THE OPTOMOTOR SYSTEM OF THE LOCUST

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The regenerating eye experiments in Chap. 5 were carried out with Dr. C.M. Bate who provided much of the histological data on the animals whose behaviour I had tested. The remainder of the work in Chap. 5 and that described in Chaps. 1-4 was carried out alone.

SUMMARY

Part I - Sensory integration in the locust optomotor system was examined by using the head movement response as an indicator of direction detection. A new finding was that movements of a single black-white edge of particular polarity (e.g. the white anterior edge stimulating the left eye) elicit head movements in the opposite direction to the stimulus. These anomalous responses disagree with the predictions of previous optomotor models. The new model, accounting for this response, consists of two opposing asymmetric (Barlow & Levick, 1965) networks, one receiving inputs from ON cells, the other from OFF cells.

Two types of optomotor neurons (as well as other motion detectors) were recorded in the optic lobes and circumoesophageal connectives; type 1 neurons code the number of ommatidia stimulated, type 2 neurons code the velocity of a movement. Both types show anomalous responses to the white anterior edge stimulating the left eye, the type 1 neurons failing to respond, the type 2 neurons showing a reversal similar to the behavioural reversal.

Tests using discontinuous movement reveal that, for the type 1 neurons, inputs from every 5th ommatidium, probably via the medullary cartridge, interact to produce directional selectivity. The type 2 neurons receive inputs from 2 cell types, a smaller field cell (dia. $1.5^{o} - 2^{o}$) interacting with its equivalent from every 5th cartridge along a row, the larger field type (dia. $2.5^{o} - 4^{o}$) interacts with its equivalent from every 8th-9th cartridge.

The time course of the interactions between the large field inputs to the type 2 neurons forms a velocity peak. The interactions between

the inputs to the type 1 neurons are brief and other mechanisms, such as selective facilitation, maintain the responses to a wide range of stimulus speeds.

The response of the type 1 neurons is not a function of contrast frequency, the same velocity eliciting maximal responses regardless of pattern wavelength. This result confirms that the inputs form asymmetric networks. The response of the type 2 neurons shows a dependence on contrast frequency but this dependence results from a switching from one asymmetric network (small field neurons) to the other (large field neurons) as pattern wavelength increases.

Part II - Alteration of a locust's arousal level, by changing the level of ambient illumination or the degree of restraint of the animal, demonstrates that animals at a low arousal level fail to make optomotor head movement or walking responses. Instead large random head movements are elicited by small flashes or tiny oscillations of a pattern. These responses are quite nonspecific as they can be elicited by stripe movement in animals whose eyes, after sectioning in 3rd instar, have failed to regenerate correctly. The large nonspecific responses result from activation of a general arousal system which must be excited to a certain degree before specific reflexes can function.

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PART 1

SENSORY INTEGRATION IN THE LOCUST OPTOMOTOR SYSTEM

Introduction

The optokinetic and optomotor responses are reflexes which enable an animal to stabilise its eyes or body against a visual background. With the fixed eyes of insects the optomotor response consists of head stabilisation. A head movement, such as tremor, stimulates the retinae and can elicit a compensatory movement which is largely controlled by visual feedback. In the standard optomotor experiment, the stimulation resulting from a head movement is simulated by rotating the background about an initially stationary animal. The head moves to reduce the visual stimulation but now by following the stimulus.

The optomotor system, from sensory inputs to behavioural output has provided a rich field for study. Many workers have concentrated on the expression of the response, analysing behaviour and motor output (e.g. Horridge & Sandeman, 1964; Burrows & Horridge, 1968a,b; Horridge, 1966e; Collewijn, 1970; Robinson, O'Meara, Scott & Collins, 1969). Apart from the intrinsic interest of eye and head movement as an example of motor integration the response is ideal for the analysis of biological negative feedback systems (e.g. Horridge, 1966e; Robinson, 1968; Collewijn, 1969). Other workers have manipulated the moving stimuli so that the resulting behaviour has allowed deductions on the nature of sensory integration within the optomotor system. This approach has been particularly popular in the analysis of arthropod optomotor systems (e.g. Reichardt, 1961; Götz, 1964; Horridge, 1966a-c; Kirschfeld, 1972, 1973). There has been much less direct electrophysiological analysis of the sensory integration in the optomotor system because of the difficulty of finding and identifying both the directional optomotor neurons and their nondirectional inputs. Indeed

only recently have responses of directionally selective neurons been compared with optomotor behaviour elicited in the same experimental conditions (Oyster, Takahashi & Collewijn, 1972; McCann & Foster, 1971, 1973). The direct analysis of sensory integration has followed two approaches; first, the analysis of the mechanism of the directional selectivity which is required to inform the animal in which direction its head or eyes must move. The second approach is the analysis of the passage of the information from the first direction selective neurons to the motoneurons.

The models for direction detection in the optomotor system which have been put forward are shown in Fig. 1. The experimentally determined mode of direction analysis in vertebrates is that shown in Fig. 1A. Both these models are asymmetric, each channel firing only if the neighbouring channel on a particular side has (excitatory) or has not (inhibitory) received the same stimulus within a given time. This model can be wired quite easily with the neurons occurring in the vertebrate retina. For example the inputs are the bipolar cells, the lateral interactions are mediated by amacrine cells while the ganglion cells are the directionally selective neurons (Dowling, 1970). This arrangement is consistent with the known anatomy (Dowling, 1970 for review) and electrophysiology (e.g. Barlow & Levick, 1965; Michael, 1968; Werblin, 1970).

Our understanding of direction detection in arthropods is not nearly so clear. Most behavioural studies have supported the symmetric multiplicative model summarised in Fig. 1Bd (Reichardt, 1961, 1969 for review). However it has been shown that this model is not exclusive and that the others shown in Fig. 1B could also be used. These models are indistinguishable in a behavioural analysis (Thorson, 1966b). The little information from direct recordings is conflicting. A model derived from recordings of fly optomotor neurons favours a symmetric interaction between the input neurons (McCann, 1963; Marmarelis & McCann, 1973) while

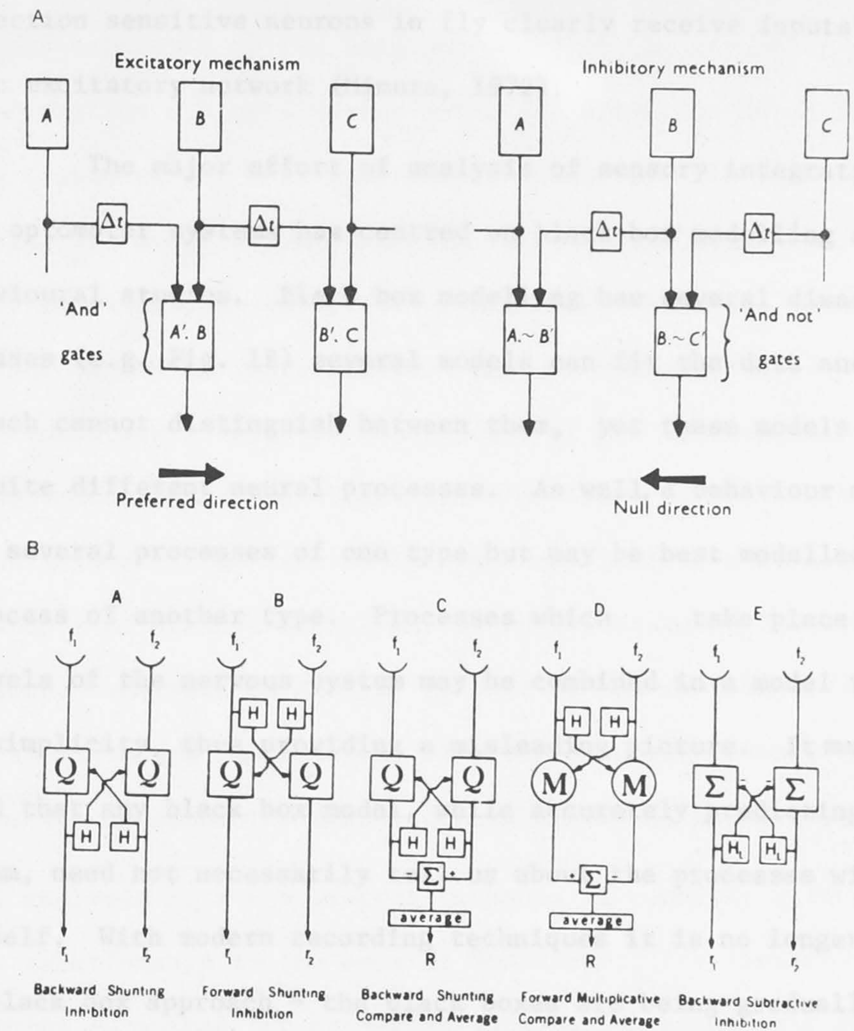


Fig. 1 Models proposed for inputs to direction detecting neurons. (A). Asymmetric models proposed by Barlow & Levick (1965) for the inputs to the directionally selective ganglion cells of the rabbit retina. The inhibitory model is usually used to explain the decrease of firing below spontaneous rate for movement in the null direction. Combination of many 'and' or 'and not' gates produces a cell with a large receptive field. (B). Mathematical models proposed by Thorson (1966b) for the inputs to the locust optomotor system. These are variations of symmetrical models with symmetrical interaction between facet pairs. d) is the crosscorrelation or multiplication model.

other direction sensitive neurons in fly clearly receive inputs from an asymmetric excitatory network (Mimura, 1972).

The major effort of analysis of sensory integration in arthropod optomotor systems has centred on black box modelling derived from behavioural studies. Black box modelling has several disadvantages. In some cases (e.g. Fig. 1B) several models can fit the data and a black box approach cannot distinguish between them, yet these models may all require quite different neural processes. As well, a behaviour may be the result of several processes of one type but may be best modelled by a single process of another type. Processes which take place at different levels of the nervous system may be combined in a model to form one step for simplicity, thus providing a misleading picture. It must always be remembered that any black box model, while accurately predicting the output of a system, need not necessarily tell us about the processes within the system itself. With modern recording techniques it is no longer necessary to use a black box approach - the black boxes are being gradually opened. We can now analyse a system in terms of its neuronal interactions and thereby describe and localise precisely what happens in the system. This approach allows the determination of the actual biological principles which govern the system.

The experiments reported here are an analysis of sensory integration within the locust optomotor system in terms of neuronal connections and interactions. One aim was to determine how the neurons are connected to create directional selectivity. The analysis was greatly facilitated by finding an anomalous response in the locust, both behaviourally and in the optomotor neurons, to movements of a single edge. Not only is this response the first reported behaviour which shows qualitative disagreement with predictions from the symmetrical networks, thereby eliminating them for the locust, but the nature of the response defines

the broad characteristics of the input networks of the optomotor neurons. With this information a simple neuron model for direction detection was devised as a framework for more experiments (Chap. 1), the value of the new model being its description of neuron interactions which could be tested easily in electrophysiological experiments (Chap. 2). Once the basic behaviour of the optomotor neurons was determined a variety of tests were used to formulate a detailed description of the lateral interactions involved in movement detection (Chap. 3). The final verification of the model and the nature of the lateral interactions lead to a revision of previous concepts of direction analysis in invertebrates. The biological mode of direction analysis is similar to that of the vertebrate and it is shown that variation and combinations of a basic neural network can account for the varieties of optomotor behaviours in different animals.

No analysis of a behavioural response is complete without considering its relationship to the overall behaviour. For instance, if the optomotor system is suited for gathering information about only the animal's movements, there must be other neurons which respond to external movements. Some neurons of this type have been found in the locust optic lobes and are described in Chap. 4. An often observed phenomenon is the apparently spontaneous doubling or trebling of firing rate of optomotor neurons. Related to this is the finding that the 'arousal' or 'excitement' of the animal greatly affects the size and even the occurrence of an optomotor movement. The effects of 'arousal' and the behaviour when optomotor responses cannot be elicited demonstrate the existence of an arousal system similar in function to the vertebrate reticular activating system (Chap. 5).

CHAPTER 1 Optomotor Behaviour

The first step in the analysis of the optomotor system was a description of optomotor behaviour to ensure the use of only behaviourally meaningful stimuli in later experiments. Most previous optomotor studies have used fly, bee or beetle and the major findings are: (1) Motion is analysed only between neighbouring ommatidia, spreading as far as sub-adjacent ommatidia in the beetle (Hassenstein, 1958) and ommatidia separated by no more than two unstimulated omma's in the bee (Kunze, 1963). In the fly stimulation of only two lamina cartridges is sufficient to elicit an optomotor response (Kirschfeld, 1972). (2) Stimulation of more ommatidia produces a larger response by a simple summation of these localised re-actions (Götz, 1964; McCann & MacGinitie, 1965). (3) The response is dependent on contrast frequency ($\frac{\text{speed}}{\text{wavelength}}$), the velocity eliciting a maximal response increasing with pattern wavelength (Götz, 1964; Fermi & Reichardt, 1963; Kunze, 1961; Reichardt, 1961). (4) The direction of the behavioural response follows a multiplicative law; if an increase of light is designated as +, a decrease as −, first in input A, then B, then the response to A+.B+ = A−.B−, and the response to A+.B− = A−.B+ these latter responses being in the opposite direction. All these findings have resulted in the multiplication or autocorrelation model in Fig. 1Bd.

A new finding in the locust are its anomalous or error responses to simple visual stimuli such as a stripe or edge. An error of this kind allows an analysis not otherwise possible and in particular allows a comparison of behaviour and electrophysiology in the error situation. This chapter describes both the normal and anomalous optomotor responses to provide a behavioural basis for the neurophysiological analysis in the next chapter.

The locusts used were female adult Australian plague locusts (Chortoicetes terminifera Walk.) from laboratory culture. The animals were fixed by the thorax leaving the head and abdomen free to move. Optomotor responses were recorded using a light flag of paper ash attached by a fine wire to the head. Movement was measured by the flag's interruption of a beam of light falling upon an illuminated photocell (Texas type LS221). This photocell consists of two cells in series with a differential output which indicates direction of movement. With a flag 2cm from the head, movements of less than 0.05^o could be measured. Thresholds determined by this method are very close to those determined by recording from neurons in the circumoesophageal connectives (Chap. 2).

Several types of stimuli were used. In one case striped patterns of different periods were inserted in a vertical drum (height, 25cm, diameter 27cm, luminance at the eye 68.4 cd/m^2) and this was rotated by hand. Direction of rotation about its vertical axis was varied randomly. The animal was placed with its longitudinal axis horizontal in the centre of this drum 6cm from its lower edge. Another stimulus consisted of stripes or edges projected onto a spherical diffuser placed over the eye and oscillating sinusoidally perpendicular to the stripe edges. Luminance at the eye was 596 cd/m^2. One eye was covered. In both cases, the whole of the other eye was stimulated. As there is an opaque patch on the dorsal surface of the eye (see Fig. 16, Chap. 2), only a few facets would not be stimulated in an open topped drum. The receptive field plots (Chap. 2) show their insignificant contribution. Pattern repeat periods subtended 6°, 15.8^o or 25° at the eye. Pattern contrast was 0.6. Single stripes subtended 7.9^o or 12.5^o. Stimulation at constant velocity was provided by a small transparent striped drum which was motor driven. A diffuser, covered so that the eye could see an area of 10° x 15° was fixed between the drum and the light source in the centre of the drum. Luminance was

26.6 cd/m^2 at the eye.

Each eye contains about 6,000 facets. The initial stimulation of both eyes is expressed as stimulation of 12,000 facets. After initial testing with both eyes, the left eye only was stimulated during all experiments. The right eye and the ocelli were covered with an opaque paint (Kodak Opaque Red). This paint was also used to blind most of the left eye leaving exposed only some facets in the flat median part of the eye. As the corneal facet diameter is 28μm the number left clear was easily checked by counting the facets under a microscope. The semidry paint was easily manipulated and removed and optomotor and histological testing after its removal showed that the paint caused no injury.

In all experiments, head movements in the same direction as stimulus movements, i.e. following movements, were expressed as the percentage of the total number of tests given.

$$\% \text{ following responses} = \frac{\text{Number of following responses} \times 100\%}{\text{Total number of trials given}}$$

The total number of trials includes trials which elicited counter movements and those which failed to elicit a response. (An exception to this is made for Fig. 9 when plotting reversal responses).

<u>Number of facets required to detect direction of motion</u>

A locust with one eye occluded and fixed by the thorax in the centre of a striped drum will nearly always move its head in the direction of motion whenever the drum is rotated (Thorson, 1966a). When the whole eye is stimulated by the stripes, these head movements are large and consistent (Fig. 2a). During the experiment the eye was gradually blinded from the periphery towards the centre with the viewing area always in the

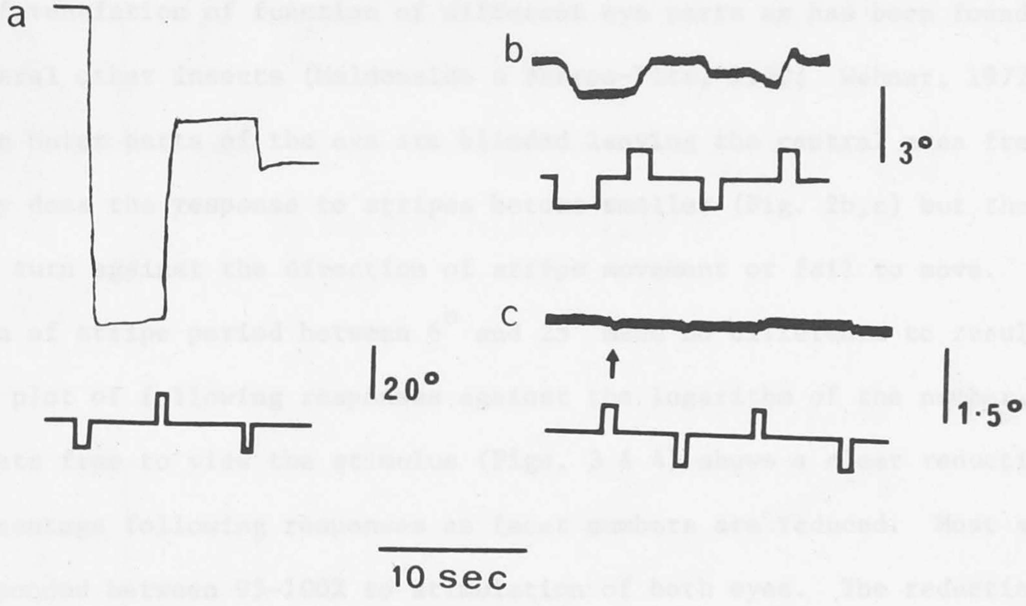
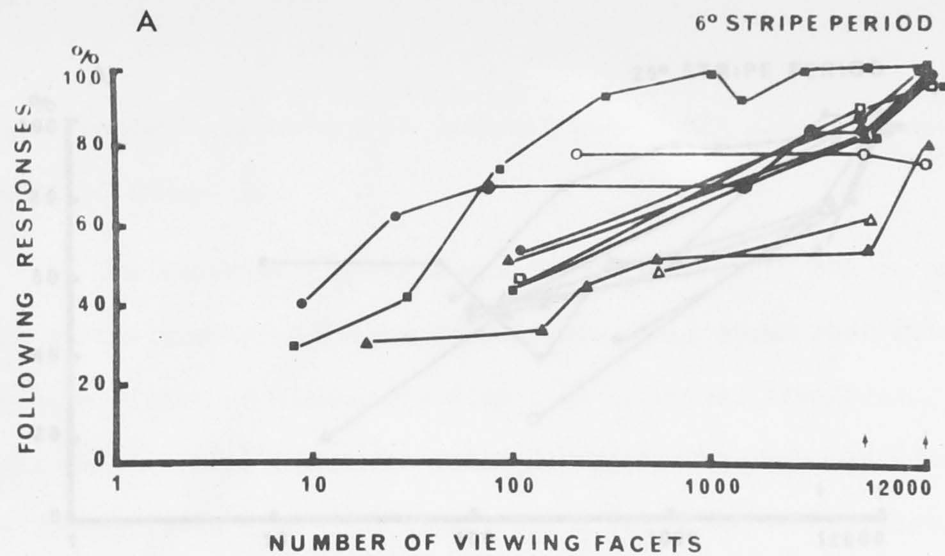


Fig. 2 Optomotor responses of a locust to movements of a striped pattern. Upper trace represents head movement output from photocell, lower trace shows duration and direction of drum movement. Upward deflection in both head movement and drum marker trace indicates movement to the right. Calibration bars indicate degrees of head turning. Angular velocities were c. 90°/sec. a) stimulation of both eyes, stripe period 6°. b) viewing area 250 facets, stripe period 25°. c) viewing area of 84 facets, stripe period 6°. Note the small responses and the error response to the first movement marked by the arrow.

centre of the eye. This central area was found to be the most sensitive area of the eye with diminishing responsiveness towards the periphery (see receptive field plots, Chap. 2). Testing different portions revealed no differentiation of function of different eye parts as has been found in several other insects (Maldonaldo & Barros-Pita, 1970; Wehner, 1972). When outer parts of the eye are blinded leaving the central area free not only does the response to stripes become smaller (Fig. 2b,c) but the head may turn against the direction of stripe movement or fail to move. Variation of stripe period between 6° and 25° made no difference to results. The plot of following responses against the logarithm of the number of facets free to view the stimulus (Figs. 3 & 4) shows a clear reduction of percentage following responses as facet numbers are reduced. Most animals responded between 95-100% to stimulation of both eyes. The reduction of responses when one eye was covered varied from 0-25%. The further reduction in percent following responses is caused by an increase in the number of errors or failures to respond. The increase in failures accounts for percentages below 50%. Figs. 3B, 4B show the same data normalised so that the response to stimulation of the whole of one eye is 100%. A χ^2 test comparing following responses when the whole eye was stimulated, with following responses when 100 or fewer facets were stimulated shows a significant difference at the 1% level. (The exceptional response of one animal in Fig. 4A may have been caused by a temporary thinning of the paint.) When fewer than 50 facets were left exposed the stimulus generated many errors or countermovements. Both errors and following movements are definitely visual, as completely blinding the eye reduced the percentage following responses to less than 5%, with the total number of trials where some head movement occurred being less than 10%. The high number of errors recorded when less than 50 facets viewed the stimulus show that there was a genuine failure to respond correctly rather than any insensitivity of the recording system (Fig. 2c). Also directional neurons in the circumoeso-



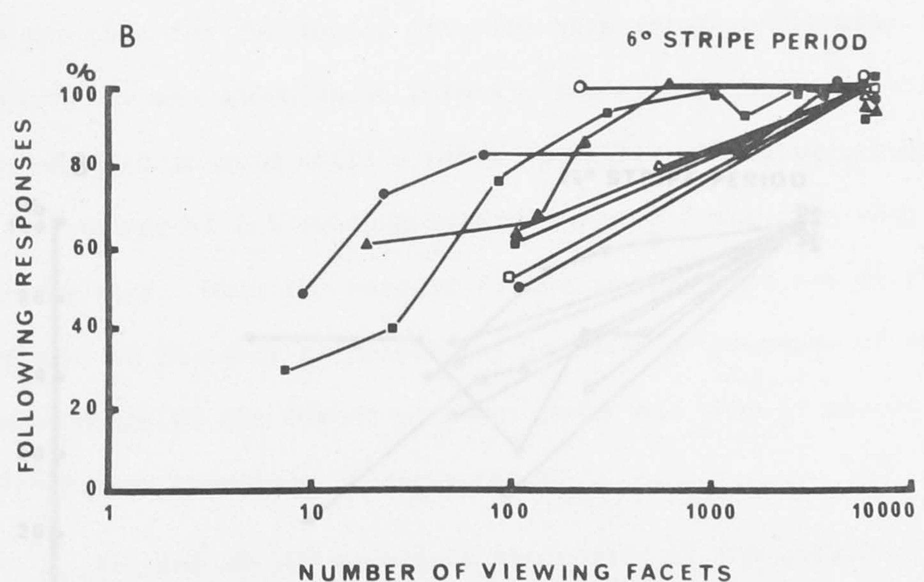
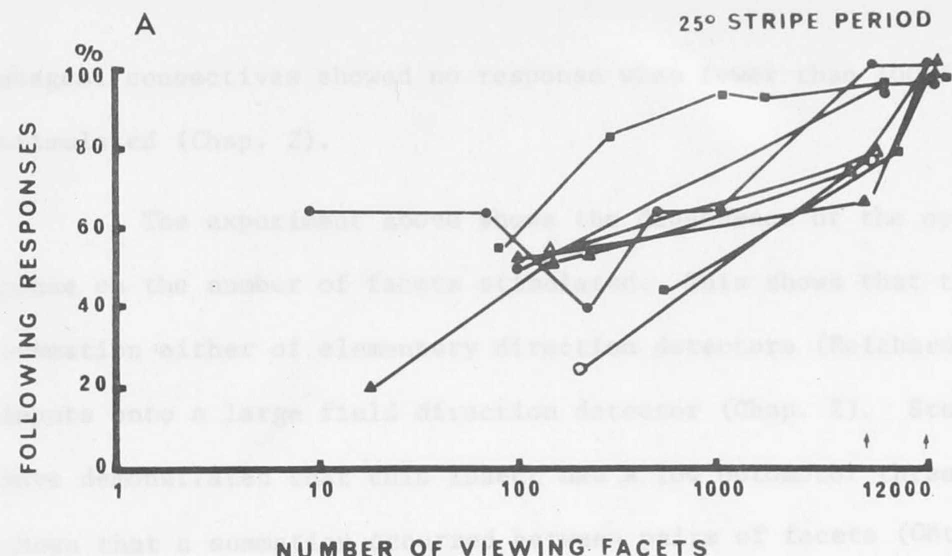


Fig. 3 Reduction in percentage following response (ordinate) to movement of 6° period stripes as the number of viewing facets is reduced (abscissa log number of facets). Each curve is obtained from a different animal and each point accumulated from 20-40 trials. Angular velocity 20°/sec. A. non-normalised data. 12,000 represents stimulation of both eyes; 6,000 is stimulation of one eye (marked by arrows). B. data normalised so that following responses for the whole of one eye is 100% in all animals.



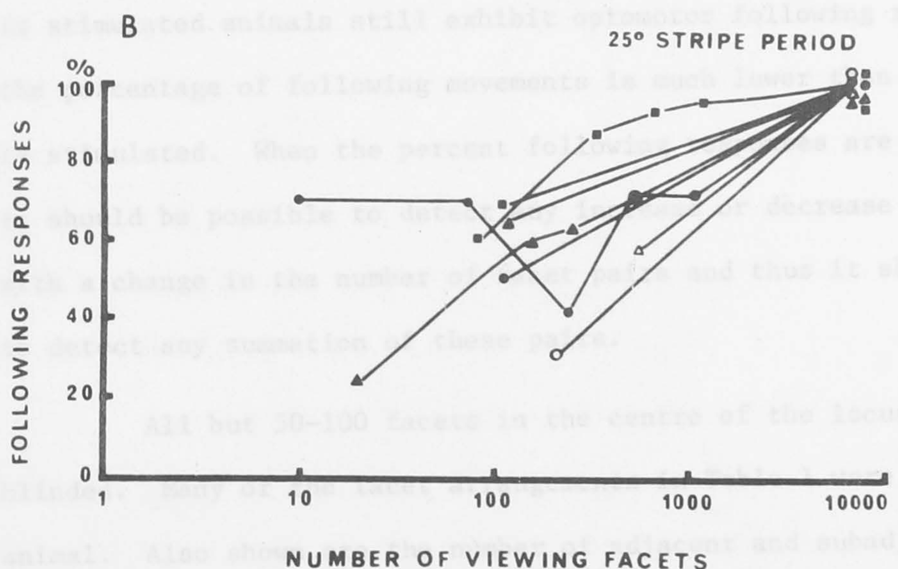


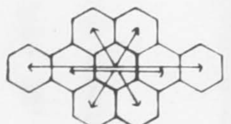
Fig. 4 Reduction in following responses to movement of 25° period stripes as the number of viewing facets is reduced. Plotted exactly as in Fig. 3.

phageal connectives showed no response when fewer than 100 facets were stimulated (Chap. 2).

The experiment above shows the dependence of the optomotor response on the number of facets stimulated. This shows that there must be summation either of elementary direction detectors (Reichardt, 1961) or of inputs onto a large field direction detector (Chap. 2). Studies on the fly have demonstrated that this insect has a low optomotor threshold and have shown that a summation occurred between pairs of facets (Götz, 1964; McCann & McGinitie, 1965). The following experiment was done to see if the same was true for the locust with its high optomotor threshold (50-100 facets). As was shown above when a circular or square area of 100 facets is stimulated animals still exhibit optomotor following responses although the percentage of following movements is much lower than when the whole eye is stimulated. When the percent following responses are at this low level it should be possible to detect any increase or decrease of performance with a change in the number of facet pairs and thus it should be possible to detect any summation of these pairs.

All but 50-100 facets in the centre of the locust's eye were blinded. Many of the facet arrangements in Table 1 were tested in the same animal. Also shown are the number of adjacent and subadjacent facet pairs for each condition calculated for horizontal movement. If a linear summation does occur, the condition with the greatest number of these pairs, i.e. condition V_5H_{20} (column 1) should show the highest percent following responses. The data in Table 1 shows that no such trend was found. The percentage following responses varied widely for each condition in different animals as did the relative performances for each condition in the same animal. A χ^2 test showed no significant differences between any of the conditions. However in 4 out of 5 animals the percentage of following responses for condition V_5H_{20} (column 1) and $V_{20}H_5$ (column 6) were slightly

Table I Orientation of viewing facets. The table shows following responses for each of the 6 conditions illustrated. The number of conventional reacting pairs of facets is shown for each condition. Conventional reacting pairs are those previously thought to interact during motion detection. These pairs are shown above the table. Data from different animals is shown down the columns, data from the same animal is read across each row. Each value was obtained from 50-100 trials. The highest value for each animal is the boxed value.



ORIENTATION OF VIEWING FACETS

	Horiz. 20 facets Vert. 5 facets $V_5\ H_{20}$	10 facets 2 x Horiz. 10 Vert. 5 facets $V_5\ 2H_{10}$	Horiz. 10 facets Vert. 10 facets $V_{10}\ H_{10}$	Horiz. 5 facets Vert. 10 facets $V_{10}\ H_5$	10 facets Horiz. 5 facets 2 x Vert. 10 $2V_{10}\ H_5$	Horiz. 5 facets Vert. 20 facets $V_{20}\ H_5$
Number of viewing facets	100	100	100	50	100	100
Number of reactive pairs	493	466	418	218	436	448
% following responses	76.4	75.0	55.9	47.8	65.8	71.4
	72.5	63.4	61.2	51.8	50.3	56.9
	54.7	52.6	82.5	55.9	53.3	58.0
	48.5	54.0	52.2	57.4	56.3	70.5
	56.5	37.8	52.5	65.6	66.6	51.7
	61.5	48.5	61.0	62.0	66.6	50.0
	51.5	41.6	54.5			57.5
	25.0	61.5	50.0			55.5
	36.7		36.3			55.5
	36.3		30.0			76.7
	44.0		51.0			66.6
	50.0		27.0			49.0

higher than those for $2V_{10}H_5$ (column 2) and $2V_5H_{10}$ (column 5) respectively in the same animal, indicating that one large viewing area performs better than several smaller ones.

