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Visual System of *Notonecta glauca*: A Neuron Sensitive to Movement in the Binocular Visual Field

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Summary. 1. Large-amplitude spikes were recorded from a movement-sensitive unit in the optic lobe of *Notonecta*.

2. This neuron is sensitive to movement of a small dark spot within the receptive field, in any direction. Movement of a background – e.g., the movement of a large striped pattern – does not elicit discharges. The movement of the striped pattern can even suppress the response to an otherwise effective stimulus.

3. The observed region of high sensitivity to moving spots is large and is found within the binocular field. Excitation involves binocular interaction: a high firing rate can be induced only if both eyes see the moving object. Covering of either the contralateral or the ipsilateral eye reduces the spike frequency to less than one-half the binocular rate (Fig. 15).

4. In the velocity range tested, from 3.5 to 350°/s, the log of the firing frequency varies linearly with the log of the stimulus velocity (Fig. 7).

5. Varying the contrast, above its threshold value, had little effect on the spike rate. At a given weak contrast, however, the neuron responded to movement in the dorsal visual field, but not to movement in the ventral field (Fig. 9).

6. Repetitive stimulation of the same part of the retinal array elicits successively smaller responses. This habituation is partly alleviated if a different group of ommatidia is stimulated (Fig. 6).

7. When a spot of suitable size was moved through the ventral visual field along a path perpendicular to the median plane of the animal, there was a discharge-rate maximum ca. 20° ipsilateral to the median (Fig. 4). A spot moving in the median plane from ventral to dorsal elicited three maxima of excitation (Figs. 3, 5, 11, 15). When *Notonecta* is hanging in its normal posture, upside down below the water surface, its visual environment is divided into three parts: the region of the deep water, the zone of te totally reflecting portion of the surface, and the zone of the transparent water surface. Each of the peaks in the response corresponds to one of these zones of the visual field.

8. The peak corresponding to the region of total reflection changed its position with the angular size of the moving spot; a small spot elicited a peak near the horizon. The larger the spot, the farther the peak shifted ventralwards (i.e., upward; Fig. 11). Due to this effect, an object moving in the plane of the water surface at any distance would excite the neuron maximally if it were of the appropriate size, ca. 1/4 the length of *Notonecta* (Fig. 13).

Introduction

A variety of movement-sensitive interneurons, with different physiological properties, have been found in the insect visual system. Many insects are known to have neurons with large receptive fields which respond when the image of the entire visual environment moves over the retina in a certain direction. (A review of the literature has been published by Northrop, 1975). Under natural conditions such cells are excited when the animal itself moves relative to the motionless surroundings.

Other large-field interneurons respond primarily to the movement of visual patterns limited in extent. Recordings from such cells have been obtained, for example, in orthopterans (Rowell, 1971), moths (Collett, 1972) and hoverflies (Collett and King, 1975). Because these neurons are not excited by displacements of the entire panorama, they signal the relative movements of smaller objects – those of a conspecific, for example, or of a predator or prey animal.

In this paper a neuron belonging to the latter group is described, a cell in the optic lobe of the backswimmer *Notonecta glauca*. *Notonecta* is a pre-

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datory water bug that is normally oriented with the back down; in this position it swims and lies in wait for prey just beneath the water surface. One goal of these studies was to examine the responses of the cell to specific optical stimuli, in relation to features of the animal's unusual way of life in its rather special optical surroundings.

Materials and Methods

The experimental animals *(Notonecta glauca)* were caught in the field. Animals kept in cold conditions were placed in water at room temperature a few days before the experiments, which were also done at room temperature.

During an experiment the animal was attached to a holder (H in Fig. 1), ventral side up, with wax-colophonium. Legs and antennae were removed. The back edge of the head was glued to the prothorax, which was fixed to the holder. The animal was positioned with its median (sagittal) plane vertical ($\pm 1°$), the long axis of the body forming an angle of 55° to the horizontal (from which the head axis may depart by $\pm 5°$). This angle is larger than would apply for an animal hanging at the water surface under natural conditions; there it would be about 31°. The head of the animal was centered in a hollow sphere of plexiglass, filled with insect Ringer. The dioptric apparatus is adjusted to water, so that under these conditions visual stimulus patterns are focussed on the retina as in the normal habitat. Artificial respiration was provided by air flowing through a small tube (T in Fig. 1) with its open end pushed over the abdomen. The surface of the Ringer solution was covered by a matt black plate (P), with a small notch through which the electrode and the holder pass; here the fluid surface was made nonreflecting with lycopodium dust (L). No specular reflections can be produced at the wall of the sphere, because the optical path between diametrically opposed points on the sphere is interrupted by the preparation.

The recording electrodes used were sharpened wires of platinum-iridium-30, insulated in glass except for an exposed tip about 50 µm long (insulation as described by Wolbarsht et al., 1960).

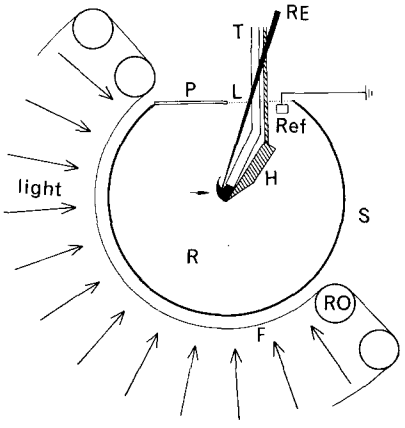

Fig. 1. Part of the experimental apparatus. *S*, hollow plexiglass sphere; *R*, insect Ringer; *P*, covering plate; *L*, lycopodium dust; *H*, holder; *T*, air-conducting tube; *RE*, recording electrode; *Ref*, reference electrode; *F*, film strip; *RO*, roller for film transport. Head (→) of backswimmer is centered in the hollow sphere

The electrode was inserted through a hole in the right side of the back of the head, just dorsal to the base of the antenna. The direction of penetration was 5° away from the frontal plane and 30° from the sagittal plane.

The stimuli consisted of geometric figures glued to a strip of transparent drawing film 0.1 mm thick (F in Fig. 1). The film strip runs outside the plastic sphere so that the stimulus moves along a semicircle around the head of the backswimmer. A synchronous motor with ten-speed gearing pulls the strip along this path, so that the stimulus patterns move at constant radius with a constant angular velocity. The ten selectable speeds range from 0.35°/s to 352°/s. A photodiode scans markings placed at the edge of the strip so as to be invisible to the animal, and provides a signal indicating velocity and position of the pattern.

The radius of the film track is 45 mm. From the center of the sphere the entire visible "stimulus stage" covers a sector of 186°, its width being 67°.

Behind this stimulus stage is a segment of a sphere made of white styrofoam, over which 54 light bulbs (each 6 V, 2.4 W) are uniformly distributed. The bulbs are supplied by direct current at an operating voltage of 96 % of their nominal voltage. The part of each light-bulb surface directed toward the plexiglass sphere is covered with white paint, and between the bulbs and the film are two spherical surfaces of matt glass. This arrangement produces a nearly homogeneously illuminated background with a luminance of $4000\,cd \cdot m^{-2}$.

The entire stimulus stage can be rotated around the plexiglass sphere so as to occupy various positions relative to the axes of the animal.

