tectal cells but they can also strongly affect the electrosensory responses. The electrosensory responses of tectal cells differ from those seen at lower levels in the electrosensory system, of receptors and cells in the posterior lateral line lobe (PLLL), in a number of ways: The tectal cells usually did not respond well, or at all, to spatially stationary stimuli such as various types of amplitude modulations of the EOD. Movement is a necessary component of effective stimuli for these cells. Receptors and PLLL cells respond well to a variety of stationary stimuli including the same types of AMs used in this study (Bastian 1981a, b). Also at least some cells in the torus semicircularis of the closely related species *Eigenmannia virescens* respond well to stationary stimuli (Scheich 1977; Bastian and Heiligenberg 1980). Many of the tectal cells lacked spontaneous activity, and the responses to objects of opposite conductivities in some cases showed larger differences than are routinely seen at lower levels. Neither the receptors nor any PLLL cells have shown sensitivity to one category of object, e.g. conductors, and insensitivity, such as is shown in Fig. 1A, to non-conductors. Likewise, lower order electrosensory cells have not been found which show nearly identical responses to objects of opposite conductivities as is shown for the tectal cell of Fig. 2A.

Jamming stimuli were found to be effective for demonstrating an electrosensory input to tectal cells by causing alterations in the responses to a moving object stimulus. The fact that the AM stimulus presented alone typically evoked no response in these cells, yet could alter the response to a moving electrosensory stimulus, suggests that the tectal cells have receptive fields made up of excitatory and inhibitory regions of roughly equal size and sensitivity. This type of receptive field arrangement would allow these higher order cells to respond to the moving objects since this stimulus would reach each component of the field sequentially rather than simultaneously. Cells in the PLLL of the weakly electric fish *Sternopygus* sp. have been shown to have this type of receptive field (Matsubara 1981). However, unlike the cells in *Sternopygus,* these tectal cells do show a decrease in response to moving stimuli when jamming stimuli are present. The jamming stimulus must exert its effects on cells afferent to the tectal cells studied. This disruptive effect could reduce the magnitude of the input to the tectum, or it could alter the patterning of the input so that it is less effective in driving these cells.

Spatially stationary visual stimuli, such as light flashes, evoked activity in units recorded in the superficial layers of the tectum and some of these responses were similar to those previously described responses of retinal afferents to the tectum (Wartzok and Marks 1973; O'Benar 1976), others were probably from the large dendritic trees of deeper cells. The more commonly studied deeper cells were insensitive to stationary stimuli but sensitive to moving visual stimuli presented alone or in conjunction with the electrosensory stimulus. The addition of a visual stimulus to an electrosensory stimulus increased the response size more than twice as often as it decreased the response and no preference was seen for headward or tailward stimulus movements being associated with the change in response size. When response shape was also evaluated a total of 55% of the cells studied showed a statistically significant change in one or both of the response properties analyzed due to the addition of a visual stimulus (see Fig. 6).

The effect of adding moving visual stimuli to the electrosensory stimulus in the presence of jamming stimuli was most often an increase in the cell's response (Fig. 8). These data also suggest that the deleterious effects of jamming stimuli are exerted on cells afferent to the tectum. If the jamming signals affected the excitability of the tectal cells directly then I should have seen some reduction in the responses to visual stimuli presented alone in the presence of jamming. Jamming stimuli did not cause decrements in the responses to pure visual stimuli, and the effects of ad-

ding the visual stimulus to the electrosensory during jamming was usually a greater augmentation than when the visual stimulus was added to the unjammed response. The tectal cells may be involved in upgrading the quality of a sensory input via the integration of information from different senses when interferring or masking stimuli are present.

The integration of the two sensory inputs involved a simple summation in some cases as is shown in Fig. 9A for tailward movements; however, in other cases the interaction was clearly non-linear. An extreme example is shown in Fig. 7B where electrosensory stimuli alone cause no response but the addition of the visual input resulted in a response consisting of two phases, one of which is clearly electrosensory. In this case the visual stimulus, which when presented alone also evoked a response, greatly facilitated the electrosensory response. This type of cell is very similar to the category of tectal cell termed 'infrared enhanced visual' recently described by Newman and Hartline (1981) in the rattlesnake tectum.

In the majority of cells studied, the receptive fields for each sensory modality were relatively well aligned, that is the responses showed at least partial spatial overlap. Two spatially separate responses were seen less often. Typically the alignment of the response could be influenced by altering the relative positions of one of the stimuli relative to the other and then moving the misaligned pair along the fish. This shows that in these cases the separate sensory inputs can function independently, and that changes in the timing of the activation of the separate receptive fields does not alter the simple summation of the separate responses. In other cases, e.g. Fig. 9 (headward movement) the spatial properties of the responses are relatively insensitive to the misalignment of the stimuli but in this case certain degrees of misalignment significantly altered the size of the response. A possible simple explanation of this phenomenon is that the tailward displacement of the object results in an inhibitory region of the visual receptive field being stimulated at a time when it does not interfere with the excitation due to the electrosensory input. The size of this inhibitory region, or the duration of its effect, would have to be large since significant displacements in the opposite direction did not augment the size of the response.

Any system relying on the convergence of vision and other sensory modalities will have to deal with the misalignment of the receptive fields for vision and the second modality caused by eye movements or by movements of the head relative to other parts of the body. The tectal cells studied here could not only be involved in processing bi-modal information in a 'sensory' context but these cells could also function as generators of error signals informing the motor systems of the degree of misalignment of receptive fields for these senses. The tectum is known to be involved in a variety of orienting behaviors (see Ingle and Sprague 1977 for review). It is possible that motor behaviors that result in more precise alignment of the receptive fields for these two sensory modalities could improve the analysis of a given stimulus via both senses. The tectal cells could signal the degree of alignment of the separate receptive fields by the duration or the intensity of their response to a bimodal stimulus.