The results of these experiments do not conform with those expected if there is a summation of pairs of facets (column 1 should show the greater percentage response level). However, there must be some form of summation as the response magnitude does increase as the stimulated area increases. As the summation is not revealed by experiments using 100 facets, it must occur over larger areas of the eye. This result suggests the presence of a large field direction detector.

Responses to a single narrow stripe

When a single narrow stripe (width 7.9^{o} or 12.5^{o}) was moved before the whole eye some animals faithfully followed even oscillations of less than 30' of arc, while others moved their heads against the stripe motion with the same precision. Comparison of results with values predicted on the assumption that following responses and countermovements could occur with equal probability showed that two animals made significantly more following responses (100%, 84.3% following; 0%, 5.3% errors; 100-200 trials/animal; $P<0.001$). Two animals made more countermovements (following 7%, 12%; errors 81%, 43%; 100-200 trials/animal; $P<0.001$). Others responded in a random manner. Thus 3 qualitatively different response classes can be distinguished: animals that followed the stripe, animals that made reversed responses and animals that made random responses to the stripe. Experiments with a white stripe on a black background produced the the same 3 response classes.

When 3 black stripes (repeat period 25°) on a white background were used, both following and reversed responses were elicited in different

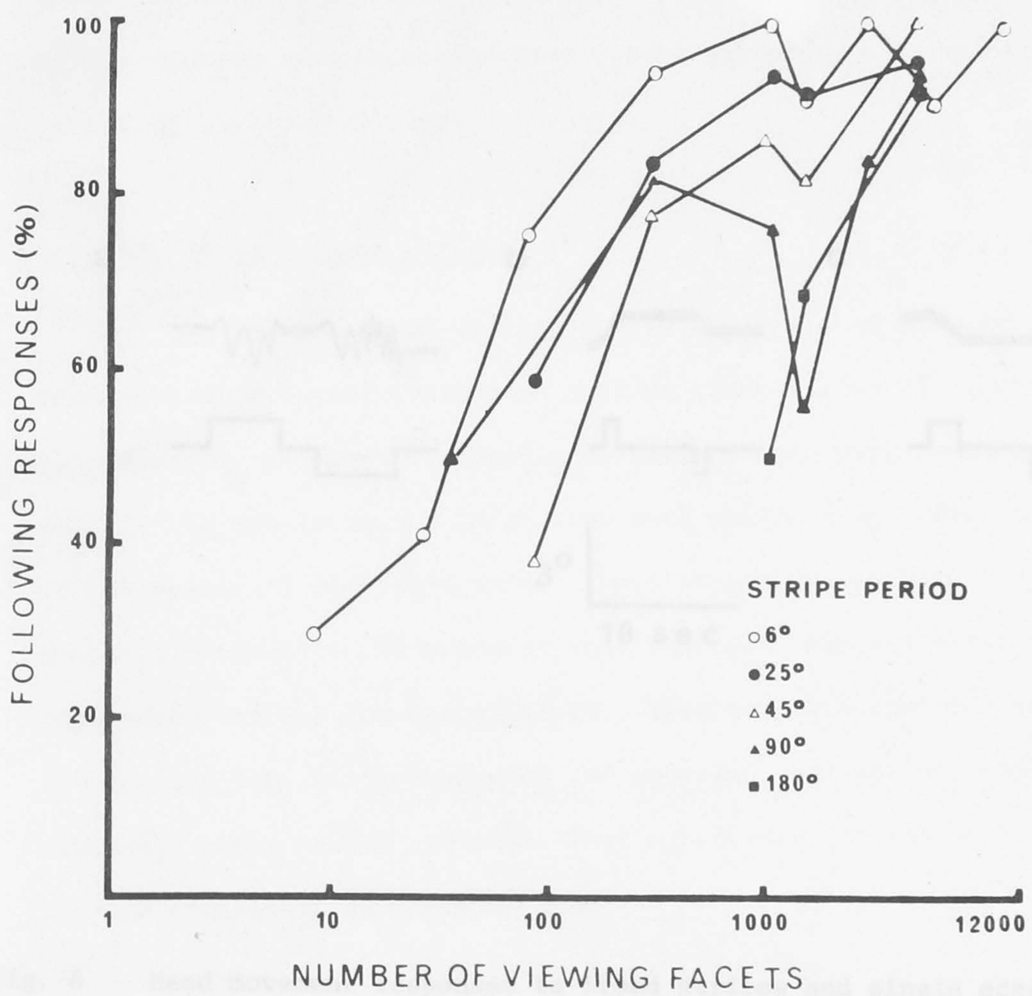


Fig. 5 The effect of reduction in viewing facet numbers on percentage following responses to stripes of different repeat periods. All data are from the same animal and values obtained from stimulation of the entire eye have not been normalized. 12,000 facets represent stimulation of 2 eyes. Angular velocity 20-90°/sec.; each point obtained from 20-40 trials. Note the decrease in performance to stripes whose repeat period is greater than 90°.

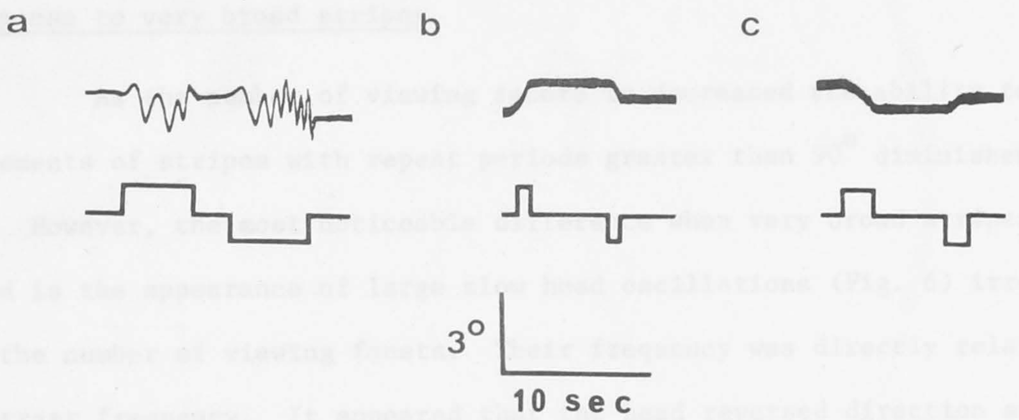


Fig. 6 Head movement responses to broad stripes and single edges. The upper trace represents head movement output from the photocell, lower trace shows duration and direction of drum movement. Upward deflection in both traces indicates movement to the right. Calibration bars indicate degree of head turning. Angular velocity of drum is 8°/sec. a) 90° period stripes stimulating 1,000 facets. b) response to a single edge, black anterior edge stimulating 35 facets. c) white anterior edge, 35 viewing facets. The size of the response to very broad stripes does not show a clear dependence on the numbers of viewing facets.

animals. In some cases, as the movement of the stripes became larger, or as the stimulus was increased from 1 to 3 stripes, an animal that had been reversing would now follow.

Response to very broad stripes

As the number of viewing facets is decreased the ability to follow movements of stripes with repeat periods greater than 90° diminishes (Fig. 5). However, the most noticeable difference when very broad stripes are used is the appearance of large slow head oscillations (Fig. 6) irrespective of the number of viewing facets. Their frequency was directly related to contrast frequency. It appeared that the head reversed direction as each edge moved through the visual field. This suggests that the broadness of the stripes temporally separated two opposing edge effects which are not separable using narrow stripes. This hypothesis was tested by using stimuli consisting of a single edge.

Responses to a single moving edge

The presence of opposing edge effects was tested by using stimuli containing a single black-white boundary. The movement of a single straight black-white edge elicited small head movements whose actual amplitude did not appear to depend on the number of viewing facets, unlike the responses elicited by a stripe pattern (e.g. Fig. 2a,b). The experimental arrangement and nomenclature referring to the edges is given in Fig. 7. If the edge was the black anterior edge the locust's head followed the stimulus movement. If the edge was the white anterior edge the response was slightly smaller and the locust moved its head consistently against the direction of stimulus movement (Fig. 6b,c). The data is given in Fig. 8. χ^2 tests on the data show differences significant at 0.1% level. The counter movements to the white anterior edge may be regarded as reversed

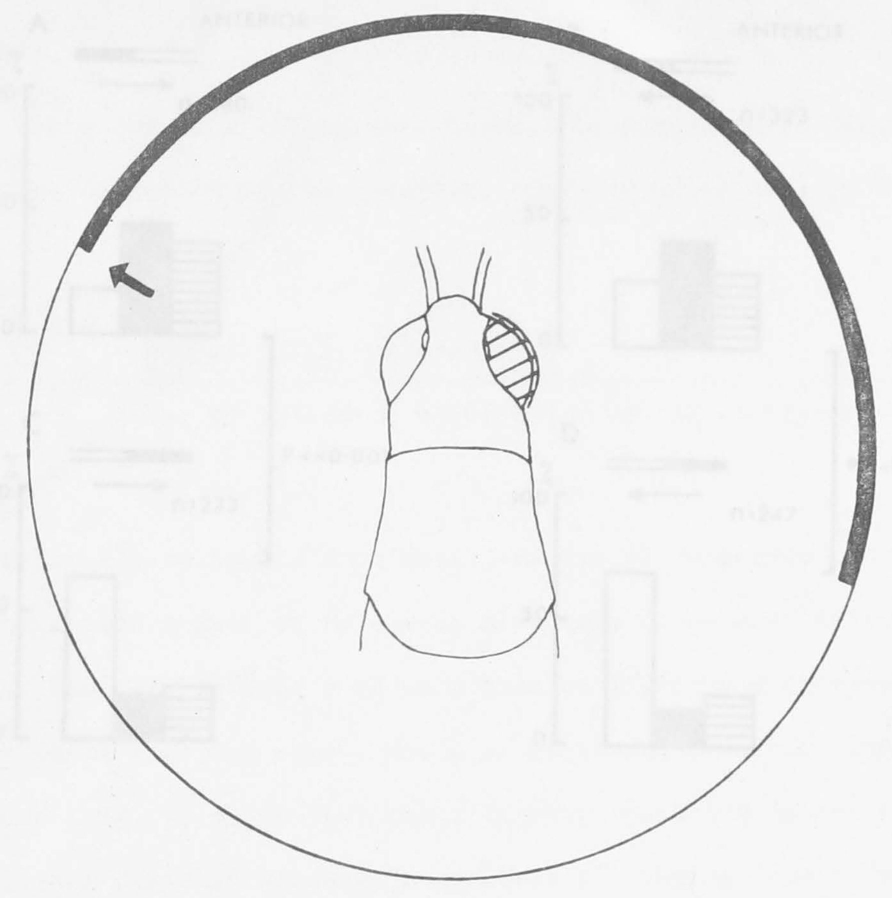


Fig. 7 A schematic illustration of stimulation with the single black-white edge. The drum is divided into two equal black and white areas. Small movements of the drum (e.g. through less than 90°) allow movement of only one boundary across the unoccluded eye. The boundary marked by the arrow shows the black anterior edge. When the white area is anterior (with respect to the locust) the edge is referred to as the white anterior edge.

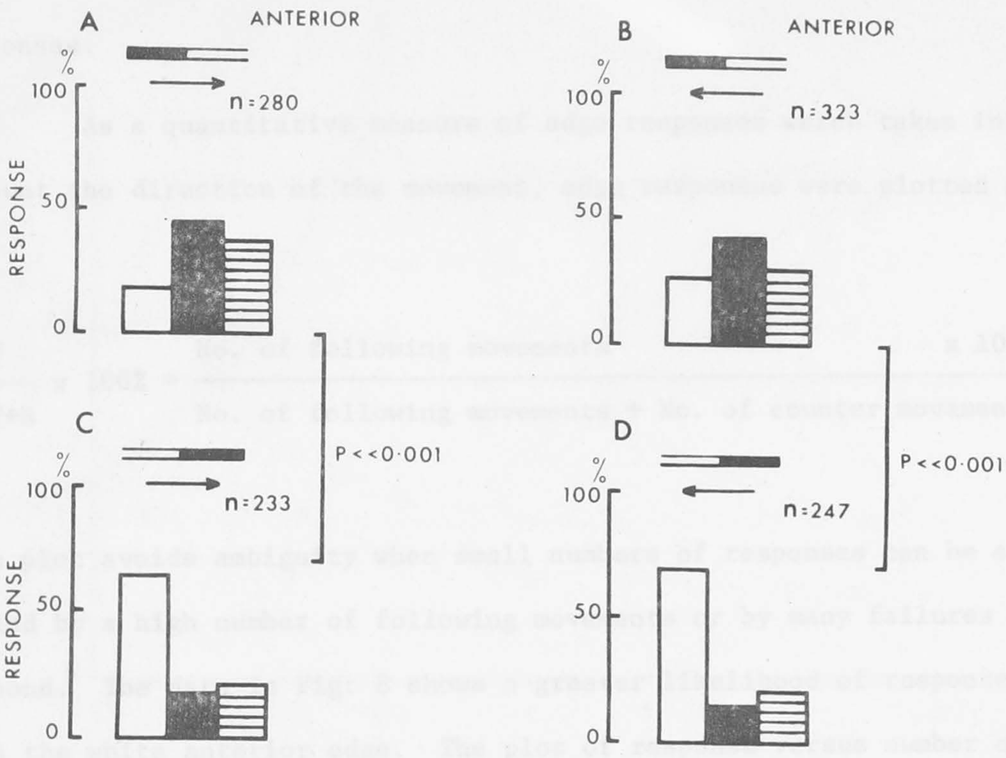


Fig. 8 Representation of percentage following responses (open blocks), percentage errors (closed blocks) and percentage failures to respond (hatched blocks) during movements of a single edge. A,B movement of white anterior edges: anterior (A), posterior (B). Movement of black anterior edge towards anterior (C), towards posterior (D). n = number of trials for each condition. Data was collected from the same 10 animals for all 4 conditions. χ^2 tests show that the differences between A & C and B & D are significant at the 0.1% level. Note the small number of following responses and the high number of errors and failures when the white anterior edge is used. Conditions A & D represent a decrease of light conditions, B & C an increase of light.

responses.

As a quantitative measure of edge responses which takes into account the direction of the movement, edge responses were plotted as

$$\frac{F}{F+R} \times 100\% = \frac{\text{No. of following movements}}{\text{No. of following movements} + \text{No. of counter movements}} \times 100\%$$

This plot avoids ambiguity when small numbers of responses can be accompanied by a high number of following movements or by many failures to respond. The data in Fig. 8 shows a greater likelihood of response failure with the white anterior edge. The plot of response versus number of viewing facets (Fig. 9) shows that the following responses to the black anterior edge diminish slightly as numbers of viewing facets decrease. In some animals the reversals diminish very slightly (i.e. $\frac{F}{F+R}$ approaches 50%) as the viewing facets are reduced but there is a wide scatter. The change of one animal from following to reversal resembles the change in behaviour of some animals when the stripe number is increased.

A total of 35 animals were tested for edge responses. Of these two locusts showed no reversal to either edge and one animal showed a reversal response to the black anterior edge stimulating the left eye and the white anterior edge stimulating the right eye - the exact opposite of the usual response.

To test that the edge responses were not phototactic responses either the black or the white anterior edge was positioned in front of the eye in the dark and the light was switched on. No consistent movement to either the black or the white anterior edge was seen. That is, 3 animals (5 trials each per edge) made 60% movements to the white area when exposed to the black anterior edge and 20% movement to the white area when exposed

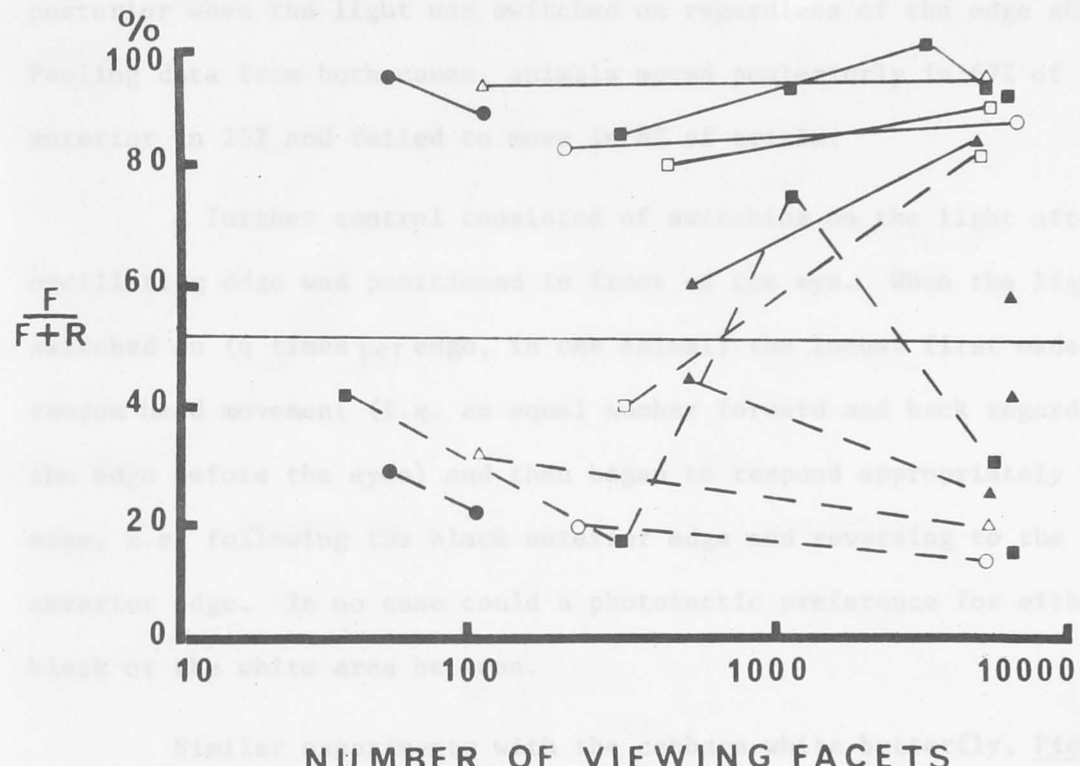


Fig. 9 The effect of reduction in viewing facet numbers on the response to a single moving edge plotted here as

$$\text{Response} = \frac{F}{F+R} \times 100\% \qquad \begin{array}{l} F = \text{no. following responses} \\ R - \text{no. countermovements} \end{array}$$

When $\frac{F}{F+R}$ = 50% the response is random, levels above 50% indicate following, and below 50% indicate reversal. Solid lines show responses of individuals (data not normalised) to movement of the black anterior edge, dashed lines show responses to movement of the white anterior edge. 20-40 trials for each point, angular velocity 8-20°/sec. Only the left eye is stimulated. Note the wide scatter of responses to the white anterior edge. See text for further explanation.

to the white anterior edge. In other words the animals tended to move posterior when the light was switched on regardless of the edge shown them. Pooling data from both cases, animals moved posteriorly in 67% of trials, anterior in 25% and failed to move in 8% of trials.

A further control consisted of switching on the light after an oscillating edge was positioned in front of the eye. When the light was switched on (6 times per edge, in one animal) the locust first made a random head movement (i.e. an equal number forward and back regardless of the edge before the eyes) and then began to respond appropriately to each edge, i.e. following the black anterior edge and reversing to the white anterior edge. In no case could a phototactic preference for either the black or the white area be seen.

Similar experiments with the cabbage white butterfly, Pieris rapae L. (Kien, 1973a), rule out that the responses could be artefacts. When the broad stripes (period 180°) were rotated around a male butterfly it responded with a smooth head movement (Fig. 10e) while the females' response was similar to that of the locust. In some cases (1 in 4) the head made only large oscillations (Fig. 10a) while in the remainder of trials oscillations were superimposed on a small directional response (Fig. 10b). When the single black-white edge was passed across the left eye the males followed the motion of both edges (Fig. 10f,g). The females' head followed the movement of the black anterior edge in both directions but the head turned in the opposite direction when the white anterior edge was used (Fig. 10c,d). The results from approximately 40 tests with each edge in each animal, expressed as $\frac{F}{F+R}$ x 100% are given in Table 2.

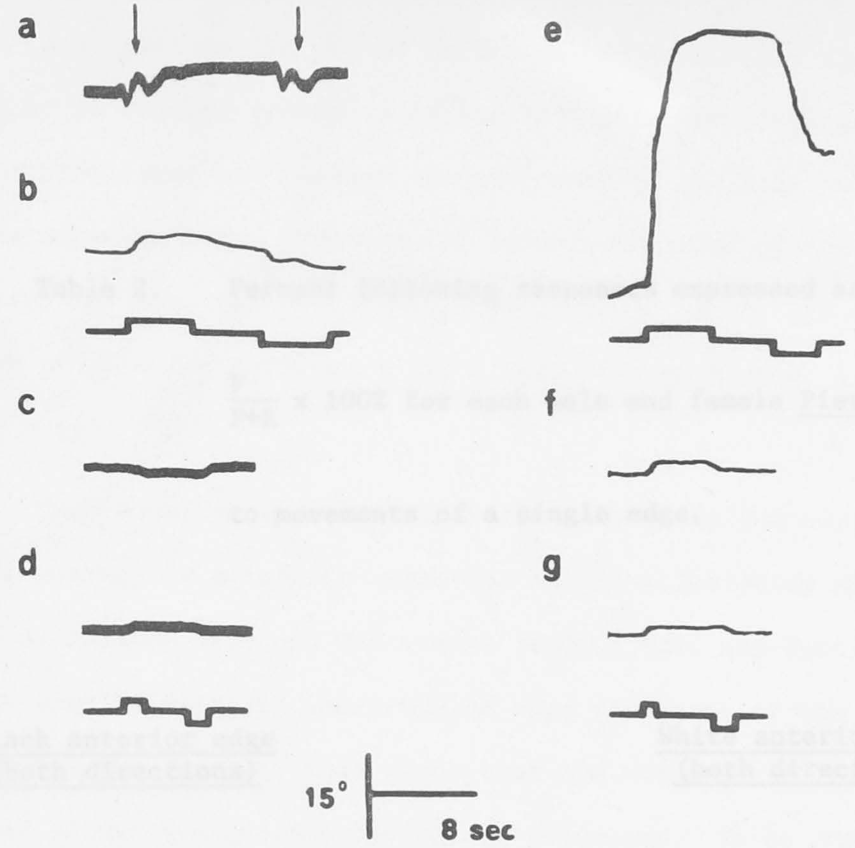


Fig. 10 The head movement responses of male and female Pieris to movement of broad stripes (repeat period 180°) and single edges. The passage of the thickened end of the antenna over the photocell registered the head movements. Upward deflection in both head movement and drum marker traces indicates movement to the right. Vertical calibration shows degrees of head turning. Speeds for large movements of broad stripes were approximately 90°/sec and for small movements of single edges 8°/sec.

a-d: responses of female - (a,b) to movement of 180° stripes (arrows point to oscillations induced by the broad stripes); (c) to white anterior edge, and (d) black anterior edge.

e-g: responses of male Pieris - (e) to movement of 180° stripe; (f) to movement of white anterior edge, and (g) black anterior edge.

Table 2. Percent following responses expressed as

$\frac{F}{F+R}$ x 100% for each male and female Pieris

to movements of a single edge.

Black anterior edge (both directions)		White anterior edge (both directions)	
MALES	FEMALES	MALES	FEMALES
72.5%	100.0%	70.5%	2.3%
97.5%	64.0%	66.6%	0.0%
91.0%	83.5%	93.5%	0.0%
84.0%	86.4%	88.5%	12.8%
	98.8%		56.7%

A χ^2 test on the pooled data shows a significant difference at the 0.1% level between responses of the female to the black anterior and white anterior edges and between the responses of the male and female to the white anterior edge. The control in three females of switching on the light after the edge had been positioned in front of the eye in the dark showed no phototactic preference (10 trials with each edge, 1 movement in 5 trials only).

This experiment demonstrates that the anomalous edge responses cannot in any way be artefacts dependent on the stimulating apparatus. There is no obvious external difference between male and female *Pieris*, such as a size difference, and thus the edge responses of the male act as a control for the female. This means that the response of both female *Pieris* and locust are genuine biological phenomena. As no phototactic preference could be demonstrated these responses must be true optomotor responses. Further evidence that these responses are optomotor responses comes from the failure of the vector edge neuron in the grasshopper to respond directionally to the white anterior edge (Northrop & Guignon, 1970) and from the responses of the locust optomotor neurons described in the following chapter.

Responses to sinusoidal oscillations

Qualitative experiments using different constant velocities and oscillation frequencies were performed to determine amplitude threshold and the range of stimulus speeds to which the animal responded. Small sinusoidal oscillations have already been found to be extremely effective in eliciting optomotor responses in the locust (Thorson, 1964). These produce small oscillations of the head. Fig. 11 shows the dependence of percent following responses on oscillation amplitude. Note that this graph shows the directionality of the response and not its magnitude. Some

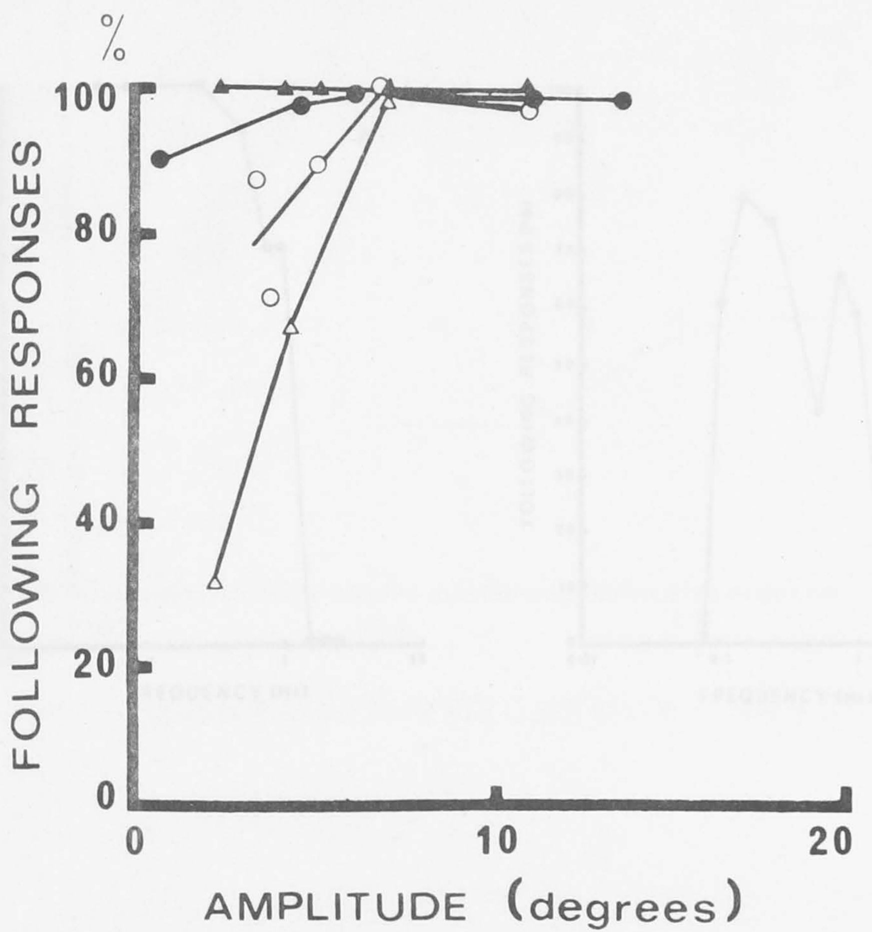


Fig. 11 Variation in percent following responses (ordinate) with amplitude of pattern oscillations (abscissa). Each curve represents data from one animal. Oscillation frequency 0.25Hz, pattern repeat period 15.8^{o}. Each point was obtained from 20 trials. Note that this plot does not show decreases in response magnitude but shows the ability of the animal to detect the direction of pattern movement.

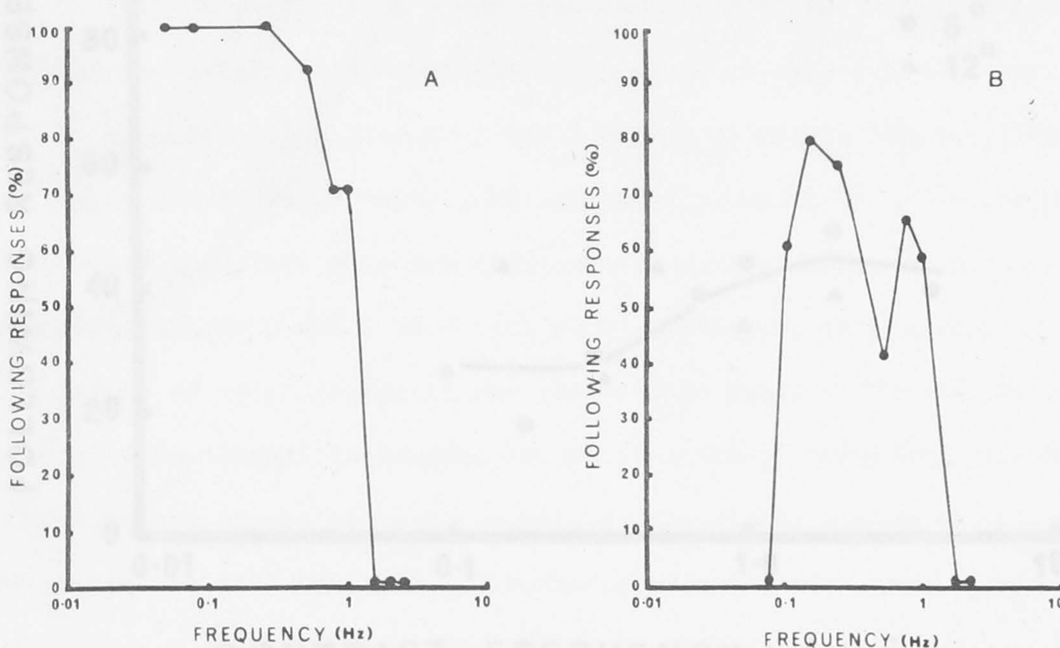


Fig. 12 Percentage following responses from one animal (ordinate) to striped pattern (period 15.8^{o}) oscillating at different frequencies (abscissa). A. stimulating the whole eye, oscillation amplitude 5°. B. the eye reduced to 500 facets, oscillation amplitude 5.5^{o}. Each point represents 20 trials.