The recorded potentials were amplified by the usual methods, filtered (lower cutoff = 1 kHz, upper cutoff = 30 kHz), and recorded on an FM tape recorder, together with the stimulus markers, at a tape speed of 38 cm/s.

Further data processing was done as follows. The action potentials are converted to square pulses. An electronic clock (made in the electronic workshop of the Fachbereich Biologie of the University) measures the time separating each impulse from a trigger signal at the beginning of each recording (with an accuracy, at this tape speed, of ± 0.25 ms). These values are read into the memory of a small computer (Wang 600) and then put out on punched tape. While the data are being entered into the computer the tape speed is reduced to 1/8 of the recording speed. The computer operates at a rate such that under these conditions spike frequencies of up to 400 Hz can be processed. A monitor is used to check whether this limit is exceeded by any sequential spike pair; it was not, in any of the usable recordings. The data on the punched tape are further processed with the Wang 600 table calculator.

In all the experiments described the background illumination was switched on exactly 15 s before the test pattern moved over the stimulus track; when the traverse was completed it was switched off unless a subsequent stimulus was to be offered within a few seconds.

Results

With the method just described, it was possible to record nerve impulses from a characteristic unit in the optic lobe of *Notonecta*, excited by certain visual movement stimuli.

The signal-to-noise ratio was very high, even when the recording electrode had a long exposed tip. The elctrode could be pushed deep into the tissue without losing the action potentials entirely. These facts suggest that the recording was from a large neuron.

In five preprarations the recording site was marked by electrocoagulation of the tissue at the tip of the electrode (10 μA for 10 ms, recording electrode negative); in serial sections of these brains, the coagulated region was found to be centered in the medulla externa. It was striking, however, that the signal-to-noise ratio was better, the closer the electrode tip could be brought to the medulla interna (lobula).

The cell can be excited by movement of an area within the receptive field (cf. p. 317), as follows. The area must stand out from the background with adequate contrast (cf. Fig. 9), must not be larger or smaller than certain limits, and must move through the visual field at a sufficiently high speed (cf. dependence of spike frequency on velocity, Fig. 7).

Change in brightness of the entire surroundings of the animal causes no (or very slight) excitation.

Motionless optical patterns were ineffective, even at the moment when they became suddenly visible to the animal by switching on the background illumination. Brightening or darkening of a small stationary surface (the end of a fiber-optic stimulator) was also ineffective.

The neuron did not respond to movement of a periodic black-white striped pattern along the stimulus track. This pattern filled the whole stage, with the stripes (ca. 16° wide) perpendicular to the direction of motion. While the pattern was being moved in any of the four directions studied – ventral to dorsal, dorsal to ventral, ipsilateral to contralateral, and contralateral to ipsilateral – in no case was the number of action potentials produced greater than that associated with spontaneous discharge of the cell (0 to ca. 10 Hz).

Several experiments clarify the necessary relationships of moved object and background. For example, a black square 14° on a side (given adequate contrast and velocity) is an effective stimulus when moved with respect to the eye. If, however, the square is motionless and only striped background moved behind it, there is no response. Movement of object with respect to background in this sense is therefore ineffective.

Moreover, the response elicited by such a black square can be inhibited by simultaneous motion of the background stripes at sufficient speed. In front of the periodic striped pattern, which moved from ventral to dorsal, a black square was moved back and forth by hand perpendicular to the direction of movement of the striped pattern. When the striped background moved at a speed of 7°/s or less it was possible to trigger excitation with the square, but when the stripes moved at 35°/s the cell could no longer be excited by movement of the square.

The response of the cell to a particular stimulus, as measured by the number of action potentials produced, can vary greatly among preparations. Nevertheless, characteristic properties can be measured; these include the shape of the spike-frequency curves when the pattern is moved over a part of the track, and the dependence of spike frequency on pattern velocity.

Dependence of Excitation on Position of the Pattern in the Visual Field

Figures 2 and some of the following illustrations show the relationship between spike frequency in successive time intervals and the position of the moving visual pattern on the semicircular track at each corresponding time. Unless otherwise stated, the position (on the abscissa) is that of the center of the stimulus figure. Such curves will be called "continuous scan curves" in the following discussion.

The abscissa in each of these figures is a time axis. During the interval delimited by the arrows the stimulus pattern moves over the stage. Because the angular velocity is constant, spatial coordinates can also be given over this region. The points on the curve outside the part demarcated by the arrows indicate the resting frequency before and after passage of the stimulus. The total time interval represented by the abscissa was divided into 40 intervals, and spike frequencies were calculated from the number of action potentials in each such interval. Except for those in Figure 5, the points represent means computed from several individual curves (cf. Figure legends).

Figure 2 shows the responses to black 14° squares moved in the median (sagittal) plane at a velocity of 176°/s, either dorsalward (——) or ventralward (------). The track was positioned symmetrically with respect to the long axis of the body. For the excitation curves labelled (1) each stimulus was presented after a pause of 20 min; the responses in curves (2) were to identical stimuli presented at an interval of 2.2 s after each Curve-1 stimulus.

In all cases, the stimuli produce marked excitation in the ventral visual field (between about +30° and +90°); they also produce a second maximum of excitation in the dorsal region. Since *Notonecta* normally has its back down (Fig. 10), the positions of these regions in space are in front and above, and behind and below, respectively. Stimulation after a long pause, with a dorsoventral movement, also excited this cell in the region between 0° and +30° (dashed Curve 1). But this excitation disappeared when the stimulus was repeated (dashed Curve 2) 2.2 s later.

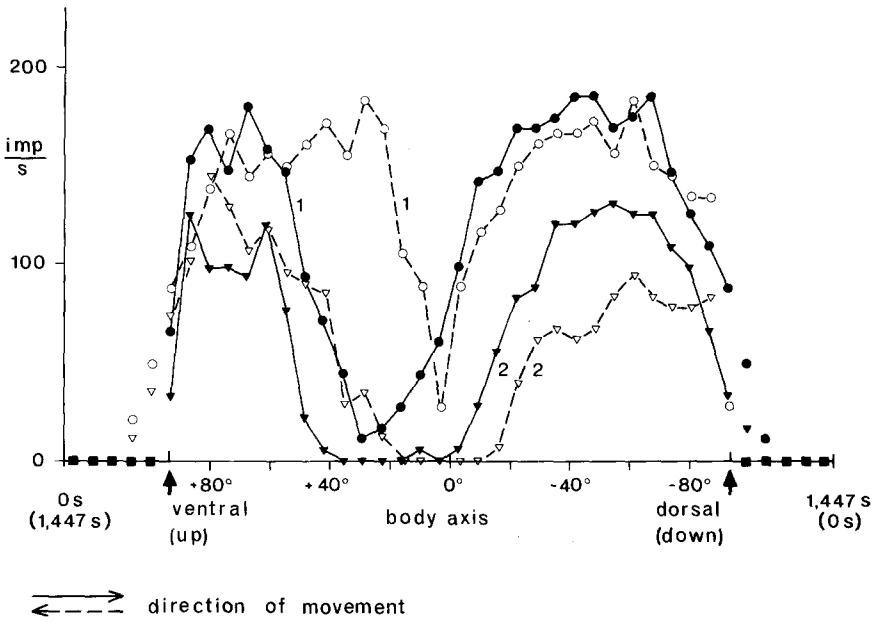

Fig. 2. Relationship between impulse frequency (ordinate) and location of a black square 14° wide (abscissa values between arrows) moving in median plane in a semicircle around the animal. Points outside the section bounded by arrows represent resting discharge before and after traverse of stimulus. Solid curves: movement from ventral to dorsal; dashed curves: movement in opposite direction. Curves labelled (1): responses to first movement stimulus after 20 min in which no stimulus was presented. Curves labelled (2): responses to repetition of the same stimulus 2.2 s later. Means of 5 single curves. Recording No. 38