Whether or not these fish make active eye movements is an open question. I have never observed eye movements in this species in experimental preparations or in individuals in aquaria, although I have seen eye movements in the related species *Eigenmannia virescens*. The other sort of motor activity that could be involved in altering the spatial relationships between visual and electrosensory receptive fields is the animal's own body movements during swimming. Since the electric organ is within the animal's trunk and tail, any movement of this part of the body will certainly alter the intensity of the electrical image caused by an object near the body and also perhaps the location of the distortion on the body surface. These animals do make very stereotyped tail movements when exploring a novelty.

Further studies of the sensory processing abilities of the tectum will explore these questions and these studies coupled with studies of the projections of the tectal efferents should provide significant insights into the role of this structure in these fish as well as in other vertebrates.

Acknowledgement. I am grateful to Dr. W. Heiligenberg and an anonymous referee for many helpful suggestions regarding the manuscript. This work was supported by NIH Grant no. R01NS-12337.

References

Bastian J (1976) The range of electrolocation: A comparison of electroreceptor responses and the responses of cerebellar neurons in a gymnotid fish. J Comp Physiol 108:193–210

Bastian J (1981a) Electrolocation. I. How the electroreceptors of *Apteronotus albifrons* code for moving objects and other electrical stimuli. J Comp Physiol 144:465–479

Bastian J (1981b) Electrolocation. II. The effects of moving objects and other electrical stimuli on the activities of two categories of posterior lateral line lobe cells in *Apteronotus albifrons*. J Comp Physiol 144:481–494

Bastian J (1981c) Visual and electrosensory responses in the optic tectum of a weakly electric fish. 11th Annual Meeting, Society for Neurosciences, Los Angeles, California, Abstr no 272-9

Bastian J, Heiligenberg W (1980) Neural correlates of the jamming avoidance response of *Eigenmannia*. J Comp Physiol 136:113–133

Behrend K (1977) Processing information carried in a high frequency wave: Properties of cerebellar units in a high frequency electric fish. J Comp Physiol 118:357–371

Bullock TH (1982) Electroreception. Annu Rev Neurosci 5:121–170

Bullock TH, Hamstra RH, Scheich H (1972) The jamming avoidance response of high frequency electric fish. II. Quantitative aspects. J Comp Physiol 77:23–48

Carr CE, Maler L, Heiligenberg W, Sas E (1982) Laminar organization of the afferent and efferent systems of the torus semicircularis of gymnotiform fish: Morphological substrates for parallel processing in the electrosensory system. J Comp Neurol 203:649–670

Drager UC, Hubel DH (1976) Topography of visual and somatosensory projections to mouse superior colliculus. J Neurophysiol 39:91–102

Enger PS, Szabo T (1965) Activity of central neurons involved in electroreception in some weakly electric fish (Gymnotoidae). J Neurophysiol 28:800–818

Hagiwara S, Szabo T, Enger PS (1965) Electroreceptor mechanisms in a high frequency weakly electric fish *Sternarchus albifrons*. J Neurophysiol 28:784–799

Hartline P (1974) Thermoreception in snakes. In: Fessard A (ed) Handbook of sensory physiology, vol III/3. Springer, Berlin Heidelberg New York, pp 297–312

Heiligenberg W (1977) Principles of electrolocation and jamming avoidance in electric fish, a neuroethological approach. In: Braitenberg V (ed) Studies of brain function. Springer, Berlin Heidelberg New York

Heiligenberg W (1980) Jamming avoidance response in *Eigenmannia*. A behavior controlled by distributed evaluation of electroreceptor afferences. Naturwissenschaften 67:499–547

Heiligenberg W, Baker C, Matsubara J (1978) The jamming avoidance response in *Eigenmannia* revisited: The structure of a neuronal democracy. J Comp Physiol 127:267–286

Ingle D, Sprague JM (1977) Sensorimotor function of the midbrain tectum. In: Neuroscience research program bulletin, vol 13. MIT Press, Cambridge, Massachusetts

Matsubara JA (1981) Neural correlates of a nonjammable electrolocation system. Science 211:722–725

Newman EA, Hartline P (1981) Integration of visual and infrared information in bimodal neurons of the rattlesnake optic tectum. Science 213:789–791

O'Benar JD (1976) Electrophysiology of neural units in goldfish optic tectum. Brain Res Bull 1:529–541

Scheich H, Bullock TH (1974) The detection of electric fields from electric organs. In: Fessard A (ed) Handbook of sensory physiology, vol III/3. Springer, Berlin Heidelberg New York, pp 201–256

Scheich H (1977) Neural basis of communication in the high frequency electric fish *Eigenmannia virescens* (jamming avoidance response). III. Central integration in the sensory pathway and control of the pacemaker. J Comp Physiol 113:207–227

Schroeder DM, Vanegas H (1977) Cytoarchitecture of the tectum mesencephali in two types of siluroid teleosts. J Comp Neurol 175:287–300

Simpson GS, Roe A, Lewontin RC (1960) Quantitative zoology. Harcourt, Brace and World, New York

Skarf B, Jones MJ (1981) Vestibular-visual interactions in frog mesencephalon during natural stimulation. Brain Res 206:457–461

Szabo T, Fessard A (1974) Physiology of electroreceptors. In: Fessard A (ed) Handbook of sensory physiology, vol III/3. Springer, Berlin Heidelberg New York, pp 59–125

Wartzok D, Marks W (1973) Directionally selective visual units recorded in optic tectum of the goldfish. J Neurophysiol 36:588–604