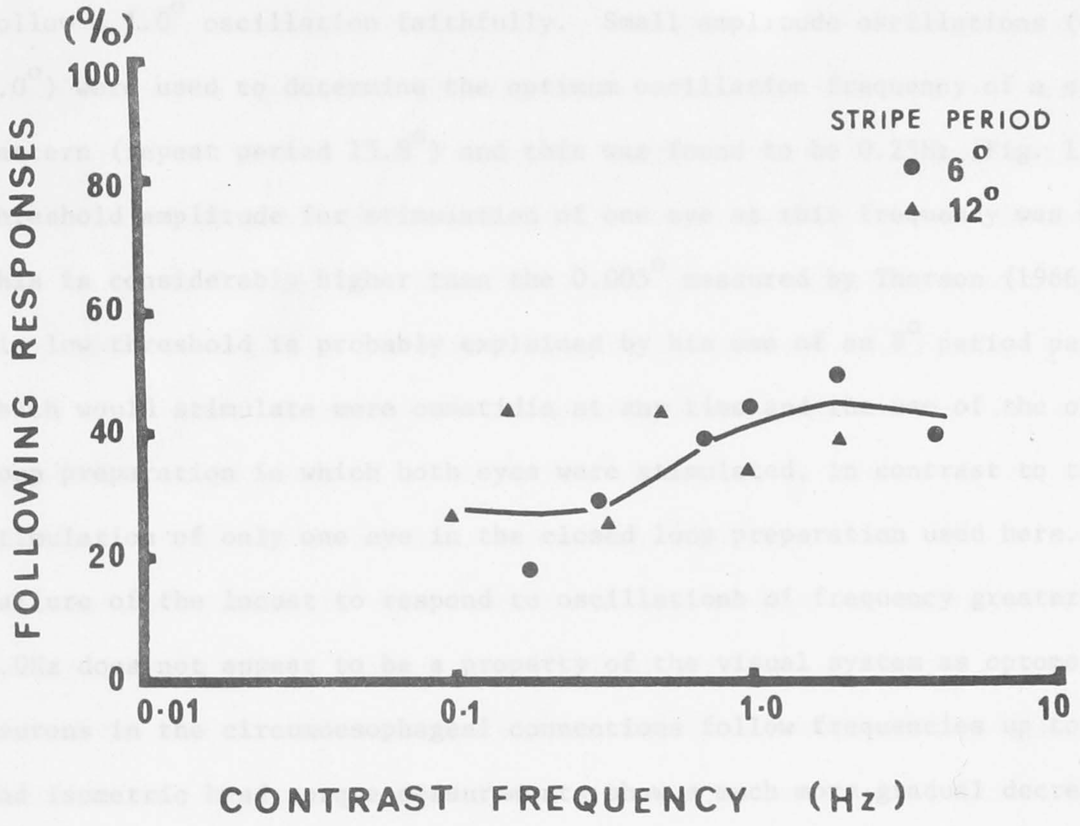


Fig. 13 Percent following responses (ordinate) to movement of a striped pattern at different constant angular velocities and contrast frequencies from one animal (abscissa). The constant velocity apparatus stimulated an area of 10° x 15°. This caused the low response level. Stripe periods were 6° and 12°. Angular velocities ranged from 1.2 to 23.9^{o}/sec. Each point was obtained from 20 trials. There was no clear difference in the angular velocity which elicited a maximum response level for each pattern. Each movement lasts 2 seconds.

animals begin to make consistent errors at amplitudes of 4.5^{o} while others follow a 1.0^{o} oscillation faithfully. Small amplitude oscillations (0.4^{o} - 9.0^{o}) were used to determine the optimum oscillation frequency of a striped pattern (repeat period 15.8^{o}) and this was found to be 0.25Hz (Fig. 12A). Threshold amplitude for stimulation of one eye at this frequency was 0.5^{o}. This is considerably higher than the 0.005^{o} measured by Thorson (1966a). His low threshold is probably explained by his use of an 8° period pattern which would stimulate more ommatidia at any time and the use of the open loop preparation in which both eyes were stimulated, in contrast to the stimulation of only one eye in the closed loop preparation used here. The failure of the locust to respond to oscillations of frequency greater than 1.0Hz does not appear to be a property of the visual system as optomotor neurons in the circumoesophageal connections follow frequencies up to 5Hz and isometric head torque measurements show a much more gradual decrease after 1.0Hz (Thorson, 1966b). The failure is probably due to properties of the neck muscles (Shepheard, 1969) and the inertia of the head.

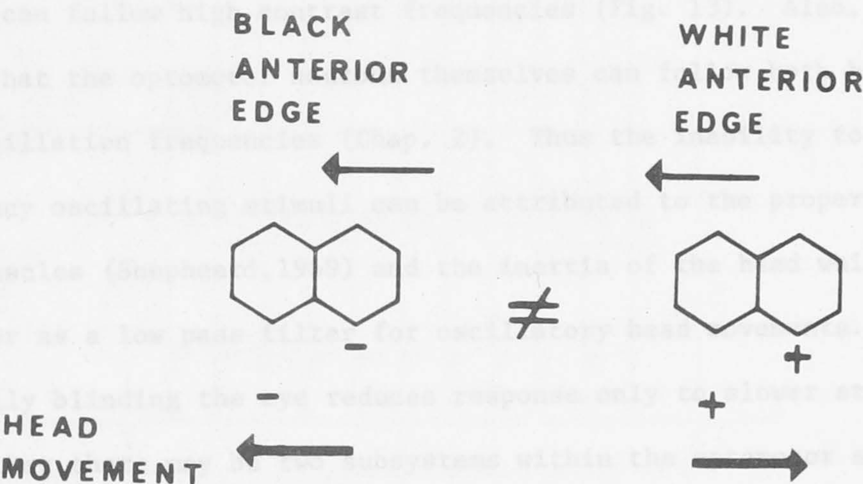
When the eye was reduced to 500 viewing facets the threshold rose to an oscillation amplitude of 5.2^{o}. In several animals the reduction of the eye decreased the percentage of following responses to slower oscillations without altering following responses to oscillations faster than 0.5Hz. An example is given in Fig. 12B. That eye reduction appears to have a greater effect on responses to slower movements is supported by data from constant velocity stimulation. The small stimulating aperture, 10° x 15°, resulted in a high incidence of response failures and a low percentage of following responses. Fig. 13 shows that the animal could respond equally and perhaps better to contrast frequencies above 1.0Hz when only a portion of the eye is stimulated.

The edge responses of the locust and the female Pieris, which have not been reported previously, provide evidence of some diversity of organisation in the insect visual system. The edge elicited reversal response of the locust fails to comply with the multiplication laws of the symmetrical model (Reichardt, 1961). The exact nature of the disagreement is shown in Fig. 14. When the black anterior edge moves posteriorly (e.g. left in Fig. 14) there is a sequential decrease of illumination on a row of facets . Movements of the white anterior edge in the same direction cause an increase of illumination on the row of facets in the same sequence. One rule of multiplication theory is that these stimuli are expected to produce the same behavioural responses since expressed as a multiplication plus x plus = minus x minus (Fig. 14). However, in the locust the two stimuli produce head movements in opposite directions, thus qualitatively failing to comply with the prediction of the multiplicative model. This failure is a definite indication that, in the locust, the sensory inputs to the optomotor system are differently arranged from those in fly or beetle.

The other experiments reported here further define the parameters of the new optomotor model required as a result of the edge responses.

The arrangement of viewing facets on the eye was found not to affect the ability to analyse direction of movements. In analogy to the findings of Mimura (1971, 1972), a certain number of non-directional cells with small oval or circular receptive fields must be stimulated to elicit a directional response in an optomotor neuron. This mechanism, consistent with the circular or oval receptive fields of known movement detector neurons in arthropods (e.g. locust, Chap. 2; fly, McCann & Dill, 1969; Mimura, 1971; moth, Collett, 1970, 1972; lobster, Wiersma & Yanagisawa, 1971), occurs not only in insects (Mimura, 1972) but also in

Fig. 14 Simplified representation of a change in light intensity falling on neighbouring ommatidia during movment of a black-white edge. An increase of light on an omma is represented by plus (+), a decrease by minus (-). Movement of the black anterior edge in one direction (e.g. to the left on the diagram) causes a sequential decrease in light (-,-) on 2 facets. Movement of the white anterior edge in the same direction causes an increase of light on the facets in the same sequence from right to left (+,+). In the multiplication theory each movement would be expressed as minus x minus, and plus x plus and these are, by definition, equal. This means that they should produce identical head movement responses. However the head movements elicited by each stimulus are of the opposite direction. Thus, this is a direct disagreement with the multiplication theory. When both edges move in the opposite direction (to the right, in the diagram) the sequence of light change on each facet is reversed. The change is now from left to right. Again it can be seen that stimuli resulting in change of light, plus x plus produce head movements opposite to those produced by minus x minus.


BLACK
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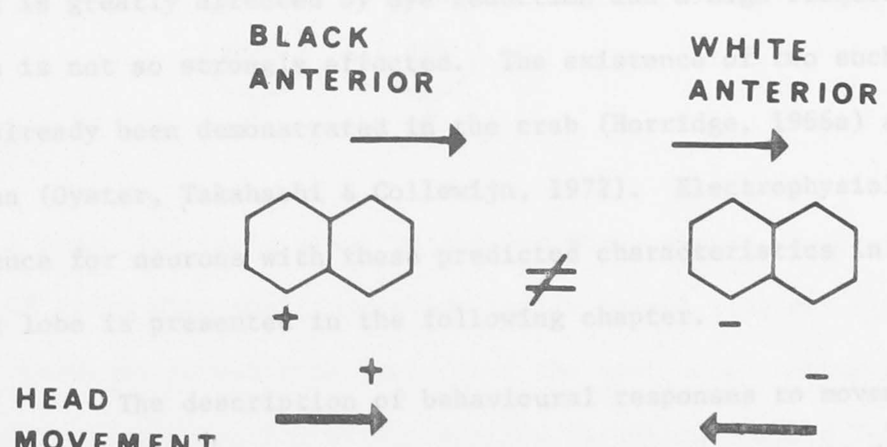
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vertebrates (Barlow & Levick, 1965; Michael, 1968; Werblin, 1970).

Following responses to different oscillation frequencies indicate that the optomotor system is most efficient at lower frequencies (Fig. 12). However results from constant velocity tests showed that the locust can follow high contrast frequencies (Fig. 13). Also, it will be shown that the optomotor neurons themselves can follow both high contrast and oscillation frequencies (Chap. 2). Thus the inability to follow high frequency oscillating stimuli can be attributed to the properties of the neck muscles (Shepheard,1969) and the inertia of the head which act together as a low pass filter for oscillatory head movements. That partially blinding the eye reduces response only to slower stimuli indicates that there may be two subsystems within the optomotor system which have different optimum frequencies of stimulation, a low frequency system which is greatly affected by eye reduction and a high frequency system which is not so strongly affected. The existence of two such subsystems has already been demonstrated in the crab (Horridge, 1966a) and the rabbit retina (Oyster, Takahashi & Collewijn, 1972). Electrophysiological evidence for neurons with these predicted characteristics in the locust optic lobe is presented in the following chapter.

The description of behavioural responses to movements of striped patterns, edges and single stripes provide a basis for comparison of behaviour with neuronal responses. Also the formation of a neuron model from behavioural responses allows the simple testing by electrophysiological recording of hypotheses arising from behavioural results. The model in Fig. 15 was designed to explain the edge reversals and fit the experimental data. It consists of two inhibitory Barlow and Levick (1965) networks placed in opposition to each other. Inputs to these networks come from the small ON cells and larger field OFF cells: both of these cells occur in the locust optic medulla (Horridge, et al., 1965).

Fig. 15 A model for input stage to the optomotor system in locust. The ON cells with small receptive fields (small circles) are connected asymmetrically so that the next order neuron is direction detecting with preferred direction forward for the left eye. The asymmetric connections form a modified Barlow & Levick network. OFF cells which respond to a net dimming of their receptive fields (larger receptive field shown by large brackets) are connected similarly but in the opposite direction so that the preferred direction of the directional neuron is also in the opposite direction. Direction analyses are made from the differences in firing rates of the opposing networks. Filled triangles represent inhibitory synapses.

This model differs from the mechanisms proposed for the fly (Mimura, 1972) in that an asymmetric inhibitory mechanism rather than an asymmetric excitatory mechanism is required for directional selectivity. However, the presence of an excitatory mechanism was not excluded by experiments reported here. Multiple overlapping of receptive fields, at least of the small ON fields, must be postulated to account for the high acuity previously observed (Thorson, 1966a). Even so, the directional neuron may only respond when a certain number of either ON or OFF cells are stimulated as a large number of facets have to be stimulated to obtain a response even though the animal responds to very small movements. If the receptive field of the directional neuron is built up in two dimentsions from the small non-directional cells it is clear that the arrangement of excited cells is not important for the overall response as long as these cells are close together. If not close, the lateral inhibitory interaction becomes weak or ineffective.

Another important feature of the ON and OFF cells is their difference in receptive field size and the consequent difference in numbers of each type required for a coverage of the visual field of each eye. It has already been found in the optomotor inputs in the rabbit (Oyster et al, 1972) and in the external tracking neurons in fly (Mimura, 1971) that directional cells with larger receptive fields are sensitive to faster movements than those with small receptive fields. Partially blinding the eye reduces the number of ON cells by the greatest extent. This may then be expected to reduce the response to slower movement and not to affect so much the response to faster movements, as indeed was found (Figs.12 and 13).

The particular directions of the inhibitory interactions on the anteroposterior axis as shown in Fig. 15 are necessary to explain the edge

responses (see Fig. 8: ON, B,C: OFF, A,D). A single edge excites either the ON or OFF system only. The white anterior edge always moves in the null direction of the system it can stimulate. The movement always excites the first cell in this system but this in turn causes the spread of the lateral inhibition and prevents the other cells from firing (Barlow & Levick, 1965). Thus, if this edge is the only moving object in the visual field, the only change in the firing of the directional neurons is caused by the first cell to be excited. This cell always activates the directional neuron in whose null direction the edge is moving, i.e. whose preferred direction is opposite to the direction of movement (see Fig. 15). In the absence of any other directional information the animal must interpret this as a movement in the preferred direction of this neuron. The response amplitude is independent of the number of facts stimulated.

The black anterior edge always moves in the preferred direction of the system it can stimulate. When the black anterior edge moves posteriorly the OFF system will be stimulated. Now the edge moves in the preferred direction of this system and the firing of all the OFF cells stimulates the neuron with back preferred direction. This causes an unambiguous response. Similarly anterior movement of this black anterior edge excites the ON cells. As the edge is moving in the preferred direction of the ON system there is a discharge in the ON directional neuron resulting in following movement. This following response, although small, should show some dependence on the number of facets stimulated. Indeed a slight trend can be seen in Fig. 9 for this edge. Thus the model reproduces the behaviour elicited by the moving edges (Fig. 9).

As this model explains the locust edge responses, it must also account for the edge responses of the female _Pieris_. A truly satisfactory model should require only a small change to abolish these

edge reversals and give the responses of the male, as one would not expect the direction detecting mechanisms in the two sexes to be completely different. In the model in Fig. 15 all edge reversals are abolished if both ON and OFF, or ON-OFF neurons connect to each directionally selective neuron. This is only a slight change in wiring or cell properties and it could easily account for the difference between male and female *Pieris*.

As a single narrow stripe activates both ON and OFF systems simultaneously its effects are quite different from those of a single edge. One edge of the stripe excites the ON system, the other the OFF system; one edge moves in the null direction of the system it stimulates. Even though the movement is in the null direction for this system, activity of the first excited cells is passed to the directional neuron. If the movement is small, a similar number of cells in the other systems, in whose preferred direction the stripe moves, are also excited. Thus, a similar discharge may reach both direction detecting neurons even though they have opposite preferred directions. This opposition, dependent on the weighting of these neurons relative to one another in the optomotor system, causes the animal to make errors. The observed variability in responses of different animals to single stripe stimuli may be caused by the variation of this weighting factor in the different animals. As the movement increases in amplitude or the stimulus in complexity, i.e. stimulates more facets for the same size movement, the difference in discharge reaching the directional neurons increases, removing any ambiguity.

The visual behaviour of *Chortoicetes* is apparently simple in that this locust shows little manoevreability in flight and fails to avoid obstacles. Also much of the flying occurs at night (Clark, 1971).

Therefore it is possible that the direction detecting networks and the optomotor system are also relatively simple. The proposed model provides accurate information only when large numbers of facets are stimulated. Its inability to provide clear information on small movements of simple visual stimuli is in accordance with the observed behaviour of this insect.

CHAPTER 2 General properties of the optomotor neurons

Neurons responding selectively to direction of motion have been recorded in optic lobes and protocerebrum of many arthropods. These neurons have receptive fields ranging from a diameter of approximately 30° (Swihart, 1968; Mimura, 1971) to the whole visual field (Collett, 1971; Bishop, Keehn & McCann, 1968). They show different frequency responses (Mimura, 1971) and different optimum stimuli, such as stripes or spots (e.g. Mimura, 1971; Northrop & Guignon, 1970; Wiersma & Yanagisawa, 1971). The reason for this variation in neuron character is not clear, for in most cases the neurons have not been directly compared with direction detecting behaviour. The one exception is the fly, where optomotor neurons and optomotor behaviour have been compared (McCann & Foster, 1971). Here the responses of the fly optomotor neurons have resulted in the formation of a model (McCann, 1973; Marmarelis & McCann, 1973) which is similar to that derived from the behaviour (Reichardt, 1961; McCann & MacGinitie, 1965) in that it consists of symmetrical correlation interactions.

It was shown in the previous chapter that symmetrical models need not be true for all insects. In particular, the edge reversal response of the locust disagrees with the symmetry arguments of a multiplication model. Rather, the model (Fig. 15) consisting of two asymmetric Barlow and Levick (1965) networks was suggested for the locust. In this model the networks are inhibitory and have opposite preferred directions, one network receiving inputs from cells responding only to an increase of light, the other receiving inputs from neurons responding to decrease of light. The optomotor behaviour should result from a comparison of the activity of the two networks. The test of this behavioural model consists of finding the neurons mediating the behaviour and comparing their responses with those

predicted by the model. This chapter shows that the activity of locust optomotor neurons confirm the validity of the optomotor model and also provides further information on optomotor integration in the central nervous system.

In overall structure the Chortoicetes optic lobe, as in other locusts (e.g. Horridge et al., 1965) is quite similar to those Lepidopteran optic lobes described in detail by Strausfeld & Blest (1970). A schematic drawing is given in Fig. 16A. At present, partly because of the difficulties in applying the Golgi impregnation technique, there is no detailed knowledge of the structure of the major synaptic areas and the cell types contained therein.

The search for optomotor neurons was initiated de novo as the two reported recordings of directionally selective neurons in acridid optic lobes (Horridge et al., 1965; Northrop & Guignon, 1970) did not give the precise location of the recording site. The constriction where the lobe joins the protocerebrum and which contains mainly fibre tracts, was probed first as the optomotor information must leave the optic lobe and can do so only via these tracts. In fact, as shown in Fig. 16A, the only region where the optomotor fibres could be recorded in the optic lobe was confined to this area. A second site where one could expect to record from optomotor neurons is in the circumoesophageal connectives as the motoneurons responsible for turning the head during an optomotor response lie in the suboesophageal ganglion (Shepheard, 1969, 1973).

During optic lobe recording the animal was fixed dorsal side up. The optic lobe was exposed by a frontal and dorsal dissection clearing superficial tissues. Electrodes approached dorsally (Fig. 16A). The mouth parts and abdomen were removed to prevent the pumping of the head fluid to reduce tissue movement. For recording in the circumoesophageal connectives

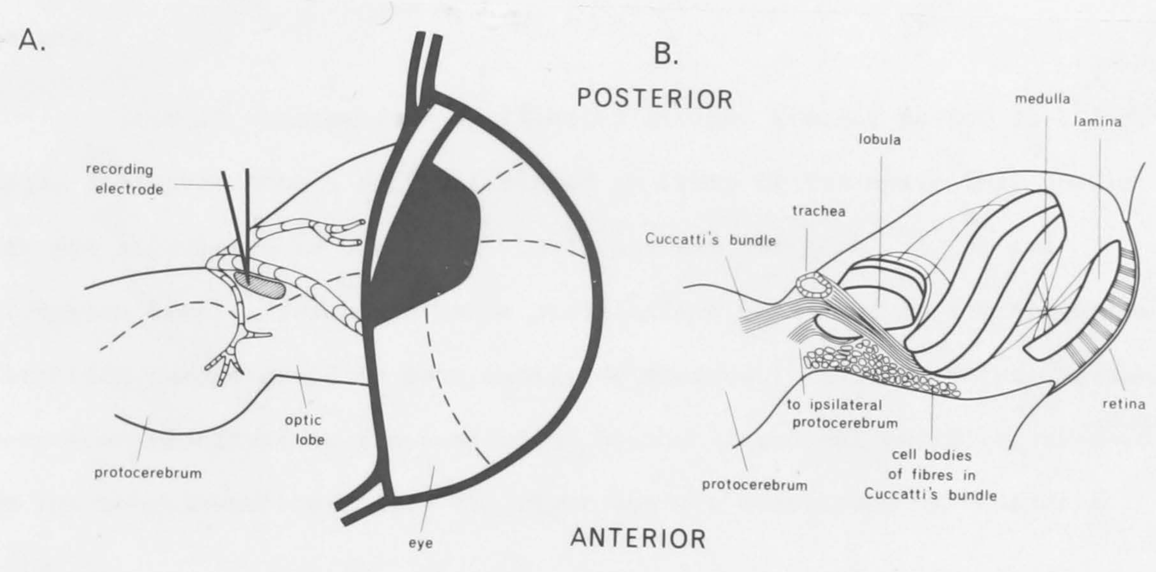


Fig. 16 (A). Camera lucida drawing of the preparation used for optic lobe recording. The shaded area shows the only region in the optic lobes where directional neurons could be recorded. (B). Schematic drawing of a horizontal cross section of the optic lobe showing the main fibre tracts in the recording area. Note the branching of Cucatti's bundle around the trachea which was used as a landmark in A.

the locust was fixed ventral side up with the head stretched back to expose the neck region. The suboesophageal ganglion and its connectives were lifted slightly and pinned to a waxed spoon. Recordings were made in the circumoesophageal connectives at their entry to the ganglion. Extra-cellular axon recordings were made with glass micropipettes filled with 2.5M KCl (resistance 10 - 30 MΩ). Signals were passed to a Grass P16 high impedance amplifier and photographed from oscilloscope display or stored on tape.

Stimuli consisted of oscillating stripes (repeat period 15.8^{o}) or edges projected onto a diffuser placed in front of the eye. Only the left eye was stimulated in this way. Luminance was 596 cd/m^2 at the eye (tungsten lamp). Triangular wave oscillations were used as the moment of direction change could be more easily determined. These produced neuronal responses identical to those elicited by the sinusoidal oscillations used in the behavioural testing. The right eye was stimulated by hand held stimuli.

Receptive fields were plotted using the constant velocity apparatus. This consisted of a small transparent striped drum (repeat period 10°) mounted with a motor on a perimeter. A diffuser, covered so that the eye could see an area of only 10° x 15°, was fixed between the drum and the light source in the centre of the drum. Luminance was 26.6 cd/m^2.

Three types of neurons responding directionally to moving stripes without habituating were found in the left optic lobe in the area shown in Fig. 16A. These neurons responded to movements in one direction with increase of spike frequency and were inhibited by movements in the other direction (Fig. 17). Two of these neuron types were ipsilateral monocular neurons. Neurons with preferred direction forward (posterior to anterior) across the eye or up (ventral to dorsal) comprised one group,

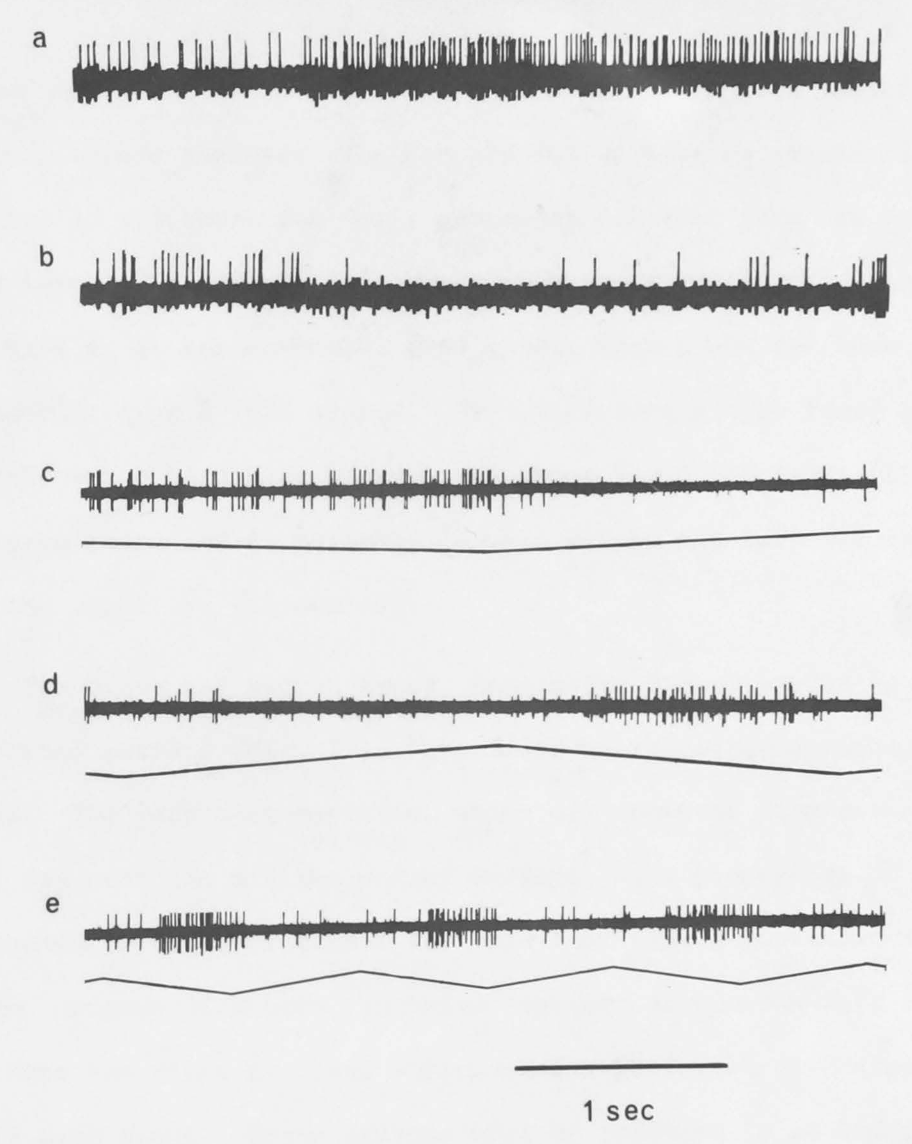


Fig. 17 A directionally selective fibre in the locust circumoesophageal connective. Movement in the preferred direction (forward over the contralateral eye) increases firing above the spontaneous rate (a). Movement in the opposite or null direction (b) causes a decrease in the firing. These fibres respond in a typical fashion to oscillation of a striped pattern in the preferred and null direction (c-e) and show no habituation. Lower trace shows movement of the pattern: c) 0.01Hz oscillation, an incomplete cycle is shown, d) 0.25Hz, e) 1.0Hz. In all cases amplitude of the oscillation was 15.4^{o}.

the other contained neurons with preferred direction back (anterior to posterior) across the eye. The forward and up neurons showed identical properties in all tests but their responses differed from the neurons with back preferred direction. For convenience the forward and up neurons will be referred to as the monocular type 1 (M1) neuron and the back neuron as the monocular type 2 (M2) neuron. The third neuron type found in the left optic lobe was a binocular neuron, the binocular directional (BD) neuron. This neuron responded to movement forward across the left eye and back across the right eye (clockwise).

Two binocular neuron types, responding directionally to movements of a striped pattern (Fig. 17), were found in the circumoesophageal connectives. The recording position, which was constant from animal to animal, was near the midline of the dorsal surface. The properties of each group corresponded to those of either the type 1 or type 2 monocular neurons, although neurons with both clockwise (forward across the left eye and back across the right eye) and anticlockwise preferred directions were found in each group. These neurons will be referred to as binocular type 1 (B1) and binocular type 2 (B2) neurons. In the left circumoesophageal connectives both B1 and B2 neurons responded to anticlockwise movements, while in the right connectives both types responded to clockwise movements. No purely contralateral neurons responding to the moving stripes were found. All neurons responded to movements whose directions were widely distributed about the preferred axis, responding to the preferred vector; e.g. anterodorsal movements stimulated both the forward and up M1 neurons.

All type 1 and type 2 neurons in the optic lobe and circumoesophageal connectives showed continual spontaneous activity, sometimes varying from 3-50 spikes/sec. Spontaneous activity was not noticeably affected by light intensity changes. The spontaneous activity of the BD neuron was much lower, usually less than 5 spikes/sec. Neurons of all types showed

phasic responses to changes in light intensity but this response was different, on, off or on-off, in each neuron of the same group. M1 and M2 neurons responded phasically to changes of light intensity on the contralateral eye but did not respond to movements. The B1, B2 and BD neurons showed the same response to light on or off on both eyes.

Responses to moving stripes

Neurons were tested with both oscillating and constant velocity stimuli. Constant velocity stimuli, starting from standstill, elicited a response (inset Fig. 28) whose latency was short and varied only slightly. The mean latency of the M1 response in the preferred direction was 83 msec (range 60-100 msec) to movements of velocity 11-24°/sec and contrast frequency 1-4 Hz. The mean M2 latency to similar movements was 62 msec (range 40-80 msec), and the BD latency was 205 msec (range 100-300 msec). The latencies of the responses to oscillating stimuli showed variations of several hundred milliseconds. The change in latencies was the only major difference found between the two types of stimulation. Oscillating stimuli were used to determine the other response characteristics and for comparison with the optomotor behaviour (Chap. 1).