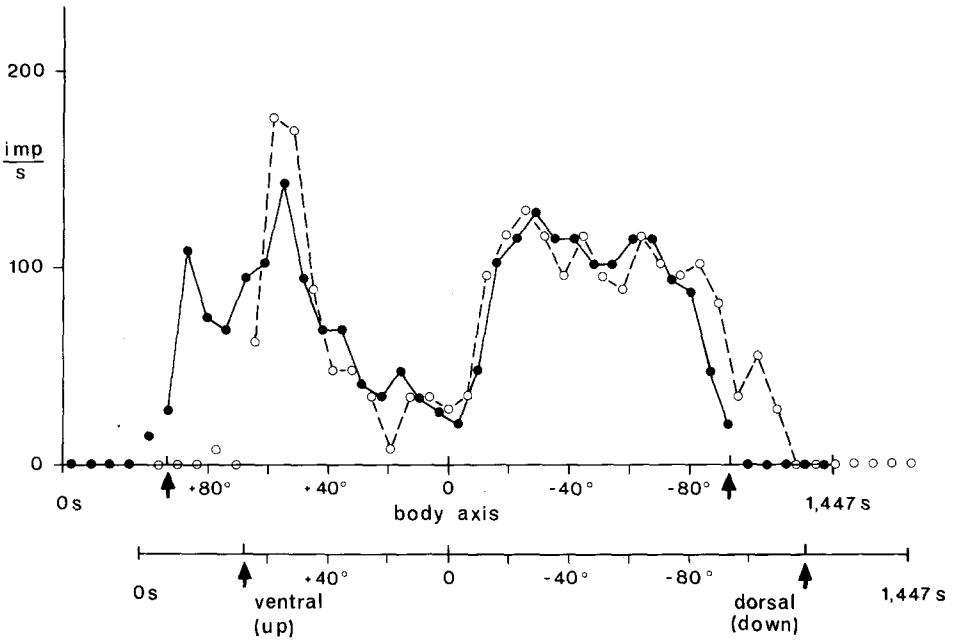

Fig. 3. Response to movement of 14° black squares in the median plane from ventral to dorsal. Upper abscissa, solid curve: stimulus stage positioned symmetrically to the animal (extending 90° dorsal and 90° ventral from the point of intersection with long axis of the body). Lower abscissa, dashed curve: response to corresponding stimulus after the entire stage was moved dorsally by 28°. Each curve mean of 4 single curves. Time interval between successive stimulus traverses, 2.2 s. Recording No. 43

The solid curve in Figure 3 shows the response of this unit in another animal to movement of the same black 14° square over the same track from ventral to dorsal. The shape resembles those of the two solid curves in Figure 2. In Figure 3, however, there is a more distinct maximum in the ventral visual field, at about +60°. The experiment was repeated 20 min later, when the stimulus stage had been rotated 28° dorsalward (dashed curve in Fig. 3). The result shows that the shape of the curve is largely independent of

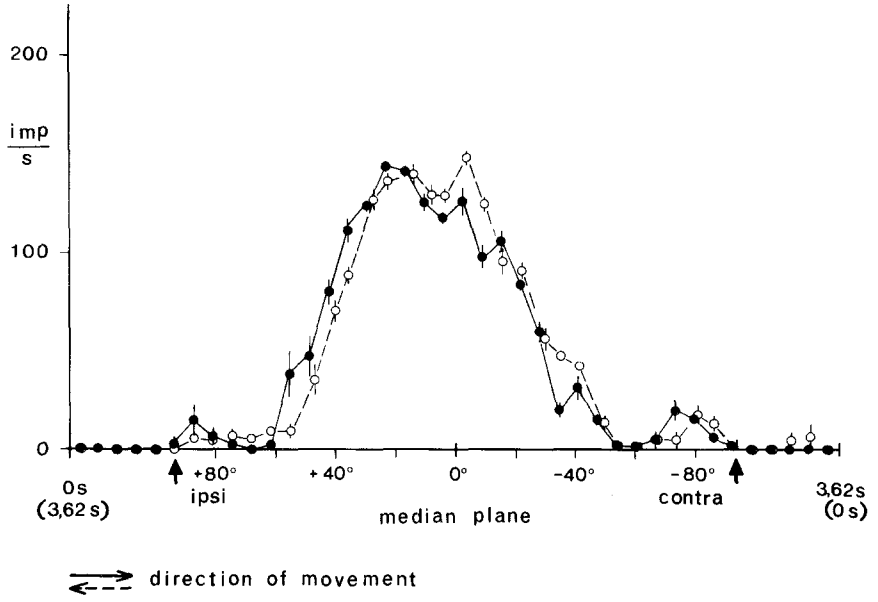

Fig. 4. Excitation of the cell by movement of a 7° black square along a track oriented perpendicular to median plane. Square crossed this plane 50° ventral to the long axis of the body. Velocity, 70.4°/s. Each curve mean of 4 curves. Vertical lines here and in next figure represent standard deviations of means ($s_{\bar{x}}$). Time interval between individual measurements 2.5 min. Recording No. 39

the position of the limits of the film strip; the only difference is that the first responses – those elicited at the edge of the stage – can be enhanced.

In the experiment of Figure 4 the position of the stage was changed by 90°, so that it was no longer in the median plane. Here the cell responds to movement of a black square along a great circle oriented perpendicular to the median plane, in such a way as to intersect it 50° ventral to the long axis of the body. Moving along this track the square traverses the zone of te visual field in which the totally reflecting water surface lies, when *Notonecta* hangs below the surface in its natural posture (cf. Fig. 10).

The two curves, for the two opposed directions of movement, have almost the same shape. The steep flanks begin about 45° on either side of the median; this is within the boundaries of the binocular visual field, which according to Lüdtke (1935) is about 90° wide in this region of the eyes. Both curves have maximum of excitation at 20° ispsilateral.

Response of the Unit to Repeated Stimuli

When identical stimuli are repeated at brief intervals the measured responses gradually decline. We shall refer to this process as habituation.

With intervals of 2.5 min between the traverses of a pattern, the response at some positions on the first scan may be greater than on the following scan. An example is given in Figure 5, which shows several traverses of the same stimulus, at 2.5 min intervals.

Habituation is much more pronounced if identical stimuli are presented at intervals of only 2.2 s. The two left-hand curves in Figure 6 show the total number of impulses fired in response to one traverse of a square; this measure decreased with successive stimuli, repeated at this interval. Examples of responses to two scans, one given 2.2 s after the other, are shown in Figure 2.

The rate of habituation was highly variable from one recording to another. For a single cell it could also differ from one place to another in the visual field. In some recordings the rate of habituation also depended on the direction of movement; in the dorsal visual field it was sometimes more rapid for dorsoventral traverses than for movement in the opposite direction.