No comparison of movement response to spontaneous activity can be made as the oscillating stimuli changed direction without a pause. Also the spontaneous and evoked activity of the neuron often varied. The most reliable measure of neuron activity was found to be the difference in spike frequencies for movements in the preferred (p in spikes/sec) and null direction (n in spikes/sec) expressed as p-n spikes/sec. The similarity of p - n curves for neurons with different p and n curves is shown in Fig. 18. Fig. 18A shows the curves derived for movements in the preferred direction and movements in the null direction. Each point is the average of 5 movements each lasting 1 second. The curves in B are the result when the n

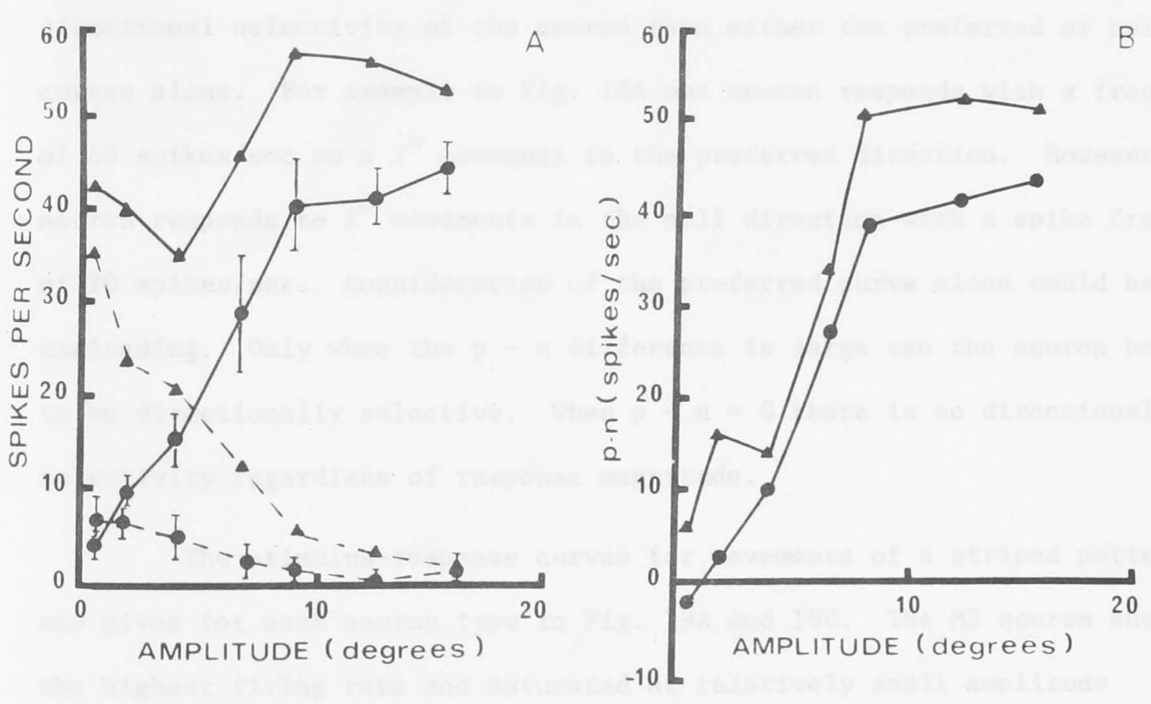


Fig. 18 Stimulus-response curves for movements of a striped pattern for M2 neurons. (A). Discharges to movements in the preferred direction (solid lines) and null direction (dashed lines). (B). The p - n curves. Stripe repeat period 15.8°, oscillation frequency 0.5Hz. In A each point was averaged from responses to 5 movements, each lasting 1 second; in B each point is derived from 10 movements. Bars in A are standard deviations. They are given here as an example of the variation in response. Notice the dissimilarity in p,n curves of the 2 neurons for small movements but the similarity of the p - n curves.

curve is subtracted from the p curve. The neuron activity might change but the absolute increase in spike frequency for movements in the preferred direction compared with movements in the null direction was almost constant for a given stimulus. The p - n value is also a truer measure of the directional selectivity of the neuron than either the preferred or null curves alone. For example in Fig. 18A one neuron responds with a frequency of 40 spikes/sec to a 2° movement in the preferred direction. However this neuron responds to 2° movements in the null direction with a spike frequency of 20 spikes/sec. Consideration of the preferred curve alone could be quite misleading. Only when the p - n difference is large can the neuron be said to be directionally selective. When p - n = 0 there is no directional selectivity regardless of response magnitude.

The stimulus-response curves for movements of a striped pattern are given for each neuron type in Fig. 19A and 19C. The M2 neuron showed the highest firing rate and saturated at relatively small amplitude oscillations (9.2^{o}). Below this amplitude there is a linear decrease until p - n = 0 between 0° and 0.8^{o} of oscillation. On the other hand the M1 neuron has a constant value of p - n (less than 5) for oscillation amplitudes below 2°. As the oscillation amplitude increases p - n also increases. This implies that the dynamic range of the M1 neuron only begins at 2° when a 15.8^{o} stripe is used whereas that of the M2 neuron begins between 0° and 0.8^{o}. The M1 neuron does not show signs of saturating for oscillations as large as 15°.

All neurons in the connectives had lower firing rates than their counterparts in the optic lobe but the stimulus-response curves for the B1 and B2 neurons showed the essential features of the M1 and M2 curves (Fig. 19C). Thresholds for stimulation of one eye were higher for these binocular neurons than for the monocular types. The B2 neuron shows an increase in the p - n value only after amplitude is greater than 4°.

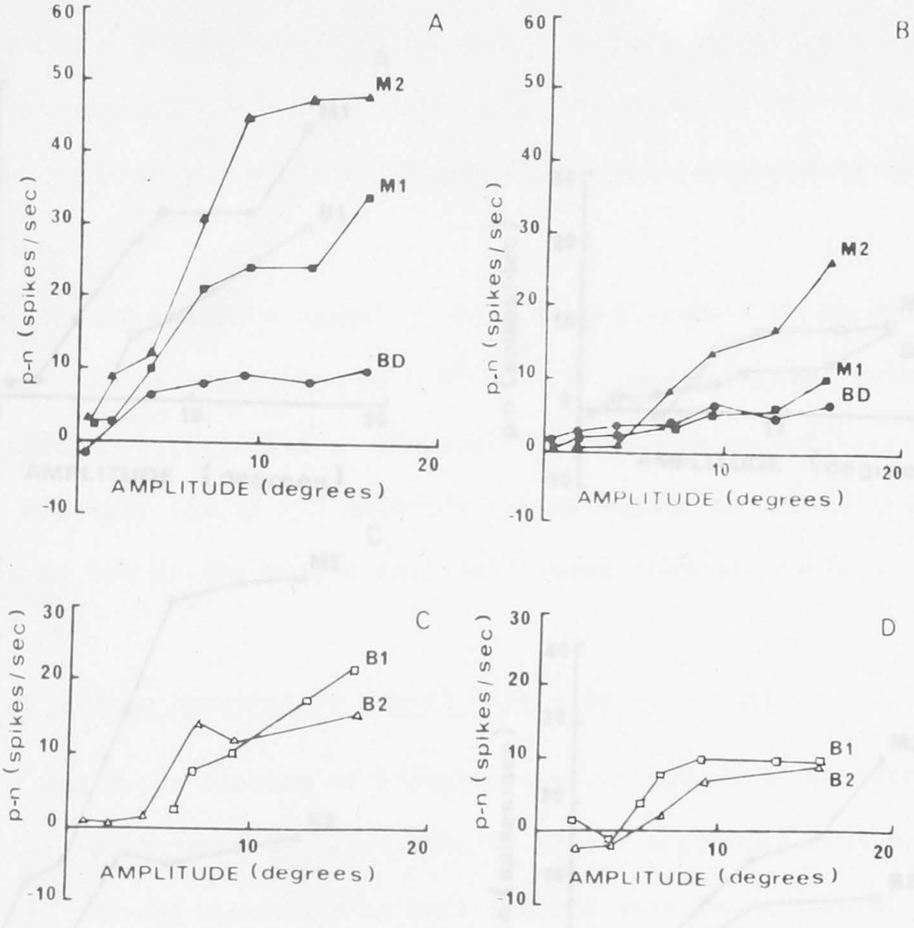


Fig. 19 Stimulus-response curves of different neuron types for movements of a striped pattern (A,C) and a single stripe (B,D). Each curve represents the averaged p - n curves of 2 neurons; –■– M1, –▲– M2, –□– B1, –△– B2, –●– BD. Pattern repeat period 15.8°, oscillation frequency 0.5Hz, stripe subtended 7.9°. p - n points for each neuron derived as before from 5 preferred and 5 null movements. (A) optic lobe neurons, striped pattern; (B) optic lobe neurons single stripe; (C) neurons in circumoesophageal connective, striped pattern; (D) same neurons, responses to single stripes.

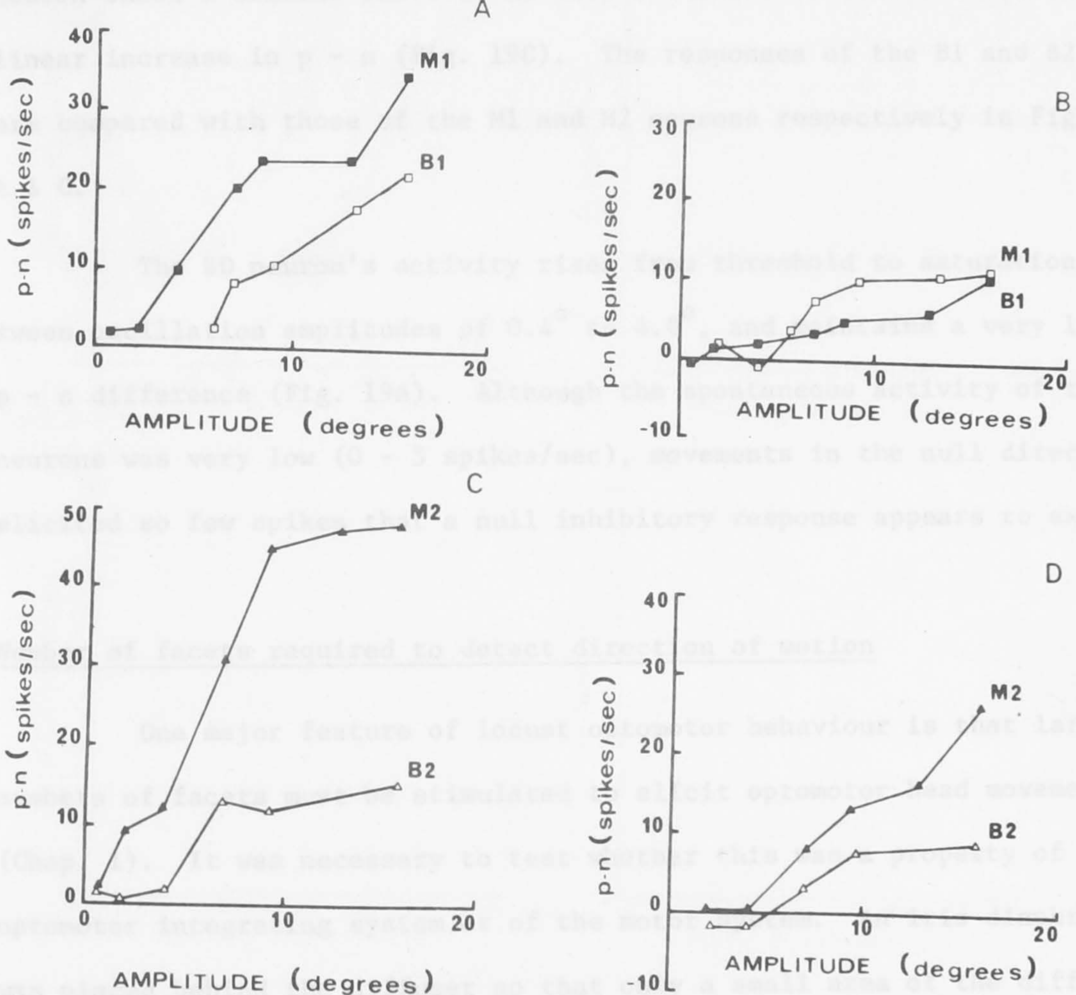


Fig. 20 Comparison of responses of M1 & B1 neurons (A) and M2 & B2 neurons to movements of a striped pattern (C) and a single stripe (B,D). Data is taken from Fig. 19. Closed symbols show monocular neurons, open symbols show binocular neurons in all graphs.

However it saturates at 6.8^{o}, slightly sooner than the M2 neuron. The B1 neuron shows a similar curve to M1 with a failure to saturate and an almost linear increase in p - n (Fig. 19C). The responses of the B1 and B2 neurons are compared with those of the M1 and M2 neurons respectively in Fig. 20 A & C.

The BD neuron's activity rises from threshold to saturation between oscillation amplitudes of 0.4^{o} to 4.0^{o}, and maintains a very low p - n difference (Fig. 19A). Although the spontaneous activity of these neurons was very low (0 - 5 spikes/sec), movements in the null direction elicited so few spikes that a null inhibitory response appears to exist.

Number of facets required to detect direction of motion

One major feature of locust optomotor behaviour is that large numbers of facets must be stimulated to elicit optomotor head movements (Chap. 1). It was necessary to test whether this was a property of the optomotor integrating system or of the motor system. An iris diaphragm was placed behind the diffuser so that only a small area of the diffuser was illuminated by the projection of moving stripes. This area was always centred on the eye centre. This is also the receptive field centre as shown in Figs. 29 and 30. p - n curves were obtained from two B1 neurons and one B2 neuron as the aperture was reduced (Fig. 21). In both neuron types the discharge to movements in the preferred direction, p, decreased and the discharge to movements in the null direction, n, increased as the aperture was reduced. In the B1 neurons p - n approached zero when 80 - 150 facets were stimulated. The B2 neuron showed that p - n tended to zero between 30 - 80 facets. This agrees well with the behavioural findings and demonstrates that the high threshold is definitely a property of the optomotor integrating system.

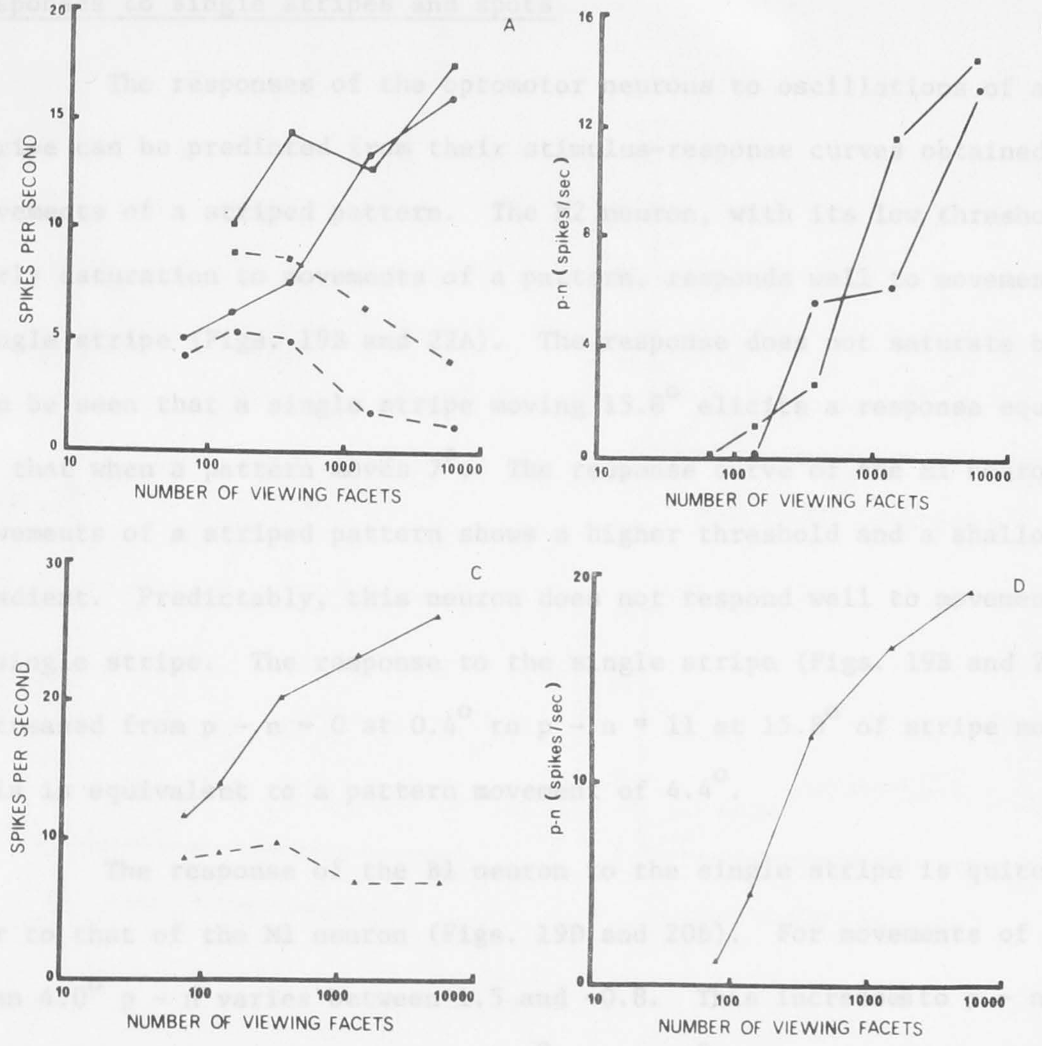


Fig. 21 Responses of 2 B1 (A,B) and 1 B2 (C,D) neurons as the number of viewing facets is reduced. (A,C) solid lines show responses to movements in the preferred direction, dashed lines show movements in the null direction. Each point obtained from 5 movements. (B,D) p - n curves. Notice how the discharges in the preferred direction decrease and the discharges in the null direction increase as viewing facets are reduced. Striped pattern repeat period 15.8^{o}, frequency 0.5Hz, oscillation amplitude 15.4^{o}.

Responses to single stripes and spots

The responses of the optomotor neurons to oscillations of a single stripe can be predicted from their stimulus-response curves obtained from movements of a striped pattern. The M2 neuron, with its low threshold and early saturation to movements of a pattern, responds well to movements of a single stripe (Figs. 19B and 22A). The response does not saturate but it can be seen that a single stripe moving 15.8^{o} elicits a response equivalent to that when a pattern moves 7°. The response curve of the M1 neuron to movements of a striped pattern shows a higher threshold and a shallow gradient. Predictably, this neuron does not respond well to movements of a single stripe. The response to the single stripe (Figs. 19B and 22B) increased from p - n = 0 at 0.4^{o} to p - n = 11 at 15.8^{o} of stripe movement. This is equivalent to a pattern movement of 4.4^{o}.

The response of the B1 neuron to the single stripe is quite similar to that of the M1 neuron (Figs. 19D and 20B). For movements of less than 4.0^{o} p - n varies between 1.5 and -0.8. This increases to p - n = 9.4 - 10.4 for movements between 9.0^{o} and 15.4^{o}. However unlike the M1 neuron the response flattens for movements of 9 - 15° at p - n value between 9 - 11. The response to 15.4^{o} movements of a single stripe (p - n = 9.4) is 0.42 of the response to a striped pattern making the same movement (p - n = 22.4). The mean value for this relationship (3 neurons) is 0.41. In the M1 neuron the mean relationship (2 neurons) of these responses is 0.24.

The stimulus-response curve of the B2 neurons to movements of a single stripe shows the gradual rise of p - n with increasing amplitude but with shallower gradient than that of the M2 neuron (Figs. 19D and 20D). However there is one slightly new feature. At low stimulus amplitudes p - n becomes negative, i.e. the response to movements in the null direction is consistently greater than that to movements in the preferred direction.

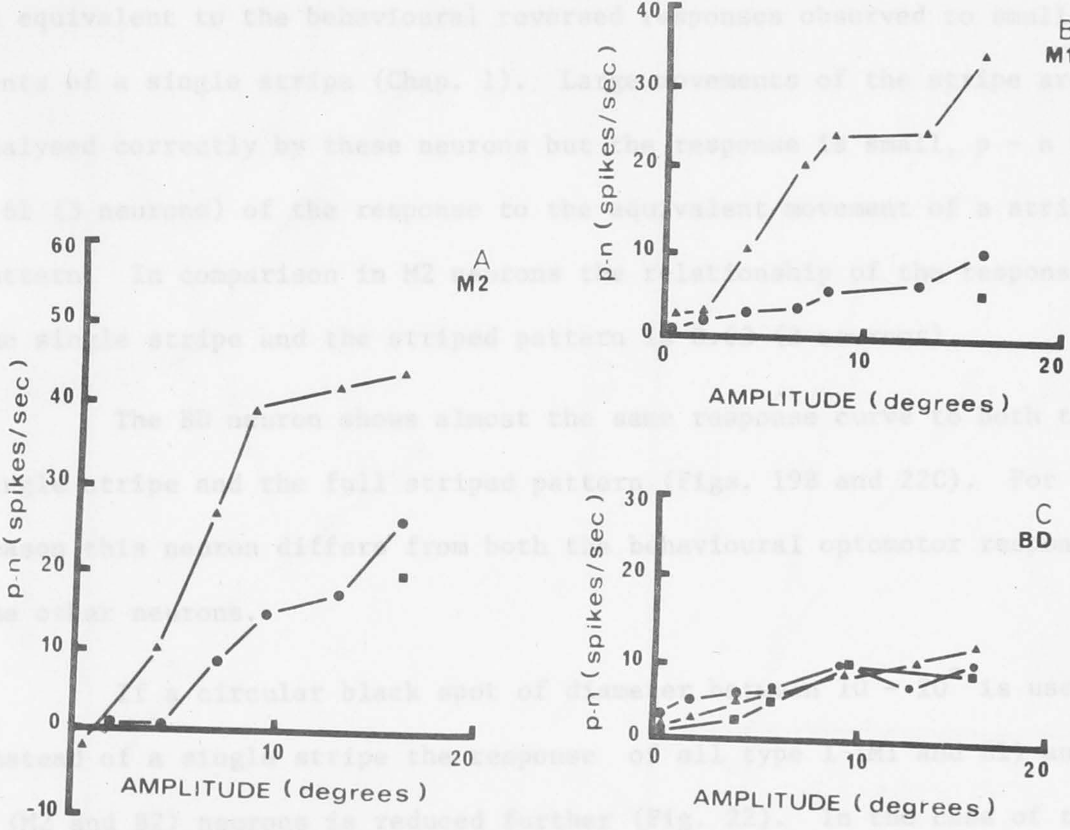


Fig. 22 Comparison of the responses of optic lobe neurons to movements of a striped pattern, repeat period, 15.8°, (—▲—) a single stripe subtending 7.9° (—●—) and a circular spot subtending 10° (—■—). Oscillation frequency 0.5Hz, p – n value obtained as before, each graph represents 1 neuron. (A) an M2 neuron, (B) M1 neuron, (C) a BD neuron. Note the good response of M2 to the large movement of the spot and the poor response of the M1 neuron.

This is shown more clearly in Fig. 23 which shows p, n and p - n curves for individual B2 neurons. This response is a reversed response and appears to be equivalent to the behavioural reversed responses observed to small movements of a single stripe (Chap. 1). Large movements of the stripe are analysed correctly by these neurons but the response is small, p - n being 0.61 (3 neurons) of the response to the equivalent movement of a striped pattern. In comparison in M2 neurons the relationship of the response to the single stripe and the striped pattern is 0.63 (2 neurons).

The BD neuron shows almost the same response curve to both the single stripe and the full striped pattern (Figs. 19B and 22C). For this reason this neuron differs from both the behavioural optomotor response and the other neurons.

If a circular black spot of diameter between 10 - 20° is used instead of a single stripe the response of all type 1 (M1 and B1) and type 2 (M2 and B2) neurons is reduced further (Fig. 22). In the case of the M1 neuron p - n is reduced to less than 5 which, from Fig. 19A, was thought to be negligible in this neuron type. The M2 and B2 neurons still give a clear response to movements of the spot (p - n ranges from 10 to 30). The BD neuron shows the same response to movements of a spot or single stripe or striped pattern (Fig. 22C). A form specificity, such as that found in vertebrate visual neurons responding only to, for example, straight edges (Hubel & Wiesel, 1965), has been thought to explain the response of the grasshopper vector edge unit to stripes and edges but not to spots (Northrop & Guignon, 1970; Northrop, 1973). However no form specificity is required to explain the failure of the type 1 neurons or the ability of the type 2 and BD neurons to respond to a moving spot. These responses could be easily predicted from their stimulus-response functions when a stripe pattern or single stripe was used. Lack of form specificity was further demonstrated by the equal responses of the neurons to curved or

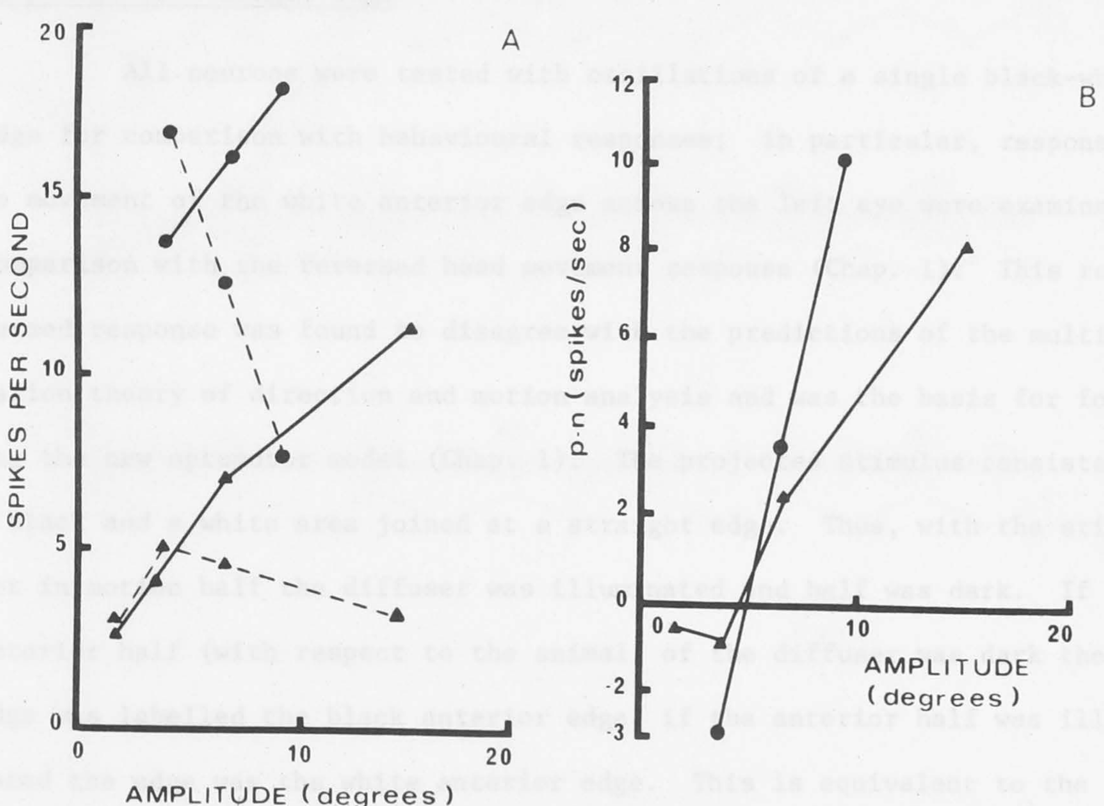


Fig. 23 Responses of 2 B2 neurons to movements of a single stripe. (A) discharges to movements in the preferred direction (solid lines) and null direction (dashed lines). (B) p - n curves. Stripe subtended 7.9°, oscillation frequency 0.5Hz. Data obtained from 5 movements in the preferred and 5 in the null direction.

straight stripes or boundaries. No change in response to the spot was seen if its shape was changed from circular to an irregular form bounded by curved or straight edges.

Responses to a single edge

All neurons were tested with oscillations of a single black-white edge for comparison with behavioural responses; in particular, responses to movement of the white anterior edge across the left eye were examined for comparison with the reversed head movement response (Chap. 1). This reversed response was found to disagree with the predictions of the multiplication theory of direction and motion analysis and was the basis for forming the new optomotor model (Chap. 1). The projected stimulus consisted of a black and a white area joined at a straight edge. Thus, with the stimulus not in motion half the diffuser was illuminated and half was dark. If the anterior half (with respect to the animal) of the diffuser was dark the edge was labelled the black anterior edge, if the anterior half was illuminated the edge was the white anterior edge. This is equivalent to the experimental situation used for behavioural testing (Fig. 7).

Both M1 and B1 neurons responded to the black anterior edge moving over the left eye, with a small directional response (Fig. 24). That is, for movements of the black anterior edge in the preferred direction (always defined by responses to movements of the striped pattern) there was a small response and a reduced response to movements in the null direction (again, with reference to movements of a striped pattern); p - n = 5.6 to 8.5 for M1 neurons, p - n = 1.8 to 15 for B1 neurons. However with the white anterior edge, there was hardly any response (Fig. 24c) and the p - n value was close to zero (p - n = 1.4 to 4.0 M1; p - n = -0.3 to 4.4 B1). The greatest response is elicited by a movement in the preferred direction causing an increase of light (black anterior edge in the preferred direction).

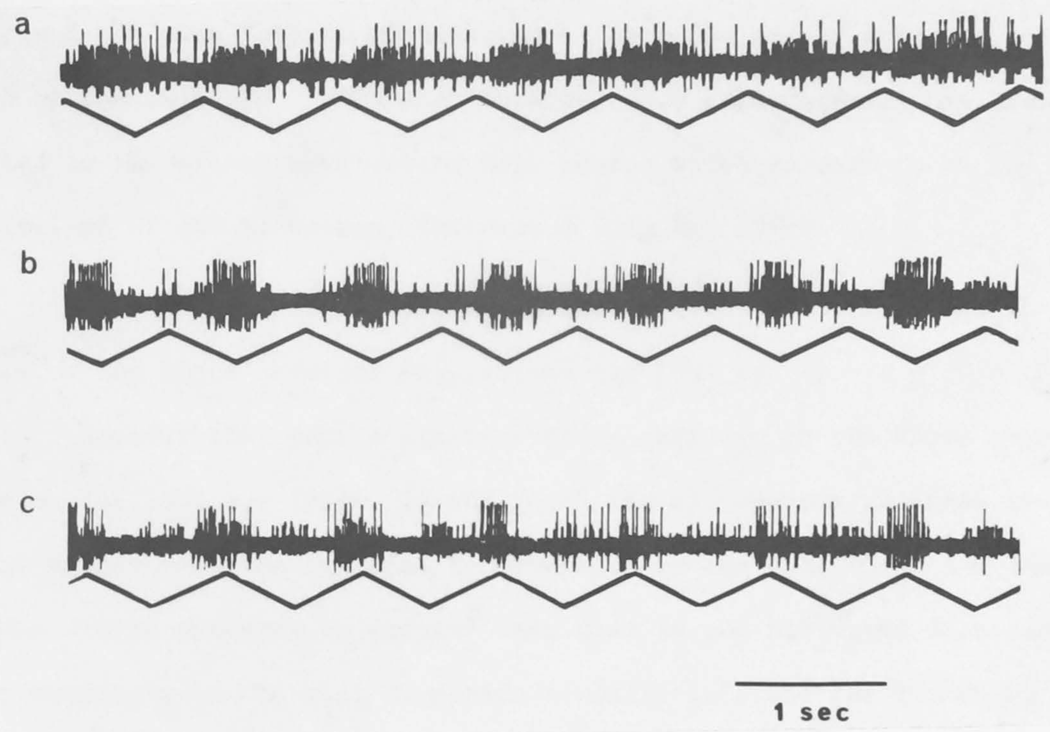


Fig. 24 Multiple recording of 2 units in the circumoesophageal connectives. The small unit is a B1 neuron, the large neuron a nonoptomotor movement detector. Responses are to movements of a) a striped pattern (repeat period 15.8°), b) the black anterior edge and c) the white anterior edge. Lower trace shows stimulus movement, down indicates a forward movement. The large neuron does not respond to movements of the striped pattern but responds directionally to edge movements, reversing the preferred direction for the white or black anterior edge (see Chap. 4). The other unit is a B1 unit whose preferred direction is forward (a). Note the lack of directional response in c. Spikes are retouched.

Movements in the null direction causing both an increase (white anterior edge) or decrease (black anterior edge) reduce firing by a small amount. For the B1 neuron the black anterior edge moving across the right eye elicited the same failure of directional response as the white anterior edge on the left eye. A similar dependence on edge polarity has been reported in the grasshopper vector edge neuron which appears to be the equivalent of the M1 neuron (Northrop & Guignon, 1970).

The M2 neurons reply with a clearly directional response to movements of the black anterior edge across the left eye (p - n = 10.8 to 23.6). However they show a clear reversed response to the white anterior edge on the left eye (Figs. 25 and 26, b and c). Here a reversed response means either that the response to movements in the null direction (defined by the stripe pattern) is greater than that in the preferred direction or that movements in the null direction actually initiate the response. A neuron responding to movements in the null direction and clearly inhibited during movements in the preferred direction is shown in Fig. 25. The second type of reversal, a response initiated by the null movement and firing maintained without inhibition during movement in the preferred direction is shown in Fig. 26c. In both cases the responses to movements both in the preferred and null direction are elicited by the movements causing a decrease in light. Both these response patterns were seen in the B2 neurons also, but to a much smaller extent, reversal being of the order of p - n = -1.0 rather than the p - n value of -8.1 in Fig. 25. The black anterior edge on the right eye elicited these responses also. The low p - n values of the B2 neurons are still sufficient to produce head movement responses as the behavioural reversals elicited by some movements of a single stripe also coincide with p - n values of only -1.0 to -3.0 in the B2 neurons.