For stimuli presented in rapid succession, habituation was most marked with repeated stimuli on the same track. The sensitivity to movement over other regions of the eye, however, was not reduced to the same extent.

The above effect is illustrated in Figure 6. Plotted here are the numbers of impulses triggered by black squares 10° on a side, traversing the stimulus stage at intervals of 2.2 s. The first four scans (1–4) were made along a different paramedial track than the subsequent set of four (5–8). In the experiment shown by the solid curve, the first four squares passed along a track shifted ipsilateral by 10°, and the following four on a track shifted contralateral by the same amount. The dashed curve reflects presentation of stimuli on these two tracks in the opposite sequence.

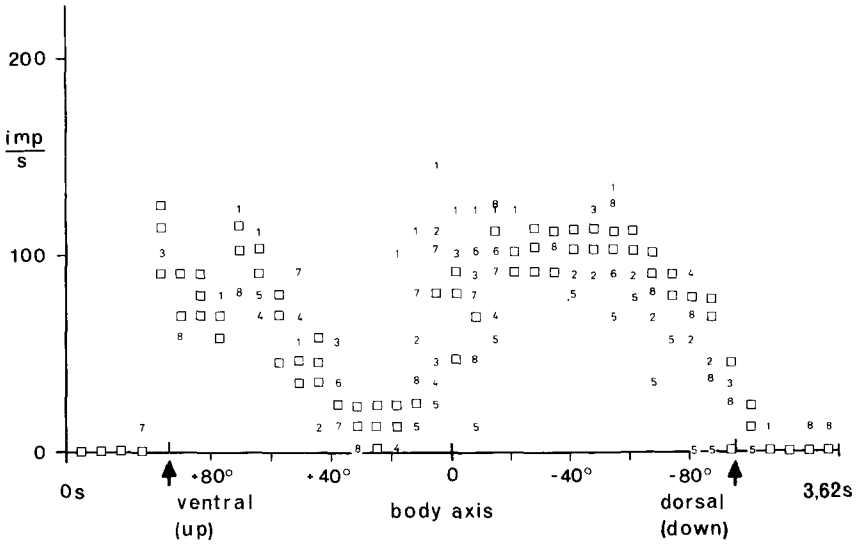

Fig. 5. Response of the cell to identical stimuli (movement of a black square in median plane, from +90° ventral to −90° dorsal) presented at intervals of 2.5 min. Single continuous scan curves are shown and identified by numbers (□ = several numbers superimposed). Square width, 14°; velocity, 70.4°/s. Recording No. 40

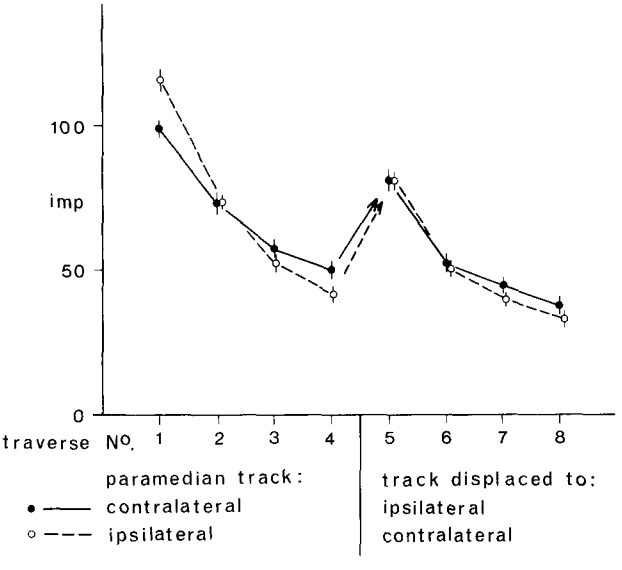

Fig. 6. Number of impulses elicited by eight single black squares moved in succession in a semicircle around the animal at uniform intervals of 2.2 s. (Abscissa gives sequence numbers of successive traverses.) Squares 1–4 moved along a different paramedian track than squares 5–8. Direction of movement, from ventral to dorsal; square width, 10°; velocity, 176°/s. $n=5$

The amplitudes of the response, which decreased during the first four traverses (1–4), recovers sharply as soon as other rows of ommatidia are stimulated by the fifth scan (point 5). On the other hand, the response to Scan 5 on each curve is lower than that to Scan 1; that is, it is lower than it would have been if no stimulus had been given elsewhere in the visual field prior to Scan 5.

These results indicate that at least two processes contribute to habituation. One of these is dependent on the maintained position of the pattern and probably takes place further peripherally than the other, which occurs independently of the position of successive stimulus patterns.

How Does Excitation Depend upon Velocity of Pattern Movement?

As speed of movement increases, all other conditions remaining constant, discharge rate also increases in the region studied, up to about 350°/s. In Figure 7 the mean spike frequencies measured in the part of the visual field between +38° and +64° ventral are plotted as a function of stimulus velocity. The stimulus was a black 14° square, moved from 90° ventral to 90° dorsal at the speeds indicated. In this double logarithmic plot, the points lie approximately on a straight line.

The continuous scan curves, measured as defined on p. 317, have different amplitudes at different velocities, but resemble one another in shape. Figure 8 shows an example of a curve measured at high velocity (176°/s; upper solid curve) and another at low velocity (7°/s, lower solid curve). Again, the stimulus was movement of a black 14° square in the median plane from +90° ventral to −90° dorsal. The dashed curve resulted from multiplication of the points in the bottom curve by the normalization factor 4.2; this is the approximate factor by which the frequency in the ventral visual region increases when velocity is

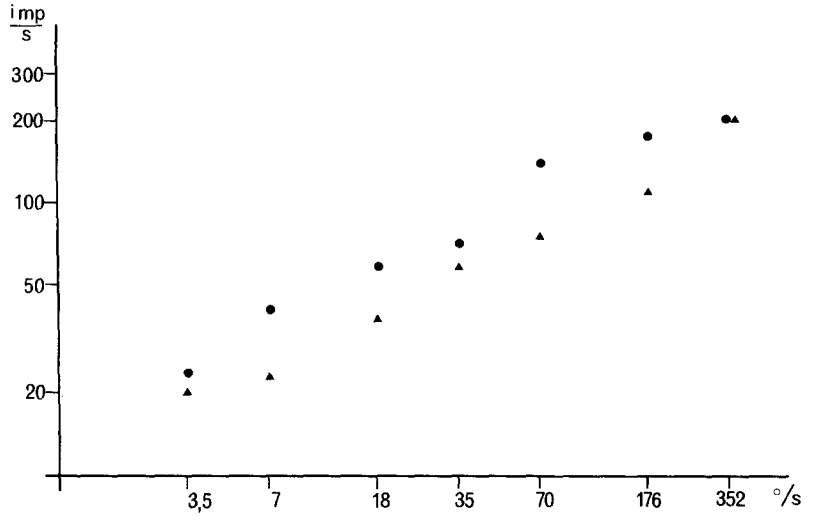

Fig. 7. Dependence of impulse frequency (ordinate) on velocity (abscissa). 14° black squares moved in median plane from ventral to dorsal. Plotted points represent impulse frequency elicited between +64° and +38° ventral. Two recordings (Nos. 28 and 38). $n=3$ in each case