The BD neuron was tested for edge responses using the left eye.

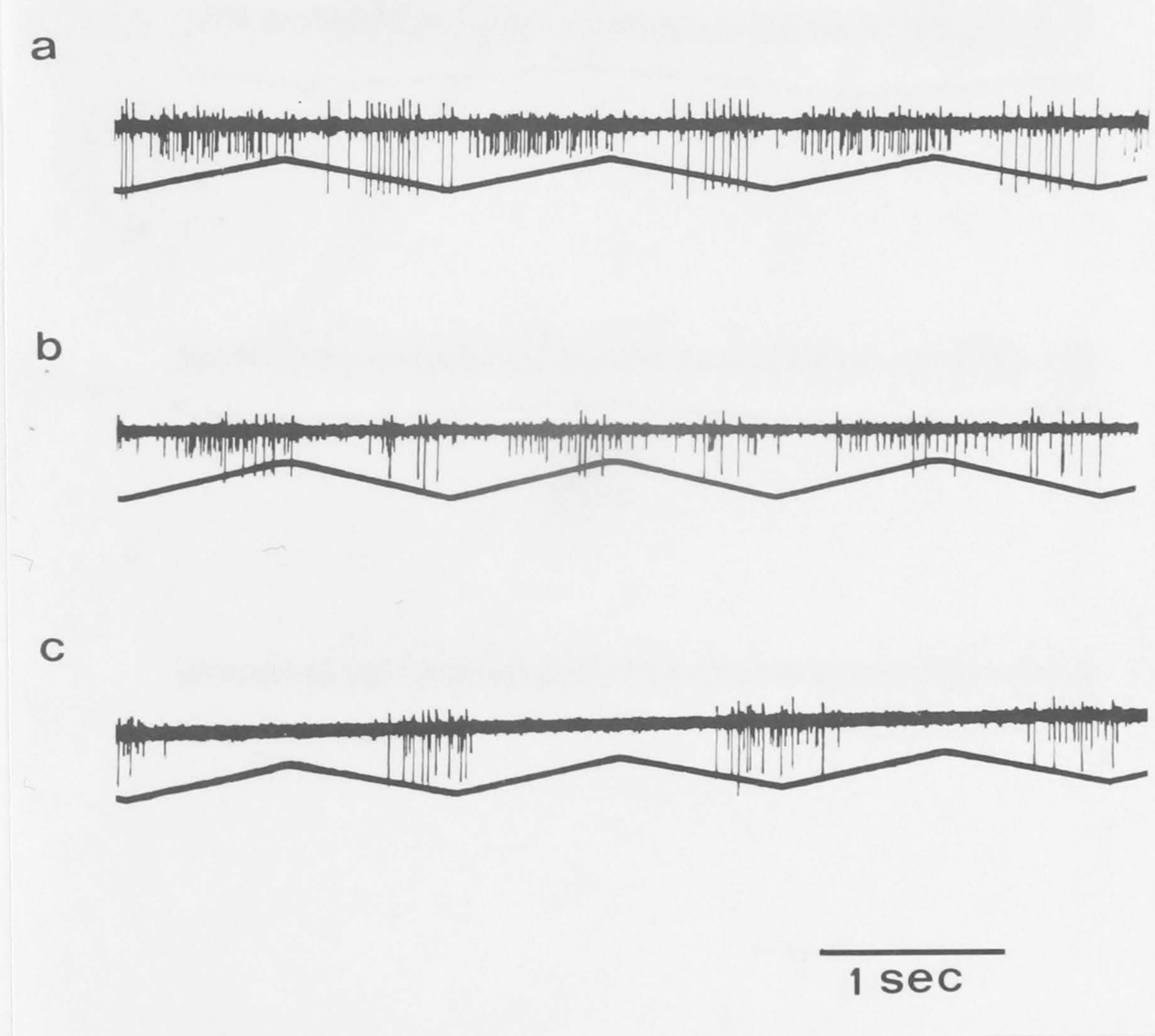


Fig. 25 Response of M2 neuron (small unit) and BD neuron (large unit) to movements of a) a striped pattern, b) black anterior edge, c) white anterior edge. Lower trace represents stimulus movement, downwards indicating a forward movement. Note reversal of response of the M2 unit in c, and the failure of the BD neurons to respond directionally in b. Spikes are retouched.

Fig. 26 Response of M2 neuron to movement of a) a striped pattern, b) the black anterior edge, c) the white anterior edge. Lower trace represents stimulus movement as before. Note the expanded time base of this record. This neuron responds to the black anterior edge although there is less null inhibition than in a. During movements of the white anterior edge (c) the response is initiated (arrows) during movement in the null direction and maintained during movement in the preferred direction. Spikes are retouched.

Unlike the other neurons the BD neuron responded clearly to the white anterior edge (p - n = 2.7 to 9.4) with a response 0.4 to 1.8 times the response to the striped pattern (the larger neuron in Fig. 25c). However, the black anterior edge failed to elicit any directional response in BD neurons. In some neurons movements of this edge elicited a small response in both the preferred and null direction (Fig. 25b) but in others movements of this edge failed to elicit any spikes at all.

Thus, all the directional neurons show unusual responses to movements of one edge, the type 2 neurons showing a distinct reversal of response to the white anterior edge comparable to the behavioural responses. This confirms that the edge responses are indeed a property of the optomotor system.

<u>Responses to varying contrast frequencies and oscillation frequencies</u>

The responses of all neurons to different frequencies of oscillation of a stripe pattern were determined (Fig. 27) and compared with responses to different constant velocities and contrast frequencies (Fig. 28). Identical results were obtained by comparing contrast and oscillation frequencies when the stripe pattern moved through an angle equal to the pattern repeat period. Therefore the oscillation frequency can be effectively compared with contrast frequency.

Both M1 and B1 neurons responded to a wide range of frequencies and velocities with a broad optimum plateau rather than a peak (Figs. 27 A & C and 28 show typical examples - 8 neurons were fully tested). Some M1 and B1 neurons preferred frequencies from 0.25Hz to 7.5Hz whereas others appeared to respond better to frequencies below 0.5Hz. In Fig. 27A one M1 unit with forward preferred direction and one with upward preferred direction are shown. The difference in frequency curves was not correlated with preferred direction as seen for the B1 neurons (Fig. 27C) where the

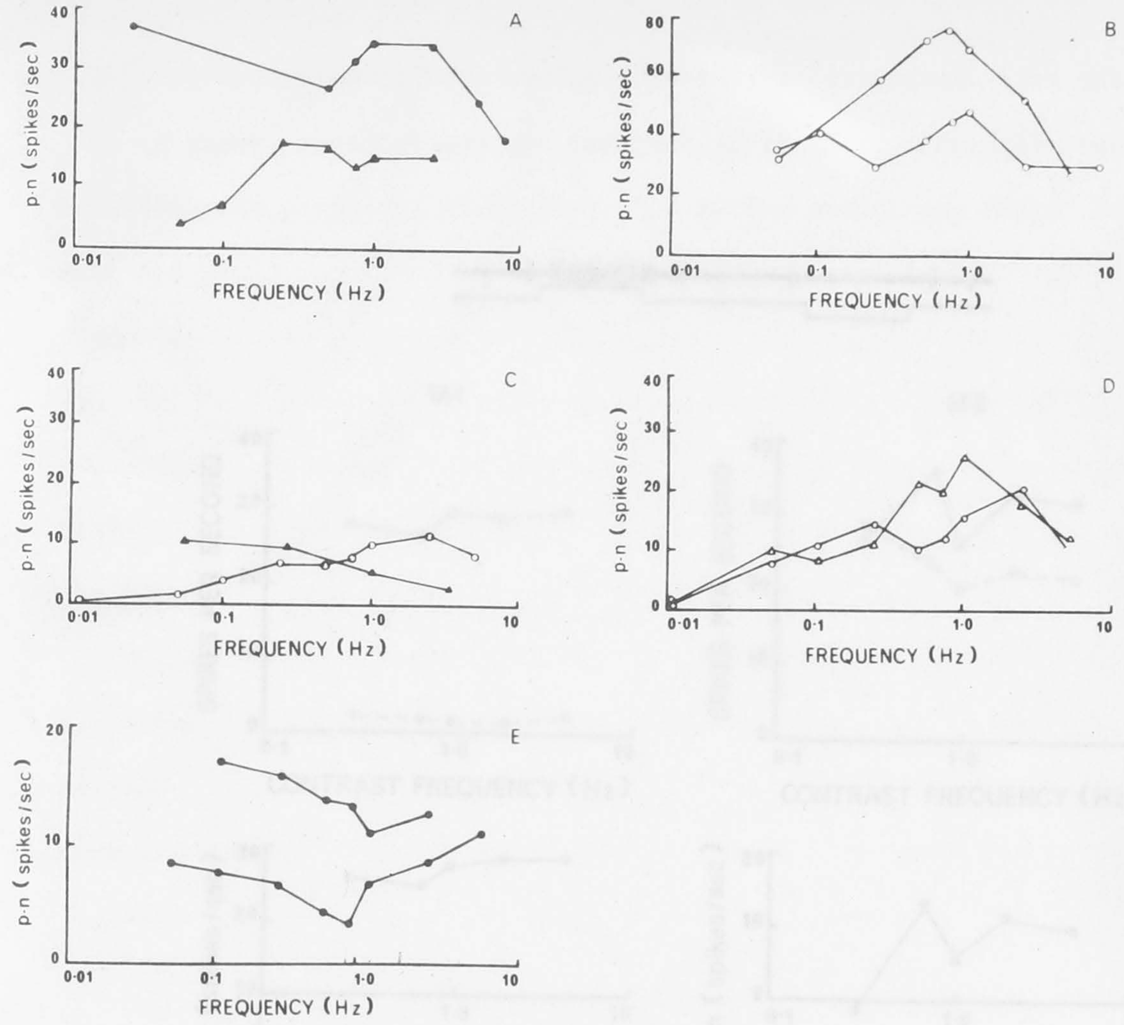


Fig. 27 Responses of individual neurons to changes in log frequency of oscillation of a striped pattern. Comparison with constant velocity testing shows that frequency of oscillation (amplitude 1 wavelength) is comparable to contrast frequency.

A. M1 neurons (preferred direction —●— forward, —▲— up)

B. M2 neurons (preferred direction back —o—)

C. B1 neurons (preferred direction -△- anti-clockwise; clockwise —o—)

D. B2 neurons (preferred direction clockwise —o—; anticlockwise —△—)

E. BD neurons (preferred direction forward —o—)

Stripe period 15.8°, amplitude of movement 15.4°. Points plotted as before.

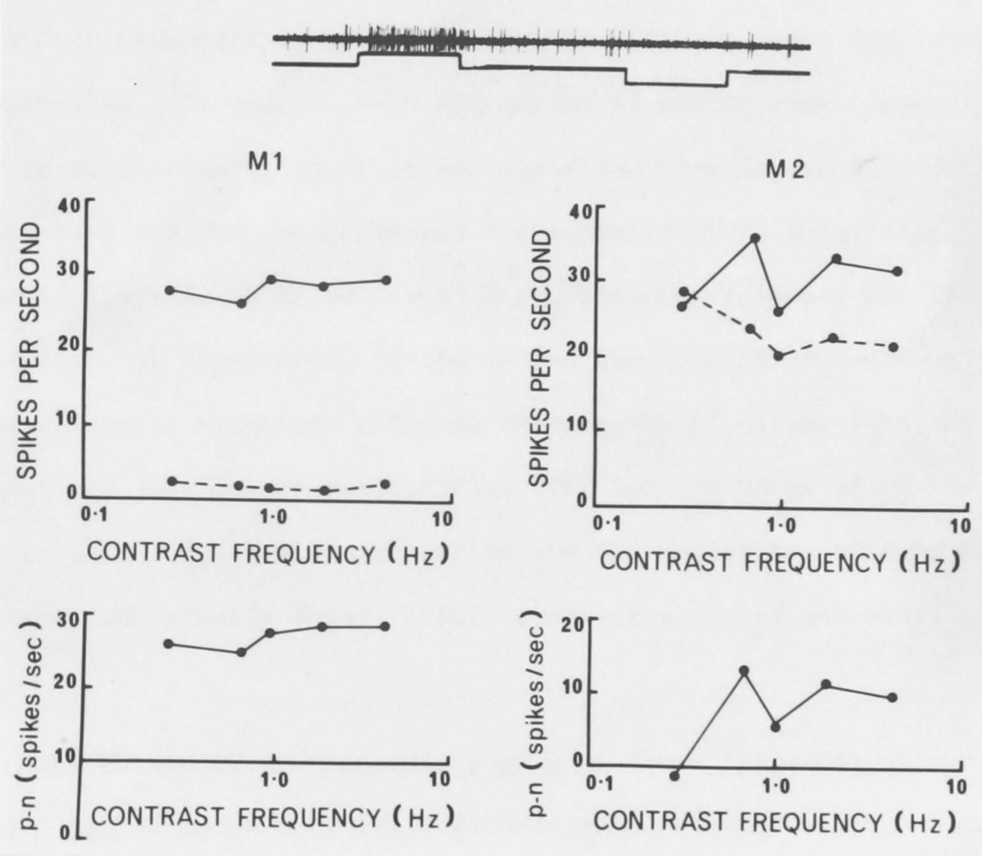


Fig. 28 Response of individual M1 and M2 neurons to constant velocity movement plotted as contrast frequency (abscissa). The actual response of an M1 neuron to a 1 second movement is shown above. The response continues for some msecs after the movement has ceased. The M1 neuron shows the same flat curve as in Fig. 27, while the M2 shows a peak at contrast frequency of 0.7Hz. In the upper graphs the solid lines represent discharges to movements in the preferred direction, dashed lines show response to movements in the null direction. Each point is the average from 5 movements each lasting 1 second. Pattern repeat period 6°.

preferred direction of both neurons was in the horizontal. The unit preferring slower oscillations was recorded in the left connective and had an anticlockwise preferred direction. The neuron preferring higher oscillation frequency responded to clockwise movements and was recorded in the right connective. As usually only one neuron of any neuronal type was recorded in each preparation it is not clear how many M1 and B1 exist in each optic lobe and circumoesophageal connective. It is impossible to determine if there is an M1 neuron of each frequency response profile (with the same preferred direction), if the up and the forward neuron always have different frequency responses although they may be of either type, or if the differences are just due to variability. The last is doubtful as the differences in the M1 neurons are echoed in the B1 neurons and because both profiles are consistently found within constant velocity and oscillating stimuli.

Both M2 and B2 neurons show a peak in their frequency curves at 0.75 to 2.5 Hz, although they still respond well between 0.05Hz and 5.0Hz (Figs. 27B,D and 28 show typical examples - 11 neurons were examined). The peak frequency for the M2 neurons was in the range from 0.75Hz to 1.0Hz (30°/sec with 15.8^{o} period stripes) and for the B2 neurons from 1.0Hz to 2.5Hz. Fig. 27D shows the responses for a B2 unit with anticlockwise preferred direction recorded in the left circumoesophageal connective and one with clockwise preferred direction recorded in the right connective. The type 2 neurons reach their peak response to the oscillating stimuli at frequencies where the behavioural response is quite poor. Thus the upper frequency limit of the behavioural response is not a result of visual integration processes. It was suggested in Chap. 1 that this limit is imposed by the properties of the neck muscles and inertia of the head. This is confirmed by the results of isometric head torque measurements where the response is maximal at frequencies between 0.5 and 0.75Hz (Thorson,

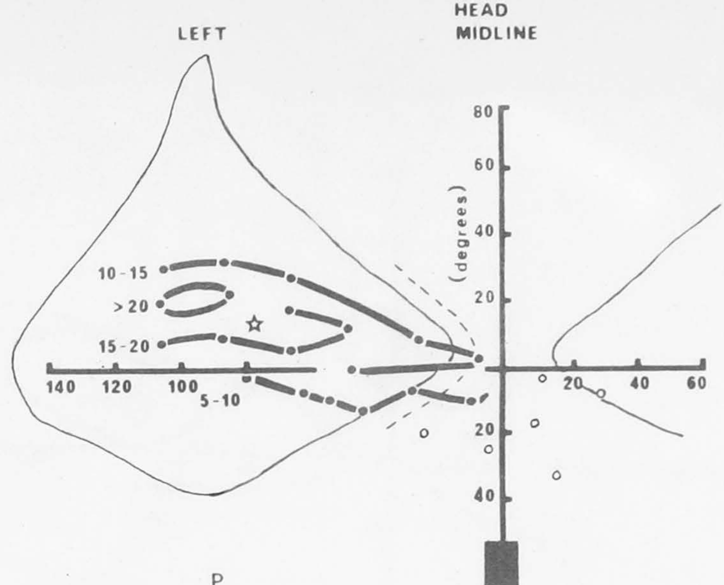
1966b), this being close to the M2 peak.

The BD neurons (3 neurons examined) show a much greater variation in p - n values for changes in stimulus oscillation frequency than they do for changes in movement amplitude (cf. Fig. 27D and Fig. 22C). Like both M1 and M2 neurons the BD neurons respond over a wide range of frequencies, from less 0.1Hz to greater than 5Hz. However, unlike either type 1 or 2 neurons the BD neuron has a dip in the curve at 0.75 to 1.0Hz, those frequencies which are optimum for the M2 neurons.

Receptive field

The stimuli used in the above tests all stimulated the entire eye. When the number of viewing facets was reduced only the centre portion of the eye was stimulated. The contribution of other parts of the eye to the response when the whole eye was stimulated was not known. Therefore the receptive field was plotted using a small (10° x 15°) stimulating aperture. Responses to movements in different directions were tested in different parts of the visual field. However no neurons showed any differences of preferred direction in different parts of their receptive fields nor did they show any inhibitory areas. Receptive field plots from 2 M1 units were almost identical. One plot is shown in Fig. 29. Here the visual field is plotted against the head axes and not the axes of each eye. The centre of the eye corresponds to a point 15° above and 85° lateral to the head mid-line. There is an area of maximum sensitivity for movements in both the preferred and null direction approximately in the centre of the visual field. The response gradually diminishes as the distance from field centre increases. Responses of movements to hand held stimuli showed that the receptive field outside the 5 - 10 contour line covered the entire visual field for the ipsilateral eye. As shown in Fig. 29 there is no response in the contralateral eye or in the zone between the eyes.

Fig. 29 Receptive field of an M1 neuron. Contour lines show responses (upper graph p spikes/sec, middle n spikes/sec and lower graph p - n spikes/sec) to constant velocity stimulation. Each point is averaged from 5 movements in the preferred and 5 movements in the null direction. The central contour indicates an area of maximum sensitivity. Maximum p - n difference was less than 30 spikes/sec. The break in the p and p - n contour lines indicates a very sudden drop dorsally from $p>10$ to $p<10$, and from $p-n>20$ to $p-n<10$. Open circles represent $p<5$, $n\geq4$ and $p-n<3$. Extent of plot was limited by perimeter movement. Qualitative testing with hand held stimuli showed that the receptive field extended over the whole eye, but only weak responses were obtained. Stimulus velocity 11.5^{o}/sec, contrast frequency 1.0Hz, stripe repeat period 10°. Each movement lasted 1.0 sec. Outline of the visual field was plotted by mounting a fine light beam on the perimeter and measuring the point at which it no longer shone on the eye. The star indicates the position of the centre of the eye. Shaded rectangle shows relative size of stimulation window. Dashed line shows area stimulated by the window when it was centred on the edge of the visual field.



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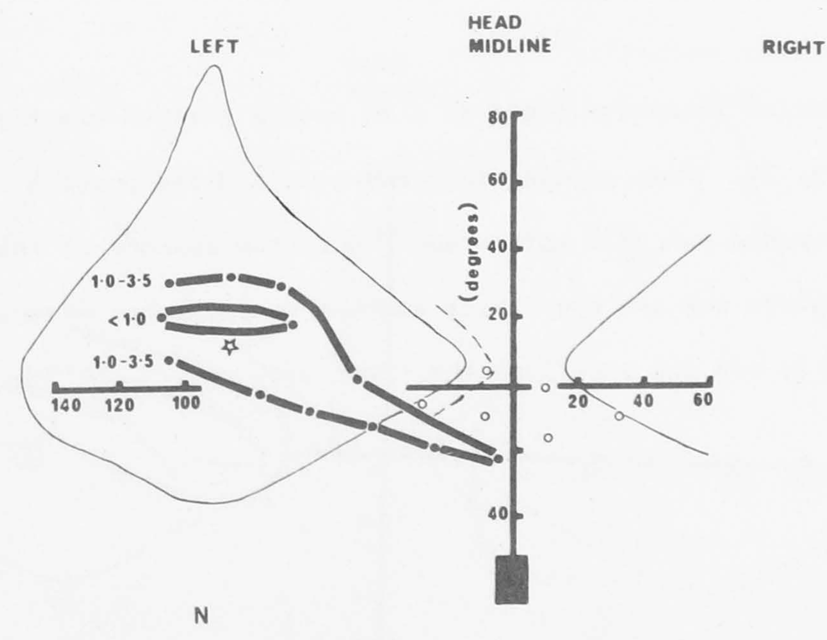

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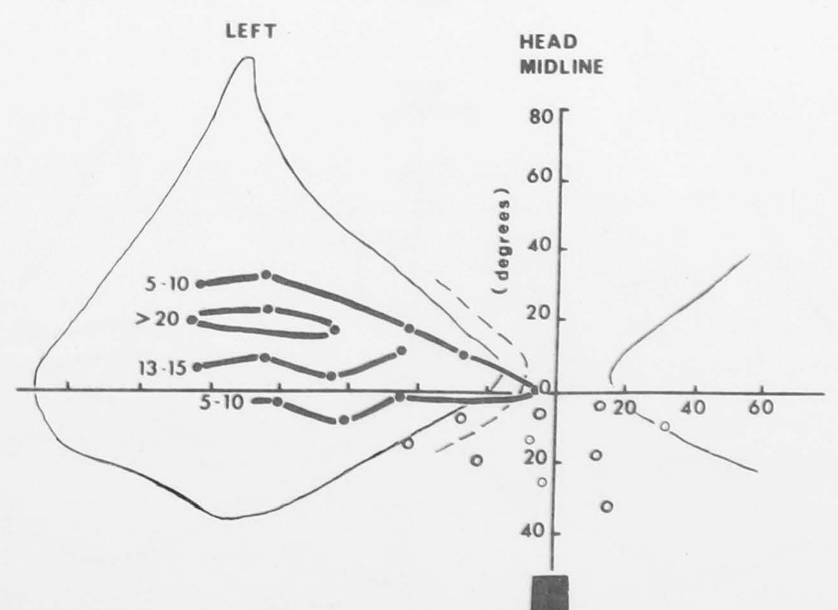
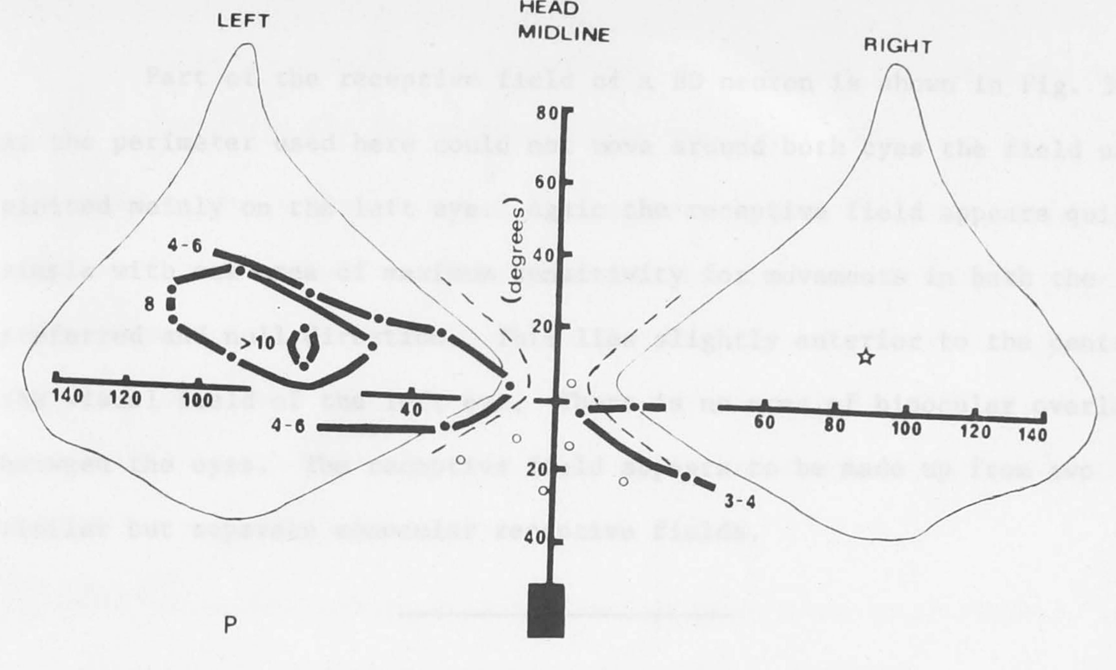


Fig. 30 Partial receptive field of a BD neuron plotted exactly as in Fig. 29. Open circles indicate $p<3$, $n>3$ and $p-n\leq 1.5$. Maximum response was $p\doteqdot 13$ spikes/sec. Note the absence of the response between the two eye fields and the reappearance of response ($p>3$, $n<3$ and $p-n>2$) on the right eye.



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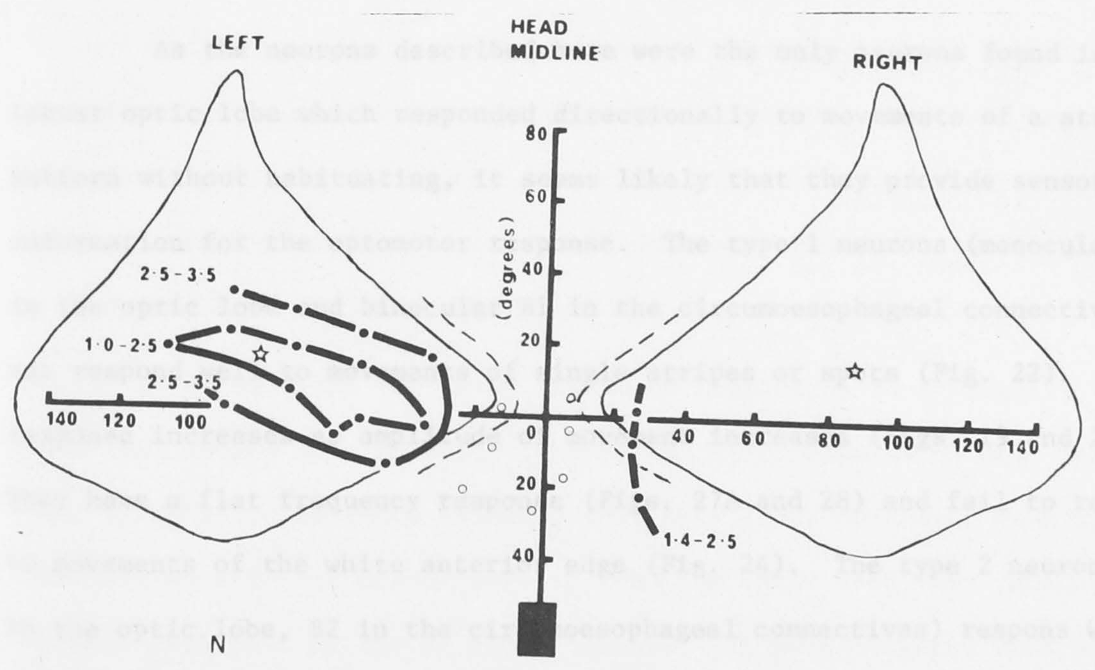

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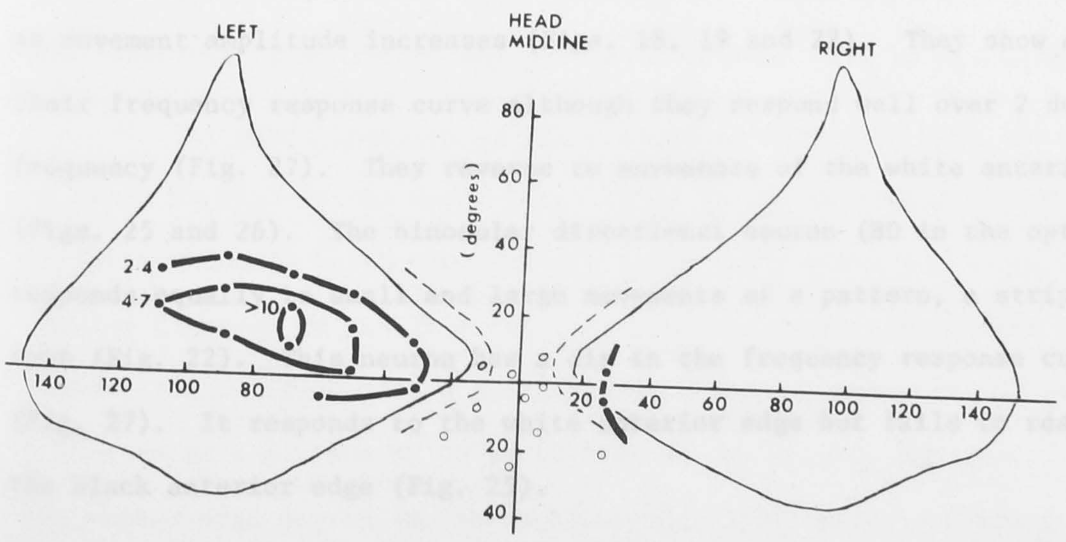


Part of the receptive field of a BD neuron is shown in Fig. 30. As the perimeter used here could not move around both eyes the field was plotted mainly on the left eye. Again the receptive field appears quite simple with one area of maximum sensitivity for movements in both the preferred and null direction. This lies slightly anterior to the centre of the visual field of the left eye. There is no area of binocular overlap between the eyes. The receptive field appears to be made up from two similar but separate monocular receptive fields.

As the neurons described here were the only neurons found in the locust optic lobe which responded directionally to movements of a striped pattern without habituating, it seems likely that they provide sensory information for the optomotor response. The type 1 neurons (monocular M1 in the optic lobe and binocular B1 in the circumoesophageal connectives) do not respond well to movements of single stripes or spots (Fig. 22). Their response increases as amplitude of movement increases (Figs. 19 and 22). They have a flat frequency response (Figs. 27A and 28) and fail to respond to movements of the white anterior edge (Fig. 24). The type 2 neurons (M2 in the optic lobe, B2 in the circumoesophageal connectives) respons well to movements of a single stripe or spot (Fig. 22) and show an early saturation as movement amplitude increases (Figs. 18, 19 and 22). They show a peak in their frequency response curve although they respond well over 2 decades of frequency (Fig. 27). They reverse to movements of the white anterior edge (Figs. 25 and 26). The binocular directional neuron (BD in the optic lobe) responds equally to small and large movements of a pattern, a stripe or a spot (Fig. 22). This neuron has a dip in the frequency response curve (Fig. 27). It responds to the white anterior edge but fails to respond to the black anterior edge (Fig. 25).