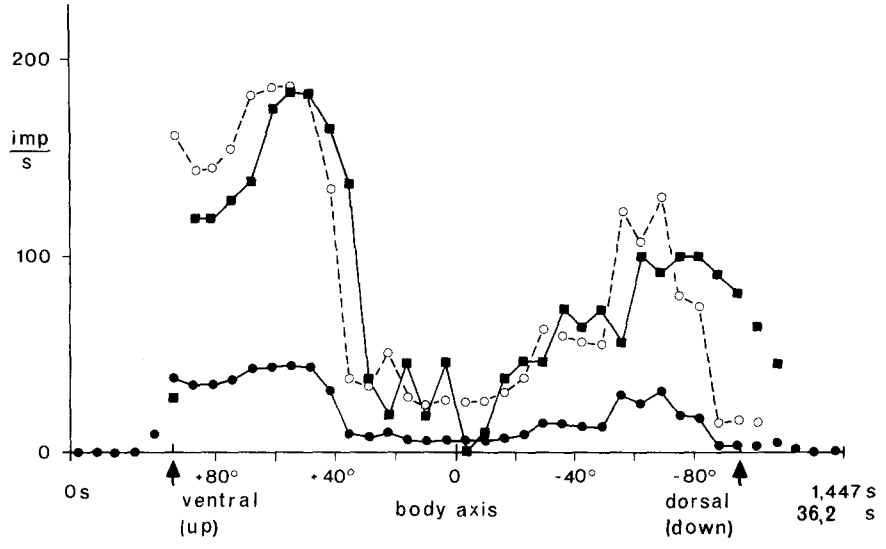

Fig. 8. Response of the cell to movement of a 14° black square in median plane from 90° ventral to 90° dorsal. Response to two different velocities (■——, 176°/s; ●——, 7°/s). Third curve (○-----) obtained by multiplying values in the second by a normalization factor. Recording No. 28

raised from 7°/s to 176°/s (cf. Fig. 7). When so adjusted, the low-velocity curve matches closely the excitation curve obtained at the high velocity.

The high-velocity curves are shifted, in toto, somewhat to the right with respect to the low-velocity curves. This shift along the time axis is compatible with a "latency" (dead time) of about 40–50 ms.

Dependence of Response upon Contrast

In order to test whether the response of the neurons depends on the contrast in the pattern, the cell was stimulated by movement of squares differing in degree of transparency. The squares that were not entirely opaque were made of film having a raster of eight black dots per degree of visual angle; the overall transmittance was determined by the diameter of the dots.

Of the responses recorded with such stimuli traversing the entire stage in the median plane, two examples are illustrated in Figure 9; for one of these the stimuli were presented in a ventral visual region (at +67°) and for the other in a dorsal region (at −60°). Both of the curves fall off gradually for contrast greater than 0.38, but at the lowest contrast the ventral response falls off sharply.

This difference in sensitivity at the lowest contrast is not limited to these selected points in the visual field. In the entire dorsal region of the visual field (associated with the broad response peak on the right

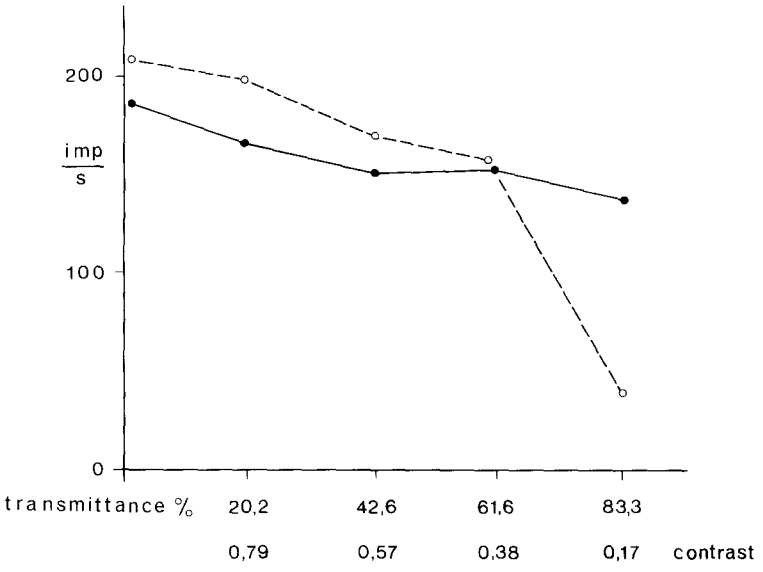

Fig. 9. Dependence of excitation upon contrast $(B_b - B_s)/B_b$. B_b and B_s are respective luminances of background and square. From continuous scan curves obtained by movement of squares varying in transmittance, two different measurement points were selected for plotting: o-----, impulse frequency at $+67°$ ventral; ●——, impulse frequency at $-60°$ dorsal. Square width, 14°; velocity, 70.4°/s; direction of movement, from $+90°$ ventral to $-90°$ dorsal. $n=4$. After each traverse stimulus stage turned by 180°. Recording No. 19

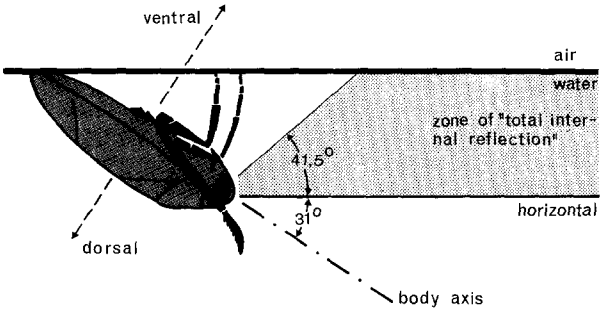

Fig. 10. *Notonecta* hanging below water surface

in Fig. 2) the unit was sensitive to the low-contrast stimulus, whereas in the entire ventral region it was insensitive.

Differences in the Shape of the Continuous Scan Curve for Objects of Various Sizes

Figure 11 shows responses of a cell to movement of different-sized squares from $+90°$ ventral to $-90°$ dorsal. The amplitudes of the curves are clearly different. In the dorsal part of the visual field, the 7° square excited this cell more strongly than either the 3.5° or the 14° square. Since the three curves were recorded in this sequence, at intervals of 20 min, they could have been affected by a change in sensitivity with time. In other recordings the optimum was associated with larger squares, up to 14° on a side. Still larger squares, with sides of 30° or more, produced marked excitation only at the ventral edge of the part of the visual field examined; such continuous-scan curves have shapes like the curve drawn with a thick line in Figure 14.

The maxima within the shaded part of the graph fall at different angular positions. The gray shading denotes the zone of the visual field in which the totally reflecting (i.e., mirroring) region of the water surface is located, when the animal hangs below the surface under natural conditions (cf. Fig. 10). The line labelled "H" marks the direction of the water horizon. The smallest square produces maximal excitation near this line. As the squares are made larger, the associated maxima move systematically away from the direction of the horizon, ventralward or $-$with respect to an animal hanging under the water surface$-$toward the front and upward.

The following table gives the positions of the maxima associated with squares of the indicated size, as found in another experiment under the same conditions:

Square width	Position of the maximum
3.5°	$+36°$
5°	$+42°$
7°	$+47°$
10°	$+49°$
14°	$+60°$

It is evident that the observed maxima shift systematically in the ventral region, the shift being greater the larger the square. This shift also appears when the rectangles moving along the track in the median plane are all the same length in the direction of motion, but differ in the perpendicular dimension.