There are similarities between the properties of only the type 1 and 2 neurons and the behavioural response. These are:

1. The magnitude, both of head movement and neural response, decrease with decreasing amplitude of movement and decrease in the number of ommatidia stimulated. The neurons in the connectives require stimulation of 50 - 100 ommatidia to elicit a directional response. This is very similar to the threshold of the behavioural response which was found to be approximately 50 facets.

2. The optomotor behaviour of the locust shows a reversal response to movements of the white anterior edge across the left eye and sometimes to small movements of a single stripe. Both type 1 and type 2 neurons showed anomalous responses to the white anterior edge, the type 1 neurons failing to respond, the type 2 neurons showing a reversal. As well the type 2 neurons in the connectives showed a reversal to small movements of a single stripe.

On the other hand the BD neuron, although responding directionally to stripe movement, showed no similarity to behavioural thresholds or edge responses. Thus there is no definite evidence that this is an optomotor neuron. It is probably an efferent neuron passing into the optic lobe (the latency is much greater than that of the M1 and 2 neurons, 205 msec compared with 60 to 80 msec). No similar neurons were found in the circumoesophageal connectives. The relationship of the BD and optomotor neurons will be discussed below.

The exact location of the neurons in the optic lobe is not known. As shown in Fig. 16 the major fibre tract in the recording region is Cuccatti's bundle which contains the large field medullary tangential fibres passing directly to and from the contralateral protocerebrum and optic lobe (Power, 1943; Strausfeld & Blest, 1970). The latencies of the type 1 and 2 neurons at a minimum of 40 to 60 msec do not suggest any specific location. The vector edge neuron (Northrop & Guignon, 1970) which appears to be

equivalent to the M1 neuron was recorded in the posterior medulla in the grasshopper. All the other reported possible optomotor neurons in insects have been recorded beyond the lobula (Collett, 1970, 1971; Bishop, 1970; Kaiser & Bishop, 1970; Bishop & Keehn, 1967; Bishop et al., 1968; McCann & Foster, 1971; Menzel, 1973). However in the fly the electrode was found to have been positioned definitely in Cuccatti's bundle in some recordings (Bishop & Keehn, 1967) and also mapping experiments in moth do not exclude the possibility that the directional neurons originate in the medulla (Collett, 1971). If the optomotor neurons are tangential fibres with large dendritic fields in the medulla, direction analysis may take place in one step from small receptive fields of nondirectional neurons to whole eye field directional optomotor neurons as found here. This would differ slightly from the fly where the field of the directional neurons covers the whole eye but different neurons have different regions of maximum sensitivity (Bishop et al., 1968). This situation in insects is different from vertebrate visual systems where directionally selective ganglion cells with fields of only 3° - 4° are found in the retina (Barlow & Levick, 1965; Michael, 1968; Werblin, 1970) and directional selectivity is sharpened in higher visual nuclei (Levick, Oyster & Takahashi, 1969).

Central connections of optomotor neurons

The directional information, once gathered in the medulla of each optic lobe is combined in the brain and passes to the suboesophageal ganglion to motoneurons which activate the neck muscles. The interconnections of the M1, M2, B1, B2 and BD neurons appear quite similar to those for comparable neurons in other insects (Bishop et al., 1968; McCann & Dill, 1969; Collett, 1971; McCann & Foster, 1971). In the brain, information from the M1 and M2 neurons of each lobe is combined to form the binocular neurons arranged as shown in Fig. 31. The binocular units behave as if

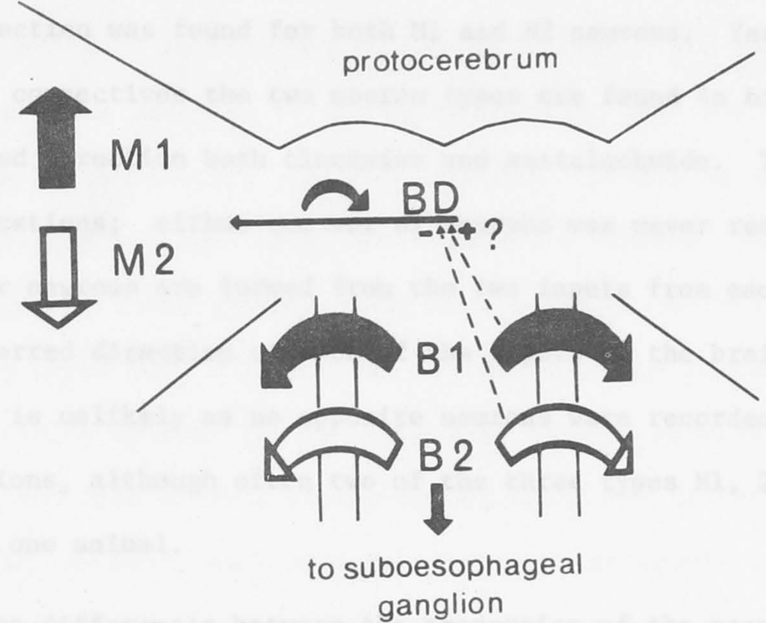


Fig. 31 Schematic summary of neuron types and their preferred direction. Monocular type 1 neurons (M1 shaded) have forward preferred direction in the left optic lobe. Binocular type 1 neurons (B1 shaded) have anticlockwise preferred direction in the left circumoesophageal connective and clockwise in the right connective. This is so for the B2 neuron (type 2 unshaded) but the monocular type 2 (M2 shaded) has a back preferred direction in the left optic lobe. Note the shift from opposing directions of type 1 and 2 in the optic lobe to similar directions in each connective. Possible inputs for the BD neuron are shown with dashed lines. Interactions between ipsilateral M1 and 2 neurons and between both ipsi- and contralateral M1 and 2 neurons are not indicated.

derived from two monocular neurons of the same type but opposite preferred direction across each eye, as occurs in fly (Bishop et al., 1968; McCann & Dill, 1969) and moth (Collett, 1971). However, in the optic lobe only one preferred direction was found for both M1 and M2 neurons. Yet in the circumoesophageal connectives the two neuron types are found in binocular form with preferred direction both clockwise and anticlockwide. This finding has two implications; either one set of neurons was never recorded, or the four binocular neurons are formed from the two inputs from each lobe by a reversing of preferred direction of each of the inputs to the brain. The first possibility is unlikely as no opposite neurons were recorded during repeated penetrations, although often two of the three types M1, 2 or BD were found in the one animal.

The slight differences between the properties of the monocular and binocular neurons favour the second possibility. The reversal to small movements of the single stripe is seen only in the B2, not M2 neurons. The reversals occur when the M2 neuron is not responding and imply the existence of an inhibition to the B2 neuron. The relationship between the response of the B1 neuron to a pattern and a single stripe is not seen in the M1 neuron. These slight differences could well be the result of various cross inhibitions between neurons with different preferred directions or of different types. These inhibitory mechanisms may also account for the transformation required to produce the four binocular neurons. For instance, inhibition of a spontaneously active neuron by a directional neuron should cause it to show the opposite directional selectivity to that of the inhibitor. Cross inhibitory mechanisms have been found between directional neurons, both monocular and binocular in other insects (Collett, 1971; McCann & Foster, 1971) and one function could be directional sharpening (Levick et al., 1969). There may also be interaction between the monocular neurons of the two optic lobes within the optic lobe itself. Some M1 and

M2 neurons showed small reactions to gross changes of light intensity on the contralateral eye. This type of interaction has been described in both fly (McCann & Foster, 1971) and moth (Collett, 1971).

The BD neuron is an efferent to the optic lobe. Its response properties, firstly its response to the white anterior edge and its failure to respond to the black anterior edge and secondly, the dip in the frequency response curve precisely where the M2 neuron shows a maximum, suggest that the BD neuron receives an excitatory input from a B1 (or two M1) neuron and an inhibitory input from a B2 (or two M2) neuron, thus representing the difference in activity between the two binocular neurons passing to each connective. The function of this neuron is not known but Collett (1972) has suggested that, in moth, such neurons provide an antagonistic surround for directional tracking neurons in the optic lobe. Another possibility is that this neuron type provides direct inhibition to neurons which respond directionally to movements of spots or edges in order to prevent them from responding to stripes (Fig. 24).

Comparison with the behavioural optomotor model

The main aim of these experiments was to see if it was possible to confirm expand or reject the model for the direction detecting mechanism proposed from the behavioural experiments in Chap. 1. It was suggested that there were two inhibitory Barlow and Levick (1965) networks with opposing preferred directions (Fig. 15). Large numbers of small receptive field ON neurons were thought to provide the input to the neuron with forward preferred direction and a smaller number of large receptive field OFF cells connect to the neuron with back preferred direction. It was also suggested that the difference in receptive field sizes of the inputs may cause the cell with back preferred direction to be more sensitive to faster movements while the cell with forward preferred direction responds to

slower movements.

The M1 and 2 neurons fit the requirements of the model very well. Firstly, the neuron with forward preferred direction, M1, responds equally over a wide range of stimulus speeds, while the neuron with back preferred direction does have an optimum response to faster stimulus movements. Secondly, the responses of the neurons are compatible with the predictions made from the behavioural edge responses. While the M1 neuron appears to have too high a threshold to reflect the small response to the white anterior edge stimulus, the M2 neuron shows the predicted reversal. The difference in response of the M2 neurons in Figs. 25 and 26 can be explained by differences in a weak cross inhibitory effect from the M1 neuron. A similar weak or variable effect from the M2 neuron onto the M1 neuron explains why the movement of the black anterior edge in the null direction, causing a decrease of light, lowers the M1 firing rate. Such a cross inhibition must be postulated to explain this effect as no combination of ON or OFF networks other than that in Fig. 32 can account for the observed behaviour. There is good evidence for such a cross inhibition between the directional neurons of each optic lobe in moth (Collett & Blest, 1966). Also a similar cross inhibition may exist between monocular neurons of the two optic lobes (see above). During pattern movement such weak cross inhibitory links would serve as direction sharpeners (Levick et al., 1969). The third agreement between model and neuron behaviour comes from the reversals to small movements of the single stripe. The model predicted that these were due to a comparison of near equal firing in neurons with opposite preferred directions. During small movements of the stripe p - n values for both M1 and 2 neurons are very low. The null response of each neuron is very similar both to its own preferred response and that of the other neuron. The only reversal to the stripe was seen in the B2 neuron and an inhibitory input from one directional neuron was thought to explain this

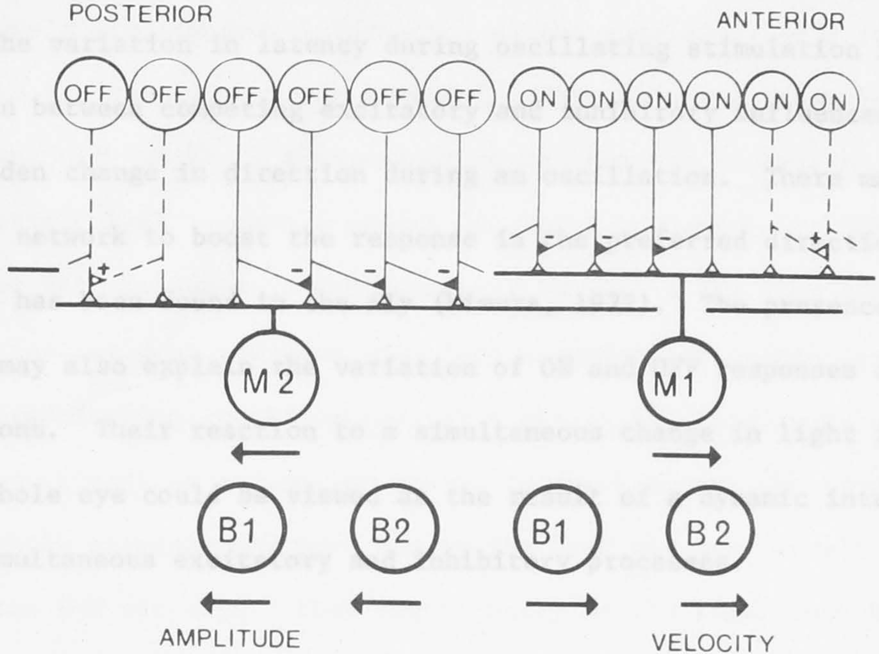


Fig. 32 Inclusion of neuron properties in the model for inputs to the optomotor system (cf. with Fig. 15 in the previous chapter). The ON & OFF cells form two inhibitory Barlow & Levick networks with opposite preferred direction as before. For simplicity the difference in the sizes of the receptive fields postulated for the ON & OFF cells is shown here by the different sized circles. The dashed lines show the possible excitatory networks. Filled triangles represent inhibitory synapses. The two directional neurons formed by these input arrangements are now the M1 and M2 neurons. From these the B1 and B2 neurons are derived in the brain. It is suggested that type 1 neurons code the amplitude of a movement or the number of ommatidia stimulated and the type 2 neurons code its velocity.

reversal. Such inhibition by one neuron and excitation by another is essentially a comparison of the activity of the two neurons.

The variation in latency during oscillating stimulation implies an interaction between competing excitatory and inhibitory influences elicited by the sudden change in direction during an oscillation. There may be an excitatory network to boost the response in the preferred direction. Such excitation has been found in the fly (Mimura, 1972). The presence of such a network may also explain the variation of ON and OFF responses of the M1 and 2 neurons. Their reaction to a simultaneous change in light intensity over the whole eye could be viewed as the result of a dynamic interaction between simultaneous excitatory and inhibitory processes.

The properties of the optic lobe neurons confirm the principles of the optomotor model derived from behavioural studies. The expansion to the model required after consideration of the neuron responses is shown in Fig. 32. The function of the difference in properties of the type 1 and 2 neurons can only be surmised. Although a crude velocity discrimination can be performed by the type 1 neurons their most precise and largest response variation is controlled by the amplitude of a movement or the numbers of ommatidia stimulated in a given time, i.e. a coarse pattern stimulates fewer omma's than a fine pattern at any one time and a single stripe stimulates fewer omma's than a full pattern. The type 2 neurons alter their response with amplitude only up to a certain displacement. The parameter which causes most alteration of the response is change in contrast frequency and stimulus velocity. While both neuron types will confuse velocity and number of omma's stimulated to a very small extent, the type 1 neurons supply information mainly on the amount of stimulation during a movement while the type 2 neurons code its velocity. These differences are emphasised in the binocular neurons of both types. Such separation of

function explains the presence of binocular neurons of both types with the same preferred direction in each circumoesophageal connective. The two neurons supply simultaneous information on the complexity of a stimulating pattern and the velocity of its movement. This allows assessment of stimulus velocity which is independent of the numbers of omma's stimulated and enables the head to make a smooth following movement. If velocity and quantity of stimulation were not separated in such a way slow movements of fine patterns could be confused with fast movements of coarse patterns. Then the head movement would consist of a series of diminishing oscillations in an attempt to reduce, by visual feedback alone, the stimulation caused both by external movement and by the head movement itself. Such oscillations are not seen. Thus the velocity of the regulatory head movement is determined by the sensory information. This sensory control is quite similar to that in the vertebrate optomotor response (Collewijn, 1969) and is a further illustration of similarities between vertebrate and invertebrate visual systems.

An unusual M2 neuron

The M1 and M2 neurons can be distinguished quite easily from each other apart from their difference in preferred direction. The M2 neurons respond clearly to movements of a single stripe or small spot while the M1 neurons do not. The M2 neurons show a peak in the frequency response curve while the M1 neurons do not. Also the M2 neurons show a reversal to the white anterior edge while the M1 neurons hardly show a directional response.

One neuron was found in the optic lobe which, while conforming to many responses of a type 2 neuron (responded to a spot, showed a frequency peak), responded to forward movements and showed no reversals of response to movements of either the black or the white anterior edge (Fig.33). It is easy to confuse rarity of recording of a neuron with its possible

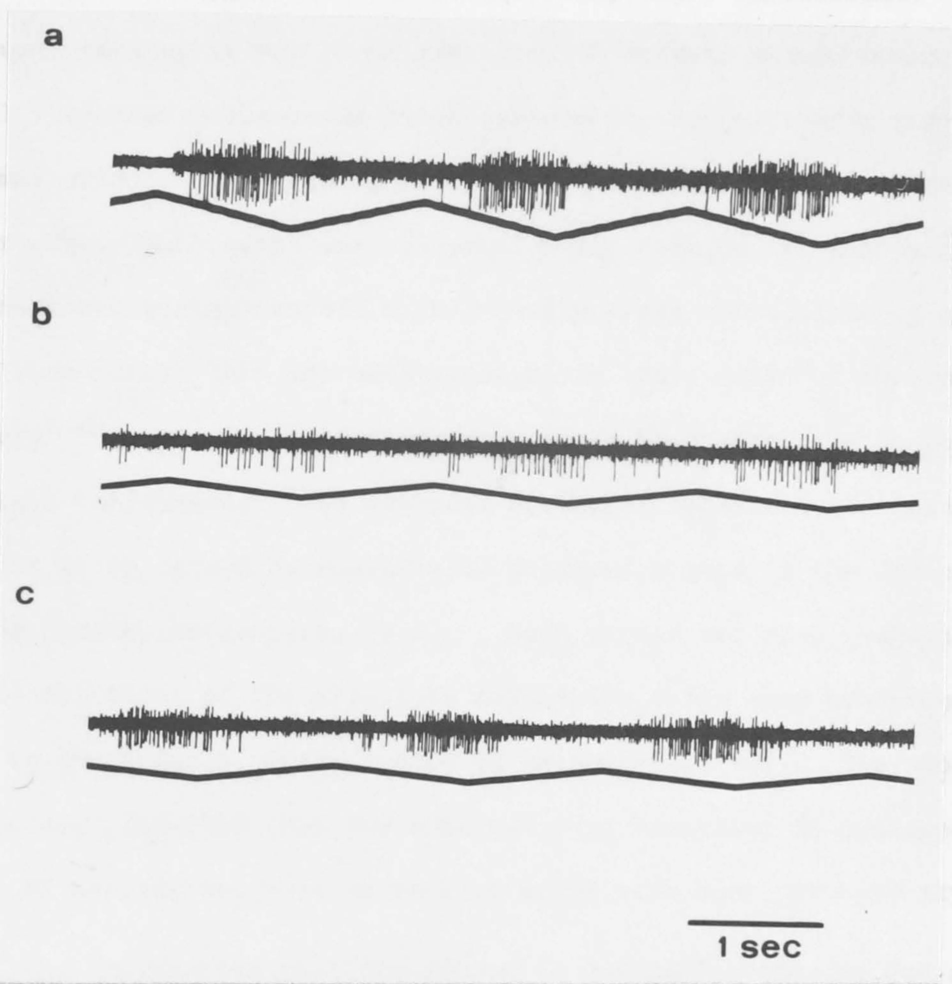


Fig. 33 Response of an abnormal M2 unit to movements of a striped pattern (a), the black anterior edge (b) and the white anterior edge (c). Note preferred direction is forward, and that the neuron responds directionally without reversal to movements of both edges. Spikes are retouched.

abnormality. However behavioural results and the responses of some non-optomotor neurons suggest that this neuron may truly be abnormal. During behavioural testing it was found that 2 of 35 animals showed no edge reversal responses; also, one animal showed the opposite edge response to the normal animal, by reversing to the black anterior not the white anterior edge. Such behaviour, conventionally regarded as abnormal, must have a neuronal basis, neurons either having wrong connections or giving unusual responses. This has been accepted in other cases of abnormal behaviour. For example, optomotor mutants can be produced in Drosophila by chemical mutagenesis. The abnormal optomotor behaviour of these mutants is thought to be caused by genetically produced errors in the direction detecting system (Heisenberg, 1972). Such errors are also postulated for the small fractions of the wild type population which show behaviours similar to the mutants (Götz, quoted in Heisenberg, 1972). Therefore, it is completely plausible that the abnormal edge behaviour is mediated by an abnormal M2 neuron, the more so as both occur with equal probability.

The explanation that the neuron is normally occurring but not usually recorded is not satisfactory. In the previous chapter it was shown that the edge responses must result from a specific arrangement of the inputs to the direction analysers. A neuron showing different edge responses requires a different arrangement of the inputs. It is unlikely that two completely different types of motion analysing networks with the same apparent function exist in each animal and only one mediates the insect's visual behaviour. Further indication that there is only one network type comes from several neurons which responded directionally to movements of only spots and edges. (An example is given in Fig. 24). These neurons, recorded both in the optic lobes and the circumoesophageal connectives, showed no responses to movements of a striped pattern or even a single stripe. However they showed a complete reversal of response to

the white anterior edge on the left eye or the black anterior edge stimulating the right eye. The preferred direction, in each case, was taken as the direction of movement of a spot to which the neuron responded. These neurons, although obviously different in type and function (see Chap. 4) from the M1 and 2 neurons, still have the same edge reversals. This is further evidence that only one type of motion analysing system exists in the locust visual system and that unusual responses such as those of the M2 neuron described here may be regarded as abnormalities.

A comparison with directional neurons in the bee

The optomotor behaviour of the bee has been studied in some detail (Kunze, 1961) but with most emphasis on particular properties such as colour coding (Kaiser & Liske, 1972) and coding of polarised light (Kirschfeld, 1973). The spectral sensitivity of the directional neurons has been measured (Bishop, 1970; Kaiser, 1972; Menzel, 1973) but almost nothing is known of their other properties. These neurons were examined here to provide a comparison with the locust optomotor neurons.

Recordings were made between contralateral lobula and protocerebrum as described by Kaiser & Bishop (1970). In the preparation used here the abdomen was removed to prevent fluid and brain movement. The isolated head and thorax preparation lives well for several hours and the longevity can be improved by feeding the bee with sugar and honey and placing it in an oxygenated atmosphere for a ½ hour before the experiment. KCl filled (2.5M) glass microelectrodes with resistances above 20MΩ provided the most satisfactory recordings.

Directional neurons similar to those described by Kaiser & Bishop (1970) were isolated. Neurons with preferred direction back across the left eye and forward across the left eye were examined. While most other experiments have dealt with colour coding Kaiser & Bishop (1970) have

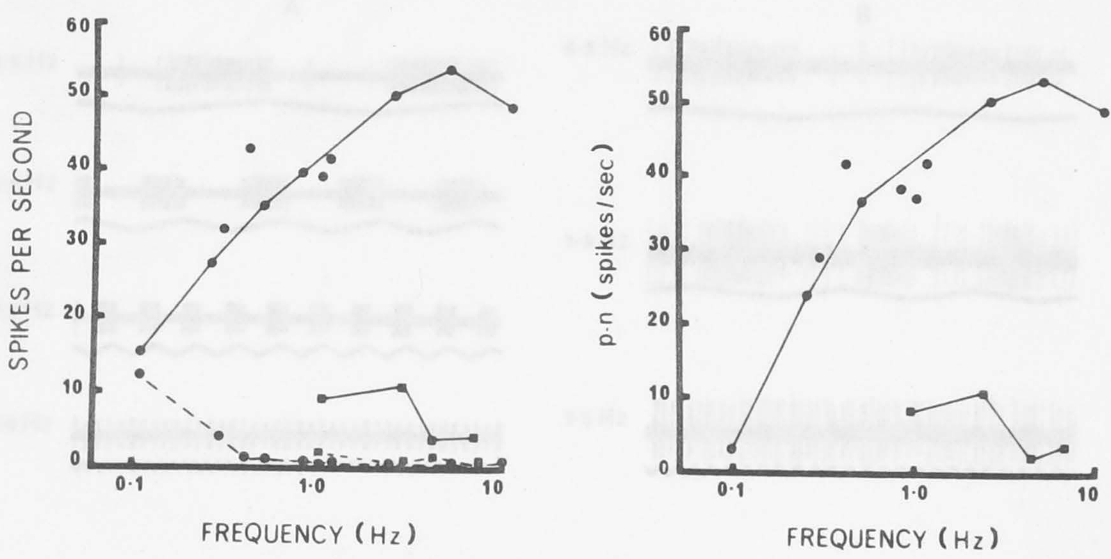


Fig. 34 Responses of bee directional neurons to variations of oscillation frequency (abscissa). Dashed line gives discharge to movements in the null direction. Data was averaged from 5 movements in the preferred and 5 movements in the null direction. Both neurons had back preferred direction across the left eye. Stripe pattern period, 15.8^{o}, oscillation amplitude 15.4^{o}. The curve for one neuron (-●-) resembles that given by Kaiser & Bishop (1970).

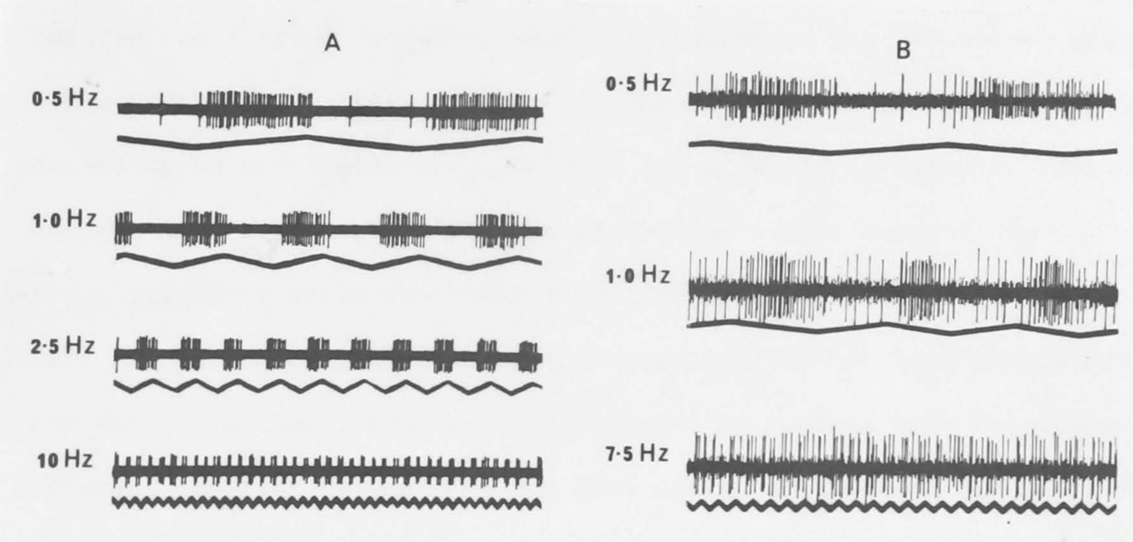


Fig. 35 Comparison of responses of bee and locust directional neurons to oscillations of different frequencies. Lower trace shows pattern movement, up represents back. (A) Responses of the bee directional neuron whose frequency-response plot is given in Fig. 34. Note the almost complete failure to fire during movements in the null direction (forward) and the ability to follow pattern oscillations of 10Hz. Because the latency of the response is longer than each half cycle the response is 180° out of phase. (B) Response of a locust M1 neuron. There is always some discharge during movement in the null direction and inhibition fails during oscillations of 7.5Hz. For both neurons pattern repeat period was 15.8^{o}, oscillation amplitude was 15.4^{o}.

plotted the response against contrast frequency in a constant velocity movement. The comparable plot, p - n against varying oscillation frequencies, is shown in Fig. 34. The response of one neuron provides a very similar curve to that of Kaiser & Bishop (1970). This shows quite clearly that the oscillation frequency used as a parameter for the locust neurons is comparable to contrast frequency. The other neuron shown in Fig. 34 appears to be quite different although its graph is incomplete. The fibre responds much better at lower frequencies and hardly responds (p - n = 2) at the frequency where the other fibre reaches a maximum (c. 5Hz). A fibre responding to lower contrast frequencies has not been previously recorded in the bee. However the existence of neurons with responses to different contrast frequencies was anticipated by Kaiser & Bishop (1970) who thought that the presence of neurons with different but overlapping frequency responses would account for the different optimum contrast frequencies for optomotor behaviour and the directional neurons.

Fig. 35 shows the responses of bee and locust neurons to oscillations of different frequencies. The discharge of the bee neurons to movements in the preferred direction is greater than that of the locust neurons. Also the inhibition elicited by movements in the null direction completely abolishes all firing whereas there is always some discharge in the locust neurons. The different optimum frequencies are easily seen.

The responses of 2 neurons with the higher optimum frequency were recorded while the oscillation amplitude was varied (Fig. 36). In the two curves, measured at different oscillation frequencies, p - n approaches zero at an amplitude of 7 - 8°. This is more than double the amplitude at which the locust M1 neuron loses its graded response. While the large amplitude at which p - n = 0 resembles the locust M1 neuron, the early saturation and the good response to a single stripe of the one neuron (Fig. 36C & D) resemble the M2 neuron. The frequency peak of this neuron

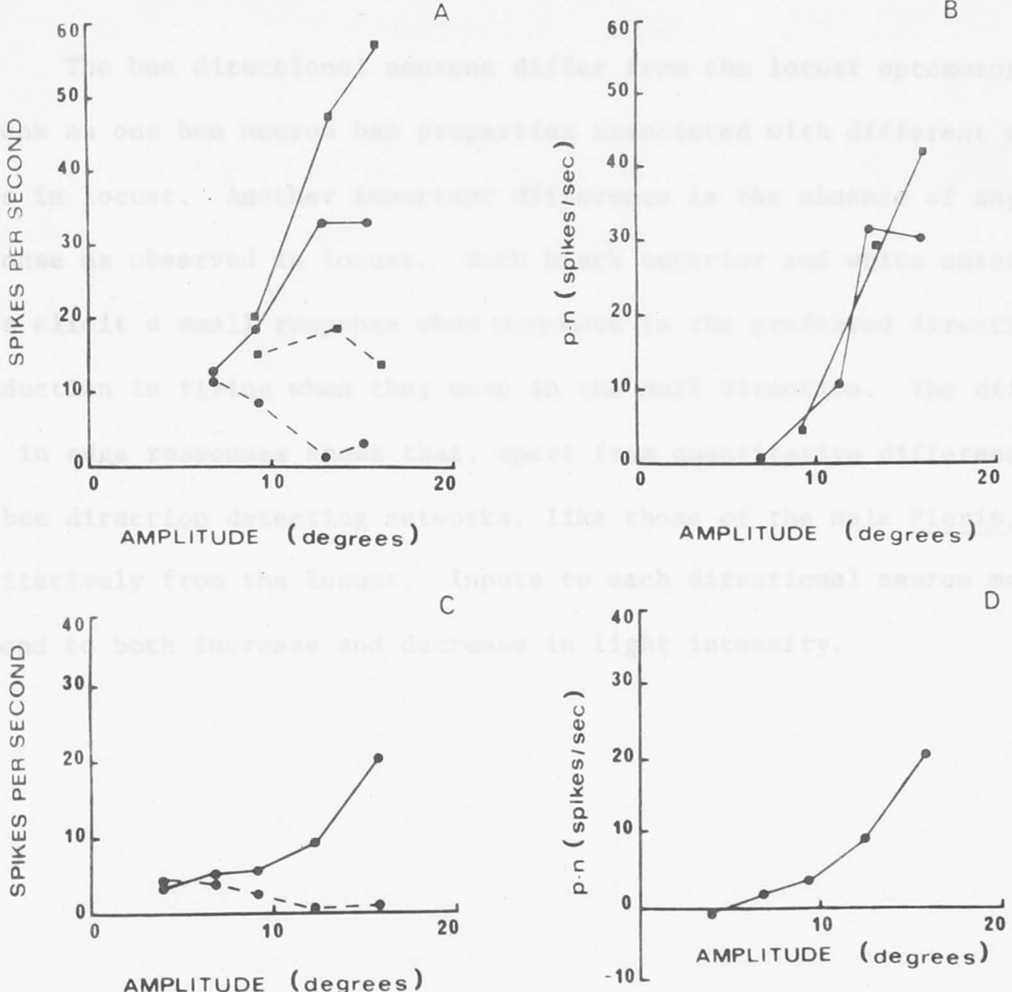


Fig. 36 Responses of bee directional neurons to variation in oscillation amplitude. A,B response to a striped pattern (period 15.8°); C,D response to a single stripe (subtending 7.9°). Data plotted as previously. —●— neuron with back preferred direction across the left eye, data obtained using oscillation frequency of 0.5Hz. This is the neuron shown (-●-) in Fig. 34 where optimum frequency is 5Hz. —■— neuron with forward preferred direction across the left eye, data obtained using oscillation frequency of 2Hz.