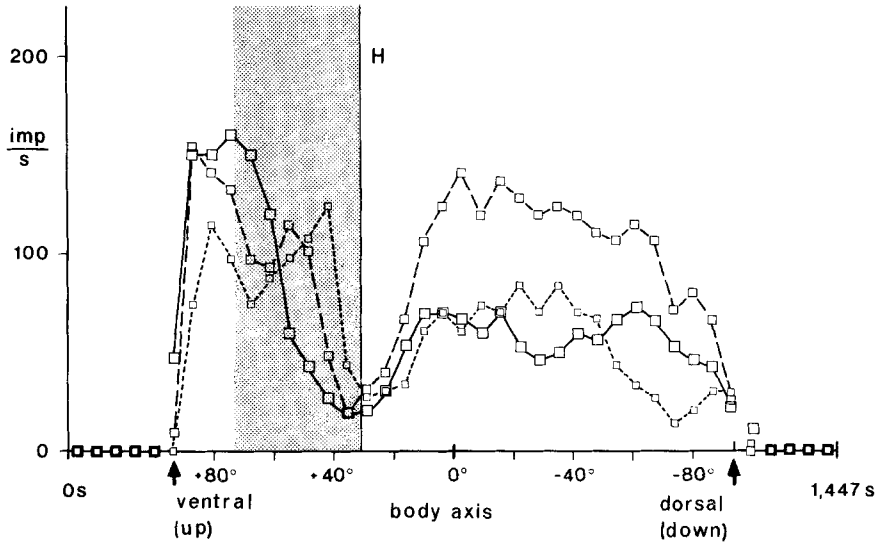

Fig. 11. Response to movement of squares of different sizes: 3.5° (···), 7° (---), and 14° (——). Gray area identifies region of visual field in which the totally reflecting part of the water surface lies, when *Notonecta* hangs below surface in normal position. H, direction of horizon. Direction of movement, from ventral to dorsal; velocity, 176°/s. Each curve mean of 6 single curves. Time interval between traverses of identical squares, 2.2 s. Series with squares of different sizes separated by pauses of 20 min

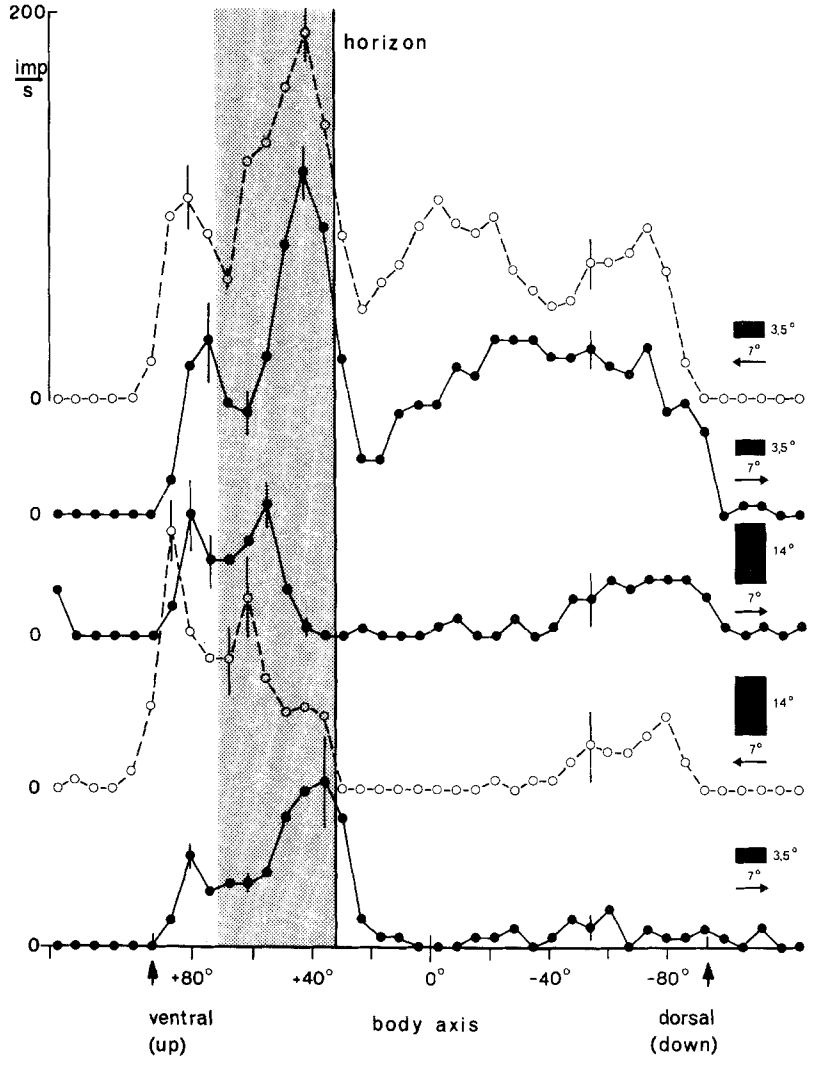

Fig. 12. Response to movement of rectangles differing in length of edges perpendicular to direction of motion. —— movement from ventral to dorsal; ------ movement from dorsal to ventral. Each point represents average of responses to six traverses at intervals of 2.2 s. Different pattern series separated by 5-min pauses

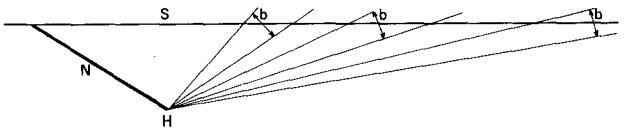

Fig. 13. Angular relationships discussed in the text

This effect is illustrated in Figure 12. The curves are shown in the sequence in which they were measured, from top to bottom. The reduction in amplitude can be ascribed to the fact that the intervals between tests of the different patterns were only 5 min. Regardless of this, however, the maxima within the shaded zone are close to the horizon line in the case of the narrow rectangle, and further ventral for the wide rectangle. This is true both with ventral-to-dorsal movement (solid curves ——) and with movement in the reverse direction (dashed curves ------).

Figure 13 is a sketch to illustrate the findings presented above. The line N represents a *Notonecta* in its natural position, at an angle of 31° to the water surface (S) with its head (H) hanging down. The thin lines indicate the visual angles subtended by the tested squares in the direction in which they produced excitation maxima in the ventral visual field in the example of Figure 11. Where these angles intersect the line representing the water surface, their chord lengths (b) are the same. The length of the lines (b) amounts to 0.18 ± 0.01 of the body length of *Notonecta*. The equivalent chord lengths computed from the data in the above table are 0.24 ± 0.02 body lengths. That is, the squares of different sizes produce excitation maxima when they lie in directions such that their images, projected onto the level of the water surface, have the same absolute sizes. For this to hold true, of course, water surface and long axis of the backswimmer's body must form the angle at which *Notonecta* normally hangs under the water surface.

The responses of a cell to sequences of six traverses of 14° squares, with the procedure described in the legend of Figure 11, were measured in 9 different animals. The peak response elicited in the region of the totally reflecting zone of the water surface occurred on the average at 63° ventral ($s_x = \pm 5.5°$; $s_{\bar{x}} = \pm 2°$)[1]. The chord length b computed from the mean position of the maximum is 0.24 ± 0.015 ($s_{\bar{x}}$) *Notonecta* body lengths.

[1] One factor that can contribute to the scatter in these angles is the error in direction of the visual field axes in the vertical direction. In this direction the error is greater than in the horizontal direction, owing to the relatively high mobility of the head before it is glued to the trunk; this error amounts to about ±5°

Parameters of the Shape of Moved Areas That Contribute to Their Effectiveness as Stimuli

In Figure 14, the response of the cell to movement of black areas differing in shape is illustrated. All the areas were moved in the median plane, from +90° ventral to −90° dorsal.

The movement of a square 14° on a side and that of a circle with diameter 14° produced very similar continuous scan curves over the entire visual field. A rectangular strip longer than the stimulus stage and moved onto the stage in such a way that only its leading, 14°-wide edge intersected the optical axes, also elicited a similar excitation curve. The shift of the curve to the right, in the ventral section, can be explained by the fact that in this case the frequency is plotted directly at the position of the edge, whereas for the circle and square it was plotted at the position of the middle of the pattern. When the long strip was moved out of the stimulus stage in such a way that only its trailing edge traversed the visual field, the cell was also excited. In this case, however, the excitation disappeared in the part of the visual field between 0° and +70°.

Movement of a stripe that subtends 14° along the direction of motion, and the full 67° height of the stimulus stage, brought about significant excitation only when it entered the stage, in a small ventral region between +75° and +90°[2].

These experiments show that the curves produced by a square and a circle closely resemble one another; the shape of these stimulus figures is not relevant to the course of excitation. It suffices that a single contour of the stimulus area intersects the optical axes of the ommatidia. Moreover, moving areas are ineffective if the edges intersecting the optical axes are too extensive.

Binocular Interaction

The most marked response of the cell was observed for movement presented within the binocular visual field (cf. Fig. 4). Does excitation also occur when the object is viewed monocularly, or is the cell sensitive only to movement stimuli seen in binocular vision?

Figure 15 shows the response to movement of a square in the median plane with the contralateral eye

[2] The excitation elicited by this pattern in the ventral region is not merely an edge effect associated only with the appearance of the stimulus at any position. After the whole stage had been shifted dorsalward by 20°, so that the traverse began at +70°, the transient excitation fell off more rapidly, to values near zero at +60° (Fig. 14b)

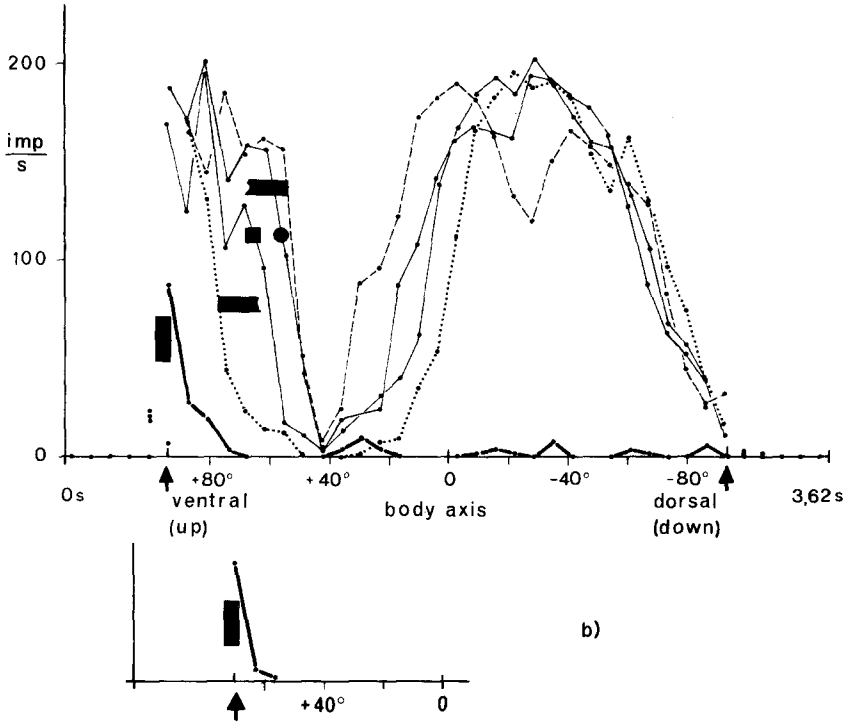

Fig. 14. Response of the cell to movement of patterns differing in shape: ■—— 14° wide black square; ●—— black circle 14° in diameter; ■--- 14° wide leading edge of a rectangular black strip longer than stimulus stage; ■··· 14° wide trailing edge of a rectangular black strip longer than stage; ▮—— 14° wide black stripe oriented perpendicular to its direction of motion and filling the entire 67° height of stage. Movement in median plane from +90° ventral to −90° dorsal; velocity, 70.4°/s; time interval between successive traverses, 2.5 min. $n=5$. For explanation of inset see text

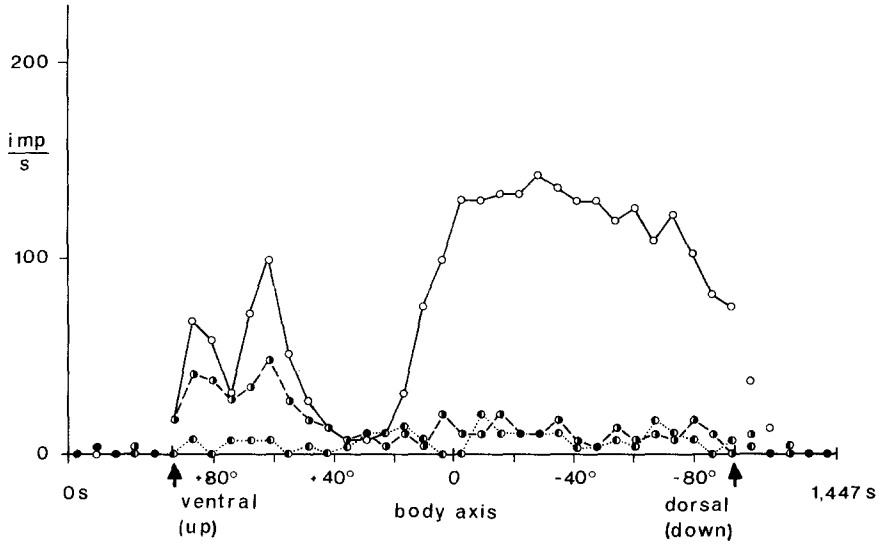

Fig. 15. Response to movement of a black square under conditions of binocular and monocular vision. Solid curve (——): both eyes view stimulus. Dashed curve (------): vision of contralateral eye occluded. Dotted curve (···): vision of ipsilateral eye occluded. Movement in median plane from +90° ventral to −90° dorsal. Square width, 14°; velocity, 176°/s. Each curve represents mean of responses to 8 traverses at intervals of 2.2 s. Recording No. 27

(------) covered and the ipsilateral eye exposed, in the reverse situation (·····; ipsilateral eye covered and contralateral eye exposed), and with both eyes exposed (——).