(Fig. 34) also resembles that of the M2 neuron.

The bee directional neurons differ from the locust optomotor neurons as one bee neuron has properties associated with different neuron types in locust. Another important difference is the absence of any edge response as observed in locust. Both black anterior and white anterior edges elicit a small response when they move in the preferred direction and a reduction in firing when they move in the null direction. The difference in edge responses shows that, apart from quantitative differences, the bee direction detecting networks, like those of the male _Pieris_, differ qualitatively from the locust. Inputs to each directional neuron must respond to both increase and decrease in light intensity.

CHAPTER 3 Mechanism subserving directional selectivity in the optomotor system

An exhaustive analysis of neuronal mechanisms of directional selectivity requires a knowledge of the properties of both the directional neurons and their nondirectional inputs. This has been achieved in some vertebrate retinae. Here the properties of each neuron group which can contribute to directionally selective ganglion cells have been determined (carp, Kaneko & Hashimoto, 1969; goldfish, Kaneko, 1971; mudpuppy, Werblin & Dowling, 1969; Werblin, 1970). A similar analysis in the insect optic lobe is at present impossible. Approximately 180 different neuron types have been identified histologically, the medullary cartridge alone contains 46 types (Campos-Ortega & Strausfeld, 1972). Many of these fibres have diameters less than 0.3μm and are at present impossible to record from.

Less direct approaches must be used to examine the mechanism of directional selectivity. One method consists of determining the properties of a variety of nondirectional neurons located more distally. But one should keep in mind that similar properties are no proof of connection. A second method is to use the responses of the directional neurons themselves to formulate deductions on the nature of their inputs. This method is followed in this chapter and the optomotor neurons' response is used to define the spatial and temporal interactions occurring between their inputs.

Spatial extent of lateral interactions

Recent analyses of motion detection (Kirschfeld, 1972; Mimura, 1972; McCann, 1973) have used discontinuous or virtual movement produced by combinations of flashes of small light spots. This method of stimulating allows precise location of both the stimulus and many of the activated neurons (e.g. receptors or lamina cartridges, Kirschfeld, 1972) and allows

a rigorous examination of the spread of the lateral interactions. As the M1 neuron does not respond to movements of a spot an attempt was made to utilise this method with flashes illuminating a single stripe. Both M1 and M2 neurons gave unreliable responses. Therefore a full stripe pattern was used in a procedure similar to that of optokinetic memory experiments (Horridge, 1966b). In these experiments the animal sees only stationary stimuli, the displacement occurring during a dark period. This is directly analogous to the light spot experiments except that because of the repetitive nature of the stripe pattern and the large area of the eye which is stimulated, the response both before and after movement is the sum of incoming stimulation.

The stimuli were arranged as in previous experiments with M1 and 2, with the white diffuser (luminance 596 cd/m^2) onto which the stripes were projected by tungsten lamp. A relay controlled shutter and a monitoring photocell were positioned in the light path. Pulse generators controlled the sequence light off, pattern movement, light on. The pattern was always moved in the dark. For these experiments only an area of 30 - 35° in diameter (equal approx. to 200-300 facets) in the centre of the eye was stimulated.

It is obvious that there should be no response when a regular striped pattern is displaced by exactly one wavelength in this stimulus sequence. However in most patterns there are spatial harmonics and subharmonics (McCann & McGinitie, 1965). These components are quite inneffective when the pattern is oscillating (Thorson, 1964, 1966a) but harmonics and subharmonics are of considerable importance in constant velocity or virtual movement experiments. Also any slight irregularities in the pattern, while unimportant in experiments where the pattern is oscillating, are important in constant velocity or virtual movement experiments. Such irregularities must abound in the patterns used here, which

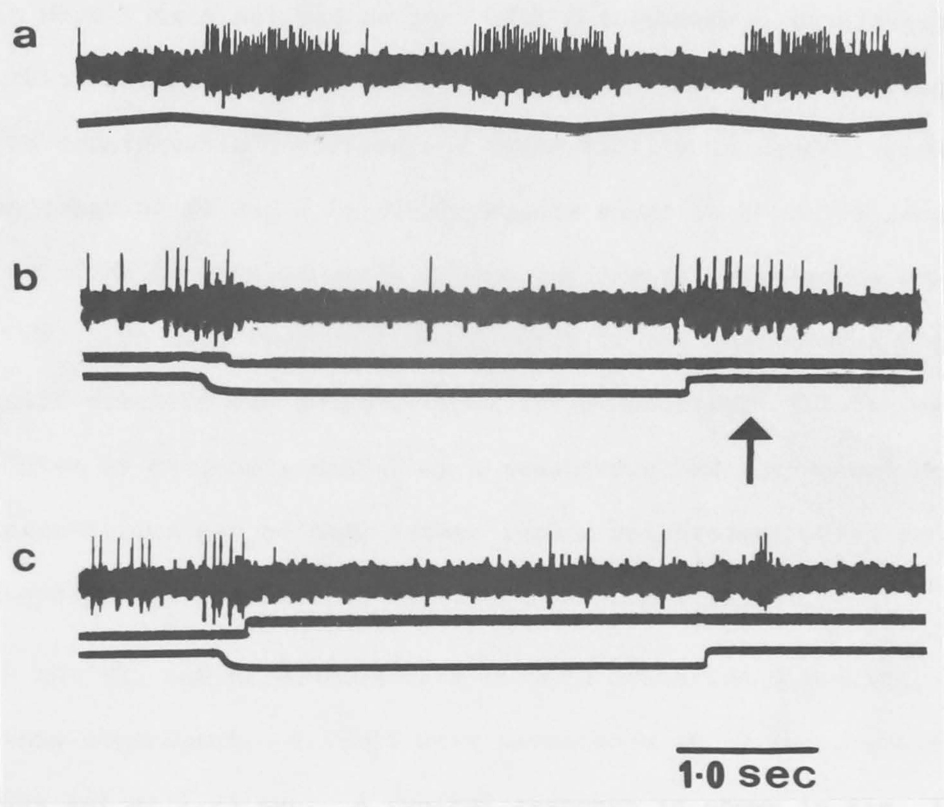
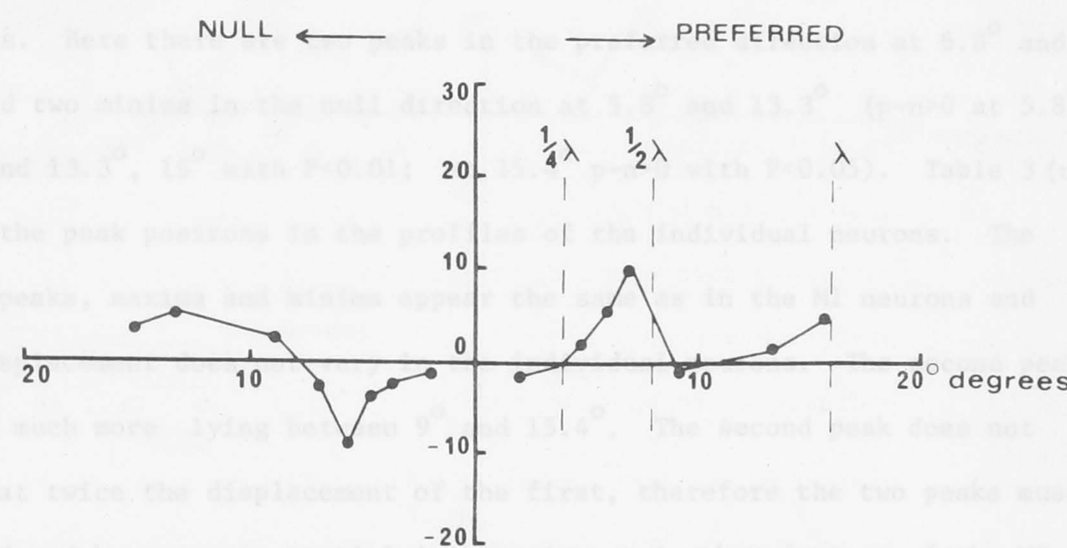


Fig. 37 Response of an M1 neuron to the test sequence used to determine the spatial extent and time course of the lateral interactions in movement analysis. (a) Responses to oscillations of the striped pattern (0.5Hz, amplitude of movement 15.4^{o}). Down on stimulus marker represents forward movement. (b) Responses to a test sequence with movement in the preferred direction. Middle trace represents pattern movement as in (a). Lower trace shows illumination of the diffuser, down indicating OFF. The arrow shows a discharge present only after movements in the preferred direction, it is absent after the pattern has been displaced in the null direction (c).

were photographic reductions of large fields of hand painted stripes. Therefore, for these virtual movement experiments, the stimulus must be regarded, not merely as a striped pattern with a fundamental wavelength, but as a pattern containing a variety of wavelengths and numerous irregularities. The considerable importance of these factors is demonstrated by the large responses of M1 and 2 to displacements equal to ½ the fundamental wavelength and of M2 to displacements of one fundamental wavelength (see Figs. 38 and 39). No such responses would occur if the fundamental frequency was quite dominant and there were no irregularities. The presence of irregularities is extremely useful as a measurement of the actual spread of lateral interactions can be made rather than a measurement which is completely dependent on fundamental wavelength of the stimulus.

Only the M2, and M1 neurons with forward preferred direction, were examined in this experiment. Stimuli were given once in 40 secs. and the dark period was set at 2.25 sec. A typical response is shown in Fig. 37. There is a small discharge at light ON when the pattern is displaced in the preferred direction but no discharge when the pattern is displaced in the null direction. Results were scored by subtracting the total number of spikes in the 2 secs. preceding light OFF from the number of spikes in the 2 secs. after light ON. The same was done with a control (light OFF and ON with no movement) and the control value was subtracted from the test values to give the final data plotted in Figs. 38 and 39. From the inset in Fig. 38 this is $\left[(C+D)-(A+B)\right]_{test} - \left[(C+D)-(A+B)\right]_{control}$. This measure was chosen as it showed the change in firing after light ON from before the test. A control must be used to eliminate ON and OFF effects. The responses of individual neurons showed similar profiles to each other although they were numerically different. For this reason standard deviations were not plotted on the mean curves but 4 x 2 χ^2 tests determined the significance of the p - n difference at each displacement. Fig. 38 shows averaged data

Fig. 38 Spatial extent of lateral interaction between inputs to the M1 neurons with horizontal preferred direction. Abscissa shows pattern displacement during a test sequence (see inset) in the preferred and null direction. The response is scored along the ordinate as Response = $[(C+D) - (A+B)]_{test} - [(C+D) - (A+B)]_{control}$ where C, D are the number of spikes during time C, D as shown in the inset. The test sequence is one where pattern displacement occurs, during the control only the light is switched ON and OFF. p-n = $response_{pref} - response_{null} = [(C+D) - (A+B)]_{pref} - [(C+D) - (A+B)]_{null}$. Also shown is the fundamental wavelength (λ) of the pattern and its fractions $\frac{1}{2}\lambda$ and $\frac{1}{4}\lambda$. Neither the peaks, minima, nor the zero values of the plots coincide with fractions of the wavelength as would be expected if all subharmonics and irregularities were absent. Curves are averaged from the responses of 4 M1 neurons. Dark period was 2.25 secs.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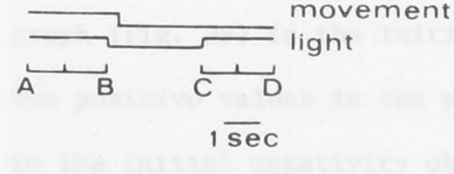
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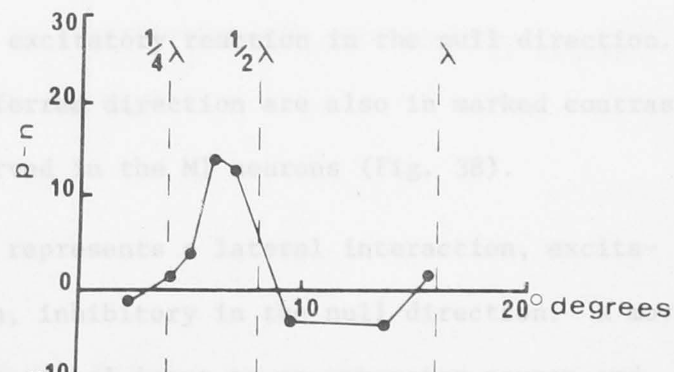
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from 4 M1 neurons as pattern displacement varied. There is a maximum in the preferred direction equivalent to the minimum in the null direction. The peak in the preferred direction occurs at 6.8°, in the null direction the minimum occurs at 5.8° ($p-n>0$ at 5.8° and 6.8° with $P<0.01$).

The responses of the M2 neurons as pattern displacement is varied are shown in Fig. 39 which also gives the mean curve obtained from 4 neurons. Here there are two peaks in the preferred direction at 6.8° and 15° and two minima in the null direction at 5.8° and 13.3° ($p-n>0$ at 5.8°, 6.8° and 13.3°, 15° with $P<0.01$; at 15.4° $p-n>0$ with $P<0.05$). Table 3 (over) gives the peak positons in the profiles of the individual neurons. The first peaks, maxima and minima appear the same as in the M1 neurons and the displacement does not vary in the individual neurons. The second peak varies much more lying between 9° and 15.4°. The second peak does not occur at twice the displacement of the first, therefore the two peaks must be produced by separate spatial interactions. Another feature of the M2 graph (Fig. 39) is the initial excitatory reaction in the null direction. The positive values in the preferred direction are also in marked contrast to the initial negativity observed in the M1 neurons (Fig. 38).

Each peak and minimum represents a lateral interaction, excitatory in the preferred direction, inhibitory in the null direction. A moving point or edge excites a nondirectional input to an optomotor neuron and activity is sent to other nondirectional inputs, probably via collaterals. This activity travels quickly to a fixed destination, it does not propagate slowly in waves. This can be shown by measurements using varying dark periods and pattern displacements and no trend in peak position with time can be seen.

As the M1 neurons show only one peak in each direction the collaterals mediating the lateral interactions can be presumed to extend only to the neighbouring nondirectional input. The double peaks and minima

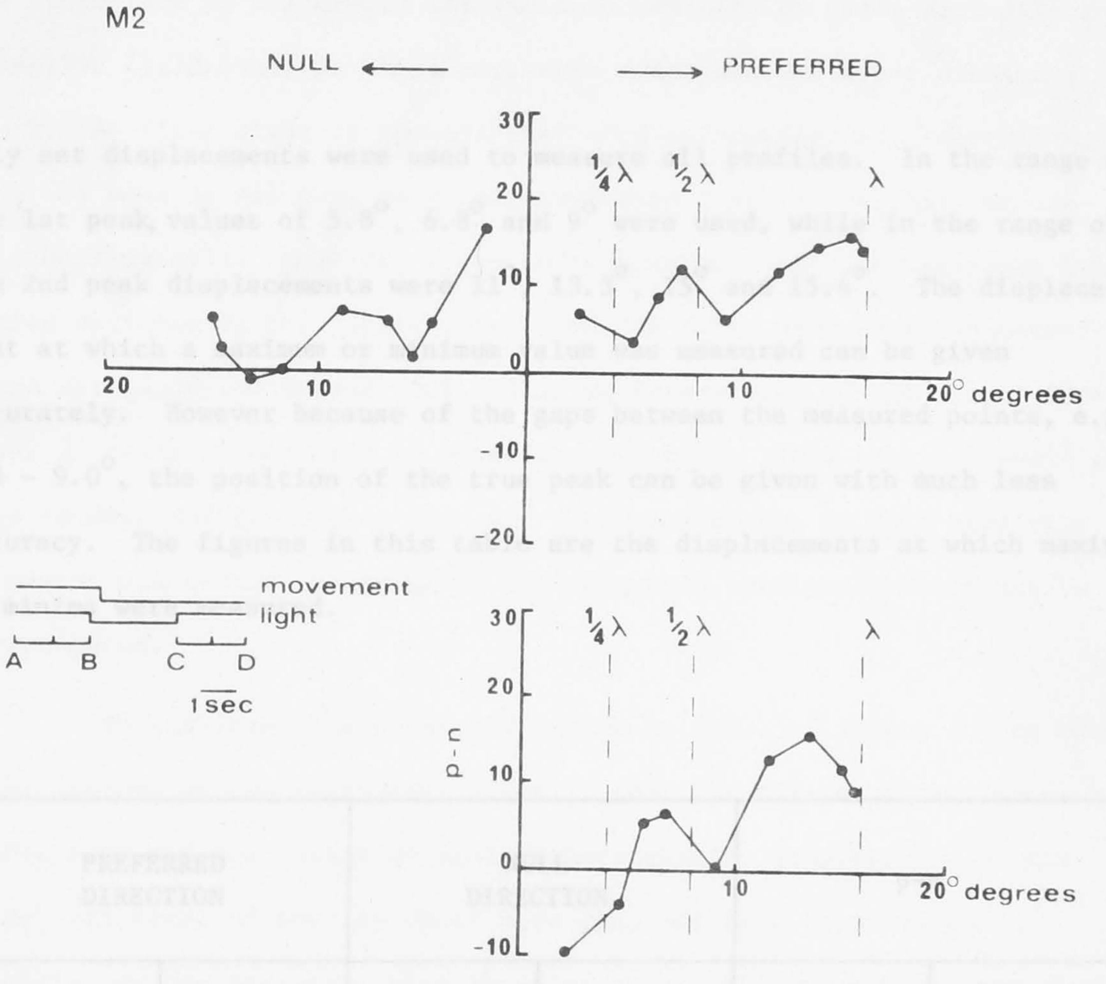


Fig. 39 Spatial extent of the lateral interactions between inputs to the M2 neurons, plotted as in Fig. 38. Note that peaks and minima do not coincide with a displacement equal to the fundamental wavelength of the pattern or its fractions. This is because of the numerous irregularities in the pattern (see text). Curves are averaged from the responses of 4 M2 neurons. Dark duration was set at 2.25 sec. p<n for displacements less than 5° and there are two peaks in both the preferred and null directions.

TABLE 3 Peaks and minima in individual M2 profiles

Only set displacements were used to measure all profiles. In the range of the 1st peak, values of 5.8°, 6.8° and 9° were used, while in the range of the 2nd peak displacements were 11°, 13.3°, 15° and 15.4°. The displacement at which a maximum or minimum value was measured can be given accurately. However because of the gaps between the measured points, e.g. $6.8 - 9.0^\circ$, the position of the true peak can be given with much less accuracy. The figures in this table are the displacements at which maxima or minima were measured.

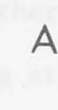
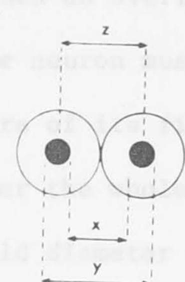
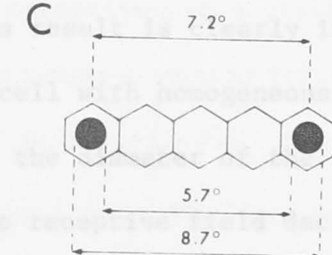
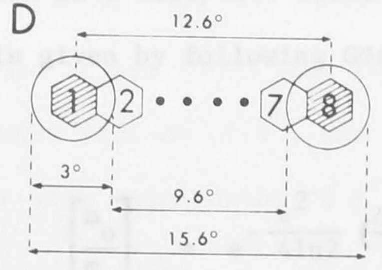
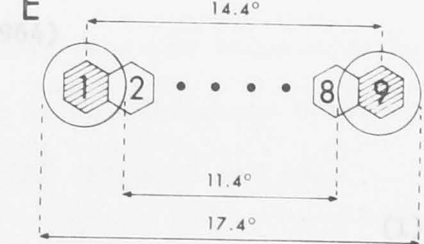
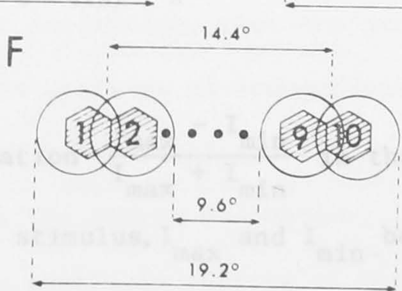
PREFERRED DIRECTION		NULL DIRECTION		p-n	
1st peak	2nd peak	1st peak	2nd peak	1st peak	2nd peak
none	13.3°	5.8°	9.0°	5.8°	13.3°
6.8°	13.3°	5.8°	13.3°	6.8°	13.3°
6.8°	15.8°	6.8°	15.8°	6.8°	15.8°
5.8°	not measured	none	not measured	5.8°	-
not measured	11.6°	not measured	11.6°	-	11.6°

in the M2 graph show no regular spacing with respect to each other and two types of interactions have been implicated. Presumably these two reactions are indicative of collateral interactions mediated by cells with different receptive field sizes or whose excitable areas are different distances apart. At first sight it appears that each interaction is represented by only one peak or minimum, each cell extending a collateral only to one neighbouring cell. However, it is quite possible that a subadjacent interaction mediated by the inputs which form the first peak could be masked by broad spread of the second peak. Also an interaction of the second type (peak 2) could be mediated by subadjacent inputs. This reaction would give rise to peak and minimum at 20 - 40° displacement but as this size displacement was beyond the range of the apparatus this point could not be investigated.

To interpret the peaks and minima in terms of inputs to the optomotor neurons we can postulate, firstly, that the fields of the inputs are homogeneous and that areas of maximum excitability (represented by the peaks) are areas of overlap where more than one cell is stimulated. Secondly, we can postulate that there is no significant overlap and that areas of maximum excitability are the centres of receptive fields with rapidly decreasing excitability towards the edges or even an inhibitory surround. In either case we must assume that each nondirectional input is the same as its neighbour.

If we assume that overlapping areas of different receptive fields make up the peaks then it is clear that the width of the peak must represent the width of 2 overlaps, with the maximum extent of the overlap being defined by the maximum displacement under the peak (see Fig. 40A). In the case of the first M2 or the M1 peak this maximum value would be between displacements of 7 - 9°. This would mean that the nondirectional inputs have homogeneous fields with a 7 - 9° diameter. It was predicted (Fig. 32)

Fig. 40 Interpretations of Figs. 38 and 39. A. The relation between measurements of the peaks in Figs. 38 and 39, and possible receptive fields of the interacting neurons. Shown are neurons with nonhomogeneous fields with excitable centres. The interaction occurs after stimulation of these excitable centres. The alternative is an interaction between neurons with homogeneous receptive fields where overlapping areas must be stimulated for the interaction to occur. B,C. Possible extrapolations from the M1 and first M2 peak to the ommatidial array. C shows a closer fit to the experimental data. D-F. Possible extrapolations from the 2nd M2 peak to the ommatidial array. D and E fit the data equally well although both show some disagreement with it.

A
z
x
y
B
5.4°
3.9°
1.5
6.9°
C
7.2°
5.7°
8.7°
D
12.6°
1
2
7
8
3°
9.6°
15.6°
E
14.4°
1
2
8
9
11.4°
17.4°
F
14.4°
1
2
9
10
9.6°
19.2°

that these cells are simple ON or OFF cells and that they respond only to the intensity modulation caused by movements of a striped pattern. The narrowness of the peaks indicates that a response is elicited only when adjacent overlapping areas are stimulated, not when an overlap and a field centre are stimulated. In other words, the neuron must discriminate between intensity changes occurring at the borders of its field but must be insensitive to intensity changes or movements over the whole field. Consider a black area moving across a receptive field diameter 8°, overlapped by its neighbours on each side for a maximum extent of 2°. As the black area moves across the overlap it alters the intensity over approximately ¼ of the field. A movement from the edge of the field to the centre would alter the intensity over ½ the field, yet this is not effective (no response at 4° in Figs. 38 and 39). This result is clearly incompatible with our assumption of simple ON or OFF cell with homogeneous fields. Furthermore, as wavelenth (λ) approaches the diameter of the receptive field (Δθ) the contrast modulation in the receptive field decreases. The modulation in a receptive field for a sinusoidally modulated intensity change is given by following Götz (1964)

$$\left[\frac{m_o}{m_i}\right]_s = e^{-\frac{\pi^2}{4\ln 2}\left(\frac{\Delta\theta}{\lambda}\right)^2} \qquad (1)$$

where m_o is the modulation $\frac{I_{max} - I_{min}}{I_{max} + I_{min}}$ in the receptive field. m_i is the modulation of the stimulus, I_{max} and I_{min} being the maximum and minimum luminances of the pattern. For a square wave stimulus such as a pattern of the black and white stripes with sharp edges Equ. 1 becomes

$$\left[\frac{m_o}{m_i}\right]_r = \frac{4}{\pi}\sum_{k=1}^{\infty}\frac{\sin\frac{k\pi}{2}}{k}\cdot h_s^{k2}(\lambda;\Delta\theta) \qquad (2)$$

where $$h_s^{k2}(\lambda;\Delta\theta) = h_s(\frac{\lambda}{k};\Delta\theta) \qquad (3)$$

and $$h_s(\lambda;\Delta\theta) = \left[\frac{m_o}{m_i}\right]_s \qquad (4)$$

and k is the kth wave with wavelength $\frac{\lambda}{k}$ in the Fourier analysis of the frequencies in the square wave. With a receptive field diameter of $7 - 9^o$, say 8°, the neuron should not be able to respond to movements of stripes with wavelengths smaller than 5.6^o, $\frac{\Delta\theta}{\lambda} = 0.7$, $\left[\frac{m_o}{m_i}\right]_r \doteqdot 0$ and response should increase until $\left[\frac{m_o}{m_i}\right]_r = 1$ when $\frac{\lambda}{\Delta\theta} = 5.1$ and $\lambda = 40.8^o$. The behavioural data in Fig. 5 shows that the response diminishes with wavelengths greater than 45°. Also it was found that the locust responds behaviourally to patterns with repeat periods of 4°, and there is no difference between responses to patterns with wavelengths of 6° and 25° (Figs. 3 and 4).

As the first assumption, that the peaks in Fig. 38 and 39 represent distances between overlaps of homogeneous receptive fields, is incompatible with both behavioural and electrophysiological data, the alternative is to use the second assumption, i.e. that the peaks represent the distances between excitable centres of nonhomogeneous receptive fields. As shown in Fig. 40 the width of the peak will equal the distance between the outer borders of two excitable areas with the maximum of the peak equalling the separation of the two excitable centres. For example, the width of the M1 and first M2 peak is c. $3 - 4^o$ (displacement 5° to a

displacement of 7 - 9°). Therefore the extent of the excitable area is 1.5 - 2.0^{o}. The peak maximum occurs at a displacement of 5.8^{o} - 6.8^{o}, thus the separation is c. 6.3^{o} from centre of the excitable areas. A similar interpretation of the second M2 peak shows that there are two excitable areas of diameter 2.5 - 4°, mean separation of 13.3 - 15°. This interpretation using excitable centres overcomes the objections to the homogeneous fields. The small diameter of the excitable areas means that any small movement will still cause a stimulus to move over an appreciable area of both types of centre, e.g. the 2° movement traversing ¼ of an 8° receptive field would now pass across the entire area of the small excitable centre and across more than ½ of the large centre. Also the smaller diameters of the centres would allow them to achieve maximum contrast modulation to shorter wavelength patterns. Maximum contrast modulation in the smaller areas would be achieved with a stripe pattern whose repeat period was 8°, the larger centres would reach maximum modulation with wavelengths from 15.5^{o}. Contrast modulation on both areas would be greater than 60% with pattern wavelength of 6°. The close agreement between excitable centre size and retinula acceptance angles (light adapted, 3.4^{o} in Schistocerca, Tunstall & Horridge, 1967) has two important implications. Firstly, if the sampling station size is close to the field size of the receptors then the properties of the receptors and the optics of the eye become the limiting factors of the response. This means that there is no further loss of information. Second, if the sampling station sizes are close to receptor field sizes, it is possible that the sampling station neurons occur in individual cartridges, either lamina or medulla and are relatively low order and simple cells.

The possible arrangement of excitable areas with respect to the ommatidial array is shown in Fig. 40B-F. The interommatidial angle between adjacent facets in the horizontal rows in the centre region of the

eye measured from cross sections is $1.8 \pm 0.3^{\circ}$. The first M2 and the M1 peak is best fitted by Fig. 40C where the inputs are sampled from every fifth ommatidium.

A similar mechanism has been found in one instance in the fly where the interacting inputs to the movement detectors are derived from subadjacent lamina cartridges (Kirschfeld, 1972). In the hexagonal array this corresponds to cartridges in every fifth row. Such a mechanism ensures a response only to movements over larger areas of the eye, not to small external movements. When the whole eye is stimulated, as it would be during a movement of the animal, the amount of stimulation received by the pairs of nonadjacent inputs would be equal to that received by pairs of adjacent inputs.

The diameter of each of these ommatidial fields is slightly smaller than that of the retinula cell acceptance angle, pointing to the present of a lateral inhibition, for which there is ample evidence in the lamina of the fly (Zettler & Järvilehto, 1972). Also the sustaining units recorded in the intermediate optic chiasma of the fly by Arnett (1971) show clear signs of lateral inhibition. The neurons mediating the M1 and first M2 peak appear to have a similar field to that of the Arnett sustaining units with a central excitable region surrounded by areas contributing an inhibitory interaction. The Arnett sustaining units have already been implicated as the inputs to both fly tracking neurons (Mimura, 1972) and fly optomotor neurons (McCann, 1973). However it must be remembered that the M1 neurons must receive inputs from ON cells and the M2 neurons must receive inputs from OFF cells, as was shown by the edge responses.

The initial negativity in both preferred and null direction for M1 neurons (Fig. 38) suggests the presence of symmetrical lateral inhibition. This too would account for the consistent 1° difference between the preferred and null peaks; addition of a symmetrical early negative peak

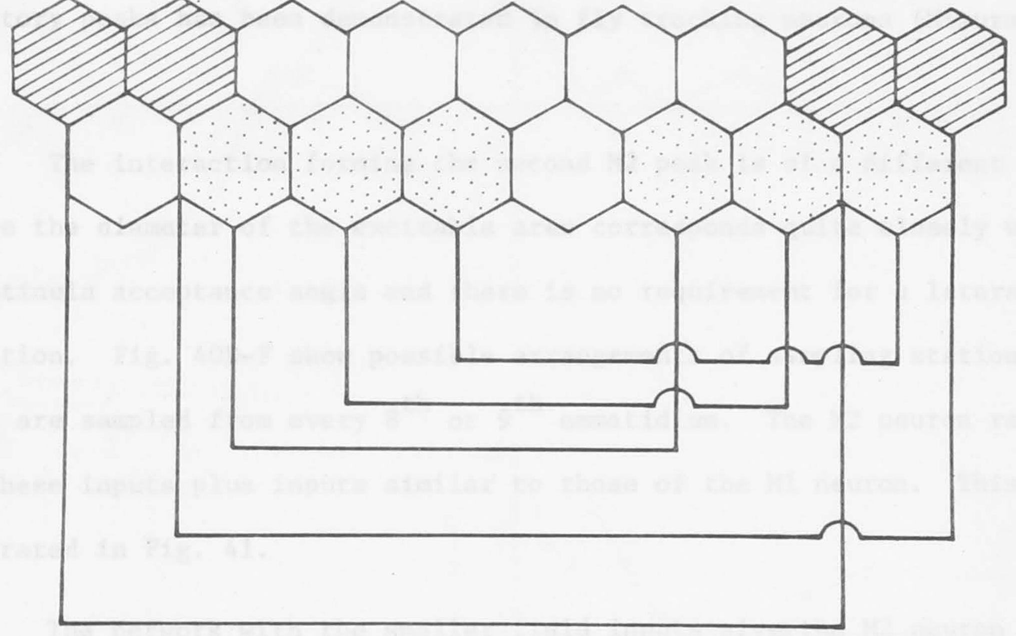


Fig. 41 Schematic illustration of the arrangement of interacting sampling stations of both M1 and M2 on the ommatidial array. Linked or interacting sampling stations are filled and their linkage shown schematically. Also shown schematically is the fact that every omma contributes to a sampling station which interacts with every 5th, or 8th or 9th sampling station along the row. Shaded areas are the smaller fields of the neurons mediating the M1 and first M2 peak. Hatched areas are the larger fields of the neurons mediating the 2nd M2 peak.

to a negative null peak would produce an earlier minimum while subtraction of an early negative peak from the positive preferred peak would be likely to increase the displacement at which a maximum occurred. A similar superimposition of symmetrical inhibitory peaks on asymmetric excitatory peaks has been demonstrated in fly tracking neurons (Mimura, 1972).

The interaction forming the second M2 peak is of a different nature as here the diameter of the excitable area corresponds quite closely with the retinula acceptance angle and there is no requirement for a lateral inhibition. Fig. 40D-F show possible arrangements of sampling stations. Inputs are sampled from every 8th or 9th ommatidium. The M2 neuron receives both these inputs plus inputs similar to those of the M1 neuron. This is illustrated in Fig. 41.

The network with the smaller field inputs gives the M2 neuron its broad frequency response while the greater distance between the larger field inputs would give an optimum in the higher velocity range (see below). The greater distance between the inputs and their larger field diameter would render this network less responsive to small movements than the more closely spaced input network. The difference between M1 and 2 thresholds can no longer be attributed to different inputs. The initial negativity of the M1 neuron is replaced by an initial positivity in the M2 neuron particularly in the null direction (2°, 4.8^o, $n>p>0$, $P<0.01$). It is possible that this is an amplification increasing both the excitability of the next sampling station and its response to very small amounts of stimulation. This process may partly account for the early saturation of M2 responses with increase in amplitude of movement. Also, this amplification may be the basis of the edge reversal response. Here the movement of the white anterior edge in the null direction provokes a response although only the first stimulated OFF channels should fire (see Chaps. 1 and 2).

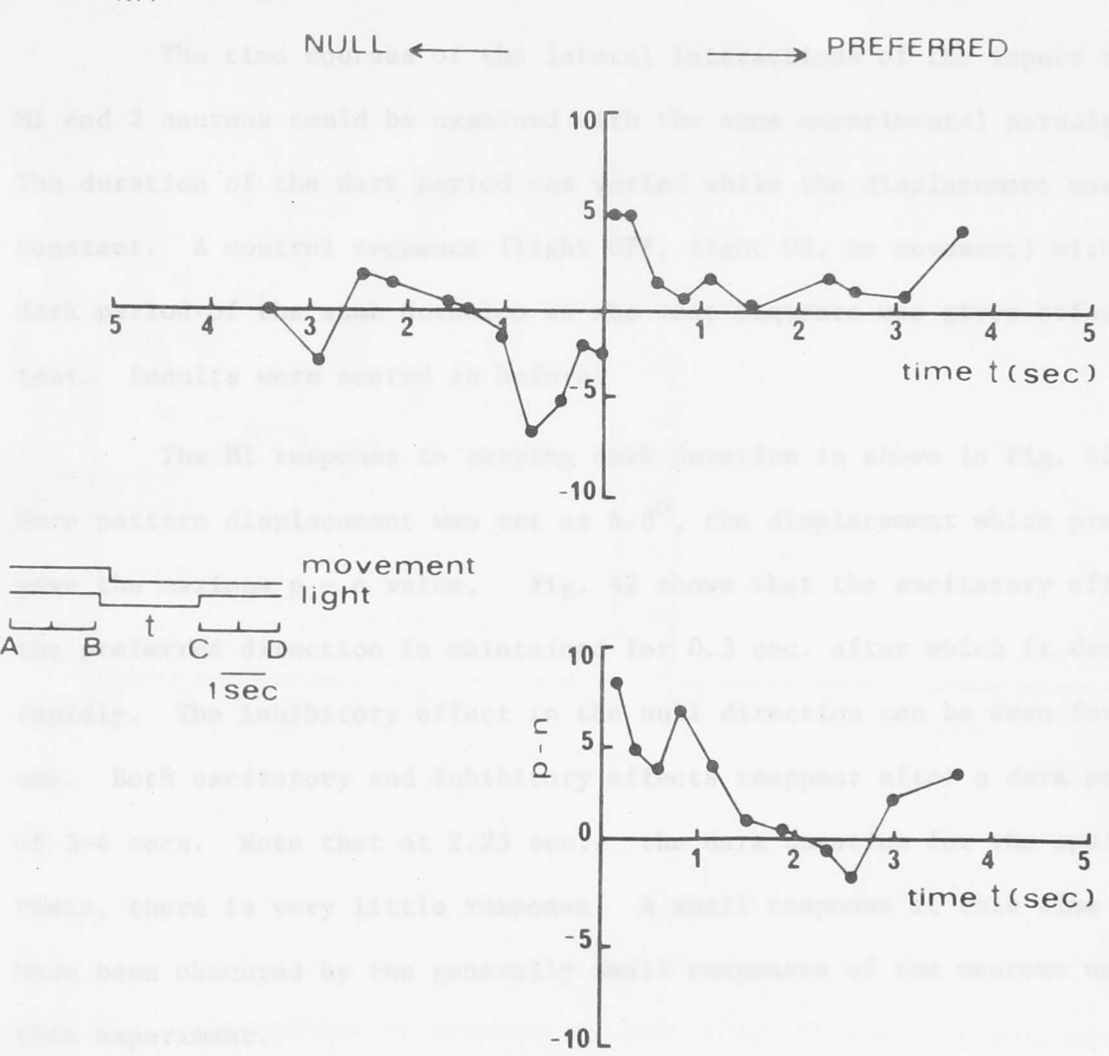


Fig. 42 Time course of the lateral interactions between M1 inputs. Plots as in Fig. 38, but duration of dark period is plotted along the abscissa (see inset). Each test value was compared with a control of the same dark duration. Displacement was set at 6.8^{o} both in the preferred and null directions. The upper plot is averaged from the responses of 2 M1 neurons, the lower plot includes responses from a 3rd neuron from which only p-n data was obtained.

Time course of lateral interactions of the M1 neuron

The time courses of the lateral interactions of the inputs to the M1 and 2 neurons could be examined with the same experimental paradigm. The duration of the dark period was varied while the displacement was held constant. A control sequence (light OFF, light ON, no movement) with a dark period of the same duration as the test sequence was given before each test. Results were scored as before.

The M1 response to varying dark duration is shown in Fig. 42. Here pattern displacement was set at 6.8^{o}, the displacement which previously gave the maximum p - n value. Fig. 42 shows that the excitatory effect in the preferred direction is maintained for 0.3 sec. after which it decays rapidly. The inhibitory effect in the null direction can be seen for 0.8 sec. Both excitatory and inhibitory effects reappear after a dark period of 3-4 secs. Note that at 2.25 sec., the dark duration for the spatial tests, there is very little response. A small response at this time may have been obscured by the generally small responses of the neurons used in this experiment.

The inhibitory reaction suggests that optimum null inhibition is elicited by movements with velocities between 4.4^{o}/sec. and 27.2^{o}/sec. Comparison with the frequency responses of the M1 neurons (Fig. 43A) shows that while null inhibition does diminish with fast movements (faster than 45°/sec.) the inhibition is still well maintained for movements as slow as 0.8^{o}/sec. (Fig. 43A, 0.025Hz, amplit. 15.4^{o}). The excitatory reaction in the preferred direction (Fig. 42) indicates that M1 neurons should respond only to movements faster than 21°/sec. Again, the duration of the lateral interaction fails to explain the response of neurons showing sustained discharges to movements in the preferred direction as slow as 0.8^{o}/sec. (Fig. 43A). Thus the time course of the lateral interaction mediated by

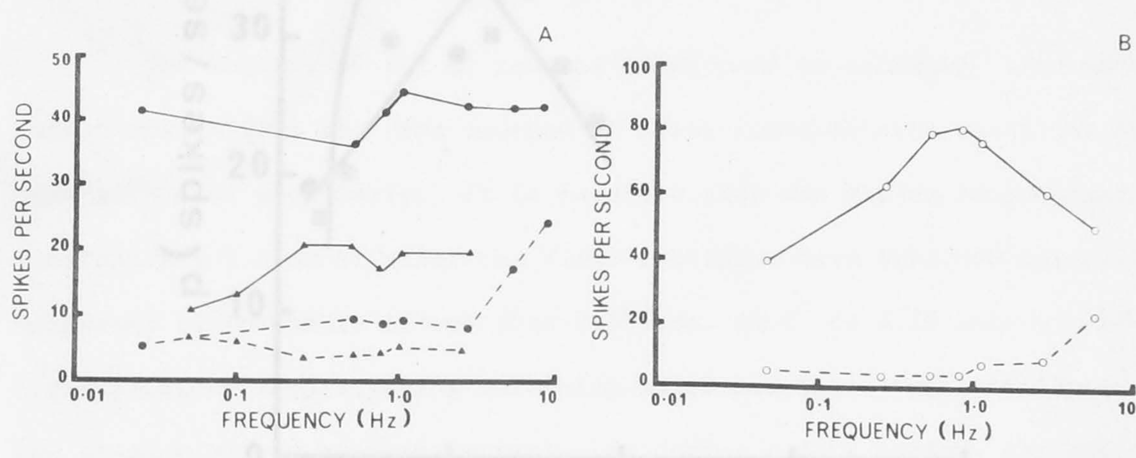


Fig. 43 Dependence of response of individual M1 and 2 neurons on oscillation frequency. Solid lines show discharges to movements in the preferred direction, dashed lines show discharges to movements in the null direction. A. Two M1 neurons (closed symbols); B. an M2 neuron (open symbols). The p-n curves of these neurons are given in Fig. 27A,B. Pattern wavelength is 15.8°, oscillation amplitude 15.4°, each point is the average of 5 movements.

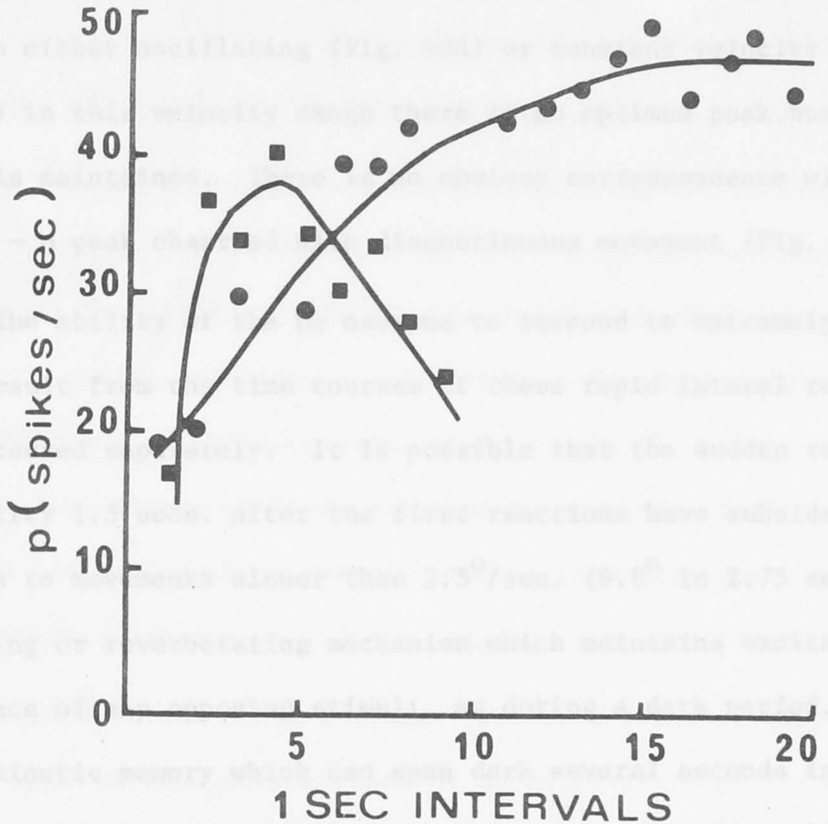


Fig. 44 The firing rate of M1 neurons (ordinate) throughout a slow movement in the preferred direction sampled over consecutive 1 second intervals (abscissa). One M1 neuron (-●-) responded well to slow movements with a gradual increase in firing rate over 14 seconds (for frequency response see closed circles, Fig. 43A). The movement here is a ½ cycle of an oscillation 0.025Hz, approx. angular velocity 0.77^{o}/sec., movement amplitude 15.4^{o}. The other neuron (-■-) did not respond well to slow movements (for frequency response see closed triangles, Fig. 43A). Shown here is a response to a ½ cycle of an oscillation 0.01Hz, approx. angular velocity 1.5^{o}/sec., amplitude of movement is 15.4^{o}. The firing rate here rises almost to a maximum after one second and declines quickly.

the nondirectional inputs can account only for the response to fast and medium velocity movements but not for the response to slow movements. Even with either oscillating (Fig. 43A) or constant velocity stimuli (Fig. 28) in this velocity range there is no optimum peak but a broad plateau is maintained. There is no obvious correspondence with the null or the p - n peak observed with discontinuous movement (Fig. 42).

The ability of the M1 neurons to respond to extremely slow movements cannot result from the time courses of these rapid lateral reactions but must be caused separately. It is possible that the sudden reappearance of excitability 1.5 secs. after the first reactions have subsided may allow responses to movements slower than 2.5^{o}/sec. (6.8^{o} in 2.75 secs.). Also a recycling or reverberating mechanism which maintains excitability in the absence of any opposing stimuli, as during a dark period, may account for optokinetic memory which can span dark several seconds in the locust (Horridge, 1966c) and up to 20 minutes in crabs (Horridge, 1968b). The mechanism of this type of oscillator is not understood but a similar situation occurs in the flight system where a single stimulus can generate activity in the motor neurons at 40msec. intervals. At present, the only explanation of these long delays is the intervention of many interneuron reverberating circuits (Burrows, 1973).

A second mechanism enabling the neuron to respond to slow movements is one independent of the lateral interactions. During a continuous slow movement the plots of the number of spikes/consecutive time interval show considerable variation during the movement. Fig. 44 shows such a plot for the neurons illustrated in Fig. 43A. The neuron which responds well to slow movements shows a gradual increase in firing rate over 14 secs. until a plateau firing rate is reached. The neuron which responds poorly to slow movements fires rapidly at the onset of the response, after the latent period shown in the first count, but the firing rate quickly declines. A

similar build up of firing rate has been reported in the moth directional neurons (Collett & Blest, 1966) and in lobster optokinetic motor fibres (Wiersma & Yanagisawa, 1971). It is absent in neurons responding only to fast movements as in the fly (Bishop & Keehn, 1967).

The gradual build up of activity in the one neuron suggests the presence of facilitation to maintain an otherwise weak response. In the absence of this facilitation, the firing, elicited by initial stimulation of the inputs, quickly declines. This facilitation must depend on the temporal patterning of incoming stimulation to the M1 neuron, otherwise responses to fast movements would be greatly elevated. Such a selective facilitation has already been demonstrated in some crustacean neuromuscular systems (Wiersma, 1970).

In summary, the broad frequency response range of the M1 neuron may be made up from the contributions of three separate processes. Firstly, the fast transmission and the duration of the lateral interactions between nondirectional inputs allow a good response to fast and medium velocity movements. Secondly, over long periods a reverberating mechanism may enhance the excitability, either of the inputs or of the M1 neuron, to allow a response to very slow movements. Thirdly, during very slow movements a high firing rate can be maintained by a selective facilitation probably within the M1 neuron itself.

The M1 neuron, to code for magnitude of stimulation as described in Chap. 2, must be able to respond quickly to any alteration in direction or magnitude of stimuli whose velocities may vary over a wide range. If the responses to slow movements were mediated by long lasting lateral interactions any sudden change, for instance in direction, would result in a competition for many seconds between incoming stimuli and previous excitation or inhibition. When the lateral excitation or inhibition are brief a quick change from one to the other is possible while the reactions for the

response to slow movements come into play only during the slow movements themselves.

Time course of lateral interactions in the M2 neuron

For the M2 neurons the displacement of the pattern was set at 13.3^{o} to coincide with the 2nd spatial peak, and the time course of the interaction contributing to this peak was measured. The variation in M2 response with dark period is shown in Fig. 45. Unlike the M1 neuron the effect in the preferred direction is quite different from that in the null direction. The large excitatory effect is most predominant in the first 0.75 sec. with a rapid decay which is complete in 2.0 secs. The inhibitory reaction elicited by movements in the null direction is smaller but longer lasting, the major depression beginning after 0.5 secs. and lasting for 2.5 secs.

The second excitatory peak at 0.4 secs., equivalent to a velocity of 33.2^{o}/sec., compares well with the 25 - 32°/sec. optimum velocity derived from oscillation (Figs. 27 and 43B) and constant velocity experiments (see below). The rapid decay of the excitation corresponds with decline in response to slower movements and the lowered excitability between 100 and 400msec. accounts for the decline in response to movements faster than 32°/sec. Neither the first excitatory peak (corresponding to a velocity of 133°/sec.) nor the first inhibitory minimum (equivalent to velocities between 30 - 65°/sec.) seem to have behavioural correlates. The second null minimum corresponds well with continuous movement responses which show a similar inhibition over a broad range of velocities. Null inhibition begins to diminish at velocities greater than 30°/sec. (Fig. 43B) which fits well with the late onset of the inhibitory reaction (0.5sec. with 13.3^{o} displacement is equivalent to 26.6^{o}/sec.). The inhibitory interaction between small field cells has a similar upper velocity limit and both

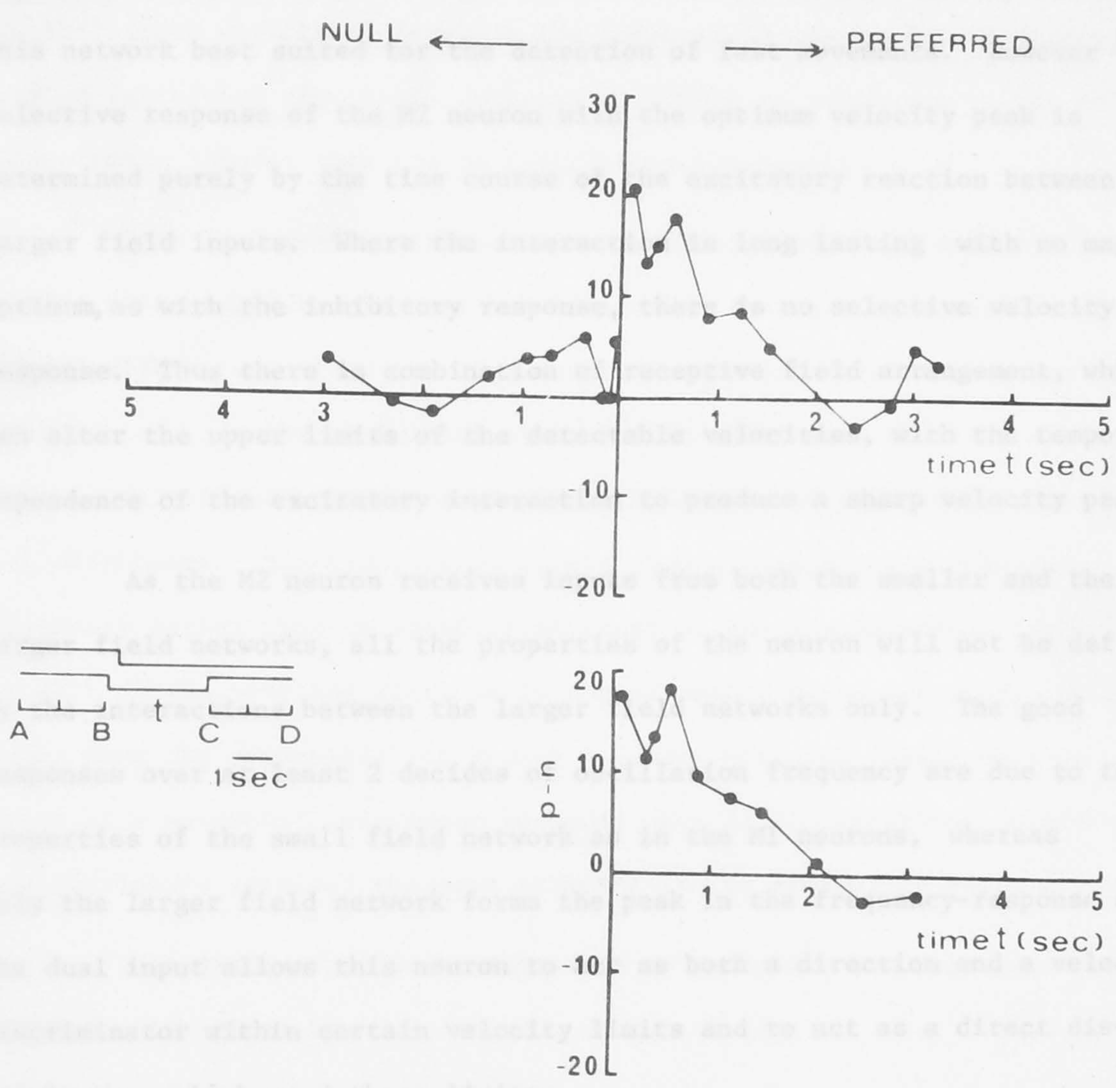


Fig. 45 Time course of the lateral interactions between the neurons mediating the 2nd M2 spatial peak. Plotted exactly as in Fig. 42. Pattern displacement was 13.3^{o} in both preferred and null direction. Each curve is averaged from the response of 2 M2 neurons.

networks fail together.

The large separation (12.6 - 14.4^{o}, see above) of the larger field inputs to the M2 neuron increases the maximum detectable velocity and makes this network best suited for the detection of fast movements. However the selective response of the M2 neuron with the optimum velocity peak is determined purely by the time course of the excitatory reaction between the larger field inputs. Where the interaction is long lasting with no marked optimum, as with the inhibitory response, there is no selective velocity response. Thus there is combination of receptive field arrangement, which can alter the upper limits of the detectable velocities, with the temporal dependence of the excitatory interaction to produce a sharp velocity peak.

As the M2 neuron receives inputs from both the smaller and the larger field networks, all the properties of the neuron will not be defined by the interactions between the larger field networks only. The good responses over at least 2 decides of oscillation frequency are due to the properties of the small field network as in the M1 neurons, whereas only the larger field network forms the peak in the frequency-response curve. The dual input allows this neuron to act as both a direction and a velocity discriminator within certain velocity limits and to act as a direct discriminator well beyond these limits.

Tests of the optomotor model

The basic difference between the model proposed for the locust optomotor system and the correlator models previously postulated for fly and bettle (see Reichardt, 1969 for review) is the use here of an asymmetric Barlow & Levick (1965) network. The asymmetric networks were required to explain the asymmetric edge responses, the different responses to the white anterior and to the black anterior edge, which were found both in the behaviour (Chap. 1) and in the optomotor neurons (Chap. 2). The spatial

plots of the lateral interactions of inputs to the optomotor neurons revealed excitation in the preferred direction and inhibition in the null direction. The obvious explanation is the presence of two Barlow & Levick networks, an excitatory network to increase the response in the preferred direction and an inhibitory network to decrease discharge to movements in the null direction. However this can be tested more rigorously.

Some fundamental difference between correlator and Barlow & Levick motion detecting networks must be utilised so that a simple experiment can distinguish between them and thus determine the nature of the system under examination. In the correlator or symmetric model each sampling station continuously correlates the light flux falling on it with that falling on its neighbours. The symmetrical models show a dependence on contrast frequency rather than on speed of movement as the instantaneous light flux on each of the sampling stations is the parameter being measured. On the other hand the asymmetric or Barlow & Levick networks depend only on the speed of a movement: any input responds only if its neighbour on one side has previously received the same stimulus (in an excitatory network).

This difference can be expressed as follows. The correlator model response R is given by

$$R = \tfrac{1}{2} \int_{-\alpha}^{+\alpha} Y_D Y_D' \left[Y_F . Y_H' - Y_F' . Y_H \right] S(\omega) \exp\left[(i\omega\Delta t)\right] d\omega \qquad (5)$$

(after Reichardt, 1969) where $Y_D Y_F Y_H$ are the transfer functions of the filters of the model related to the weighting functions of the time domain by Fourier transforms; Y' designates the conjugated complex of Y. $S(\omega)$ is the spectral density of G(t) where G(t) is a fluctuating light flux whose average value is 0, i is $\sqrt{-1}$ and $\omega = \frac{2\Pi}{\lambda} . w$, λ is pattern wavelength and w is angular velocity of the movement. This can be expressed by

$$R = f(\bar{I}, \frac{w}{\lambda}, m_o) g(\lambda;\Delta\phi) \qquad (6)$$

where $g(\lambda;\Delta\phi)$ is the interference function created by the spacing of the ommatidia, $\Delta\phi$ being the interommatidial angle. If $\lambda >> \Delta\theta, \lambda > 2\Delta\phi$ (where $\Delta\theta$ is the diameter of the sampling station field) then $0 < g \leq 1$. Therefore if $\bar{I}$ and m_o are constant

$$R = f(\frac{w}{\lambda}) \qquad (7)$$

Therefore the correlator model depends on contrast frequency.

The general Barlow & Levick model is described easily in terms of its logic (Zorkoczy, 1966). An excitatory network with inputs derived from OFF cells only (as in the M2 neuron) is modelled as follows.

Let a_p $p=1,2,3,....n$ be a set of equivalent binary variables of inputs. An OFF response is given by

$$T(a) = a_p^* \times \overline{a_{p+1}} \qquad (8)$$

where x is logical disjunction which gives the value 1 at time t if and only if the variables it connects each have the value 1 at time t, otherwise it gives 0.

$\bar{a}_p$ is a negation which gives 1 at time t if and only if a_p has the value 0 at time t, otherwise it gives 0.

a_p^* gives the value 1 at time t if and only if a_p had the value 1 at time t-1, otherwise it gives 0 (delayed by unit time).

With 2 inputs a_p and a_{p+1}, if at time, a_{p+1} equals 0 (or turns OFF) if and only if a_p equals 0 at time t-1, we have formed an asymmetric excitatory reaction (Ma_p), with

$$M(a_p) = T(a_p^*) \times T(a_{p+1}) \qquad (9)$$

When the reaction is extended over the whole set of a_p we have

$$M_s(a_p) = \sum_{p=1}^{n} T(a_p)^* \times T(a_{p+1}) \quad (10)$$

and this defines a complete Barlow & Levick network. The main operators are delay, contrast and summation. This can be expressed as

$$R = f(\Delta t; m_o; \Sigma) \quad (11)$$

where Δt is the delay required between stimulating adjacent inputs. Contrast is independent of velocity (Equs. 4-7) and if we consider the size of the individual reactions as we did in Equs. 5-7 then

$$R = f(\Delta t) = f(w) \quad (12)$$

where w is the angular velocity and there is a constant distance between sampling stations.

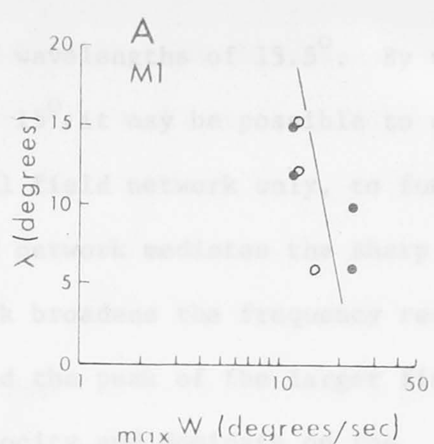
Thus the two networks can be distinguished on the basis of their different dependences, the correlator model on contrast frequency and the asymmetric network on velocity. It is relatively simple to discover the nature of the movement network by experimentally determining whether there is a functional dependence on contrast frequency or velocity. This dependence can be shown by finding which velocity elicits the maximum response at each pattern wavelength and plotting $_{max}w$ against λ. If there is a dependence only on velocity the result should be a line, w = const. whereas if there is a dependence on contrast frequency the result should be $\frac{w}{\lambda}$ = const.

The M1 and 2 neurons were tested with the constant velocity apparatus (see Chap. 2). Only lower wavelengths could be used as very

broad stripes begin to elicit sequential edge responses.

The M1 neuron was tested first, as it was previously shown to receive only one type of input. The w,λ plot for M1 neurons is shown in Fig. 46A. The w on λ regression line has a slope $\frac{w}{\lambda} = -0.56$. This is not compatible with correlator predictions as a zero or negative term for contrast frequency is meaningless. (The reaction would be optimum at $_{max}w = 0$ at $\lambda = 45^{o}$). The result is clearly that predicted for an asymmetric network where $_{max}w$ = const. The scatter which gives the line its slope is derived from the difficulty of assigning the optimum velocity from a broad, flat velocity-response curve. Here 5 of the 7 points lie between 11.5 and 15°/sec. while λ is more than doubled showing that $_{max}w$ is not dependent on λ and lies close to 11.5^{o}/sec. This test confirms the asymmetric nature of the inputs to the M1 neuron showing conclusively that the spatial interactions of Fig. 38 are due to the presence of two separate networks, an excitatory and an inhibitory network.

When similar tests were repeated on an M2 neuron the results appeared to fit the predictions of the correlator model (Fig. 46B). The $_{max}w$ on λ regression line has a slope of $\frac{w}{\lambda} = 1.8$. However several factors must be considered before this data can be interpreted correctly.
1). It was shown that the M2 neuron receives inputs from two separate networks, each capable of producing its own w,λ function. The output of the M2 neuron can be a result of activity in either or both of these networks. 2