With either of the two eyes prevented from seeing, the response was much reduced over the entire region of the median visual field examined (180°). When only the ipsilateral eye was exposed (------) a greater excitation was produced than that resulting from stimulation of the contralateral eye alone.

In trials in which 8 squares traversed the stimulus stage in succession, the total number of action potentials produced was 746 for the binocular case, 151 with the contralateral eye covered, and 67 with the ipsilateral eye covered. The sum of the two monocular responses is much less than the response produced when both eyes can see.

The marked excitation of the cell by movement of a suitable object in the binocular visual field thus arises by way of a binocular interaction.

Discussion

It is highly probable that all the records described here reflect the activity of the same unit in the visual system, one sensitive to moving optical stimuli. In the different preparations, the complex responses to the various stimuli were similar.

This unit is probably very large; the amplitude of its action potentials was relatively large even with low-resistance electrodes.

The tip of the electrode lay in the medulla externa. But it is not unlikely that the action potentials arise in the medulla interna (lobula). The amplitude of the recorded potentials increased, the closer the electrode tip approached the lobula. Attempts to penetrate the lobula directly were unsuccessful.

The cell responds to the movement of stimulus areas as long as the angle they subtend is not too large; it does not respond to movement of a periodic striped pattern (16° stripes, 67° in extent). Therefore under natural conditions relative motion of the surroundings produced by *Notonecta*'s own movement would not produce excitation of this unit. But the movement of an object of appropriate size – for example, a prey animal – can serve as an effective stimulus. (With respect to the significance of similar properties of cells in the orthopteran CNS cf. Palka, 1969, 1972).

Over the range of velocities studied, between 3.5°/s and 350°/s, the logarithm of impulse frequency increases as a linear function of the logarithm of angular velocity. In other studies of movement-sensitive insect interneurons the discharge rate has been shown to increase with angular velocity up to similarly high values. In direction-specific units in the visual system of *Calliphora*, for example, impulse frequency rises in proportion to the logarithm of angular velocity; when stimuli are presented briefly in the most sensitive region of the visual field, the velocity can be increased to similar orders of magnitude with no occurrence of saturation (Collett and King, 1975).

The physiological responses of the neuron in *Notonecta* resemble those of the "DMD (Descending Movement Detector)" neurons of orthopterans in several respects. Both neuron types have large receptive fields (for the DMD neuron see Rowell, 1971). In both cases movement of a small area that stands out from the background has an excitatory effect. Both cell types fail to respond when very extensive contours move relative to the axes of the animal; the stimulus shown to be ineffective for orthopterans was relative movement of the surroundings when the animal was turned (Palka, 1967; Horn and Rowell, 1968), while with *Notonecta* a periodic striped pattern was moved around the stationary animal. The response to a normally excitatory stimulus is suppressed in both cell types when there is simultaneous movement of extensive structures in the visual field, at sufficiently high speeds (for the *Notonecta* neuron see p. 317 of this paper; for the DMD neuron see Palka, 1967, 1972; Rowell, 1971). The latency indicated by the displacement of the excitation curves of the *Notonecta* neuron with different speeds of movement is about 40–50 ms – on the same order of magnitude as the minimum latency of 30–50 ms found for the DMD neuron (Rowell, 1971).

The *Notonecta* neuron described here is particularly responsive to stimuli within the binocular field of view. The results show that the excitation involves binocular interaction; when either of the two eyes is prevented from seeing, excitation is reduced to a fraction of the original level.

The significance of the binocular interaction is not yet clear. The neuron was found to be excited both by objects moving at a distance of a few millimeters in front of the eyes (a little ball hanging on a hair) and by the movement of objects some meters away (a person in motion). This result is inconsistent with the notion that binocular interaction might cause the cell to respond only to movement stimuli at certain distances. (See Burkhardt et al., 1973, for a general discussion of binocular distance measurement by insects.) Experiments designed to clarify the situation are now in progress.

The optical environment of an animal hanging at the water surface is divided into three sections – the region under water, the zone of totally reflecting water surface, and a zone 97° in extent just above the animal, in which the water surface is transparent.

There is a similar subdivision in the responses of the cell to movement stimuli. It appears especially clearly in the continuous-scan curves for movement in the median plane of objects that are not too large (cf. Figs. 3, 5, 11, 12, 14, and 15). A maximum lies between 30° and 70° ventral to the long axis of the body, where the totally reflecting part of the water surface is located when the animal is in its normal orientation, waiting for prey. There is a second, broad sensitive zone in the part of the eye that sees the underwater region. A notch in the curve is evident at ca. 70° ventral; it is particularly distinct when the cell is stimulated by several traverses in rapid sequence (Figs. 3, 12, 15). This notch lies close to the boundary between the transparent and the totally reflecting water surface. Further ventrally the sensitivity increases again.

Movement stimuli in the three receptive-field zones thus demarcated elicit different responses of the cell. The angular diameter of objects effective as stimuli can be much larger in the ventral part of the field (comprising the transparent water surface) than in the central part which includes the totally reflecting surface. In the part of the visual field encompassing the underwater region, the cell was more sensitive to objects of low contrast than in the water-surface zones.

It is conceivable that the differing responses of the cell to movement stimuli in the various parts of the visual field are to some extent due to the structure of the periphery of the eye. According to Bedau (1911) there is a boundary between a ventral part of the eye, which views the water surface and in which the divergence angles are narrow, and a dorsal part with wider divergence angles. In the extreme ventral region of the eye there is a third zone where the divergence angles are again larger (Zänkert, 1939).

When *Notonecta* hangs below the water surface with its characteristic body orientation, the zones of maximal excitability are superimposed on the three zones of the optical environment. (For a discussion of the significance of spatially invariant mapping to abilities such as pattern recognition in insects, see Wehner, 1973). For *Notonecta* in this position the observed "size-constancy phenomenon" holds for the plane of the water surface; the movement of squares of different sizes in the ventral eye region between +30° and +70° produced excitation maxima at positions that shifted systematically with the size of the square (cf. Fig. 11). In the direction in which the maxima of excitation were produced, the squares – of different sizes in terms of the subtended visual angle – had the same absolute size, about 1/4 the body length of *Notonecta*, when they were projected upon the water surface (cf. Fig. 13). This could mean that objects of this size moving in the water surface excite the cell maximally at any distance, so that a high level of excitation would be maintained as they approached or receded.

Animals smaller than *Notonecta*, moving in the water surface, are the backswimmer's prey. Prey at the water surface is first localized by means of the sense of vibration (for literature on vibration sensitivity see Wiese, 1974). The accuracy of localization is between 2° and 20° (Markl et al., 1973). The backswimmer turns so as to bring the object into the zone of highest sensitivity of the movement-sensitive cell described here. It slowly swims toward the prey, led by vibration stimuli, and then – from a distance of a few centimeters – propels itself sharply forward by strong rowing motions. This phase of prey capture is triggered by visual stimuli (Baerends, 1939). The present results indicate that during this phase the cell is excited by the prey. It is conceivable that the neuron described here participates in control of the final surge forward. Following a computation in which the signals from this neuron are processed together with those from the corresponding unit on the opposite side of the body *Notonecta*, remaining just under the surface of the water, could swim directly toward the prey agitating the water surface. Further experiments are needed to test whether this notion in fact applies, and these are now in preparation.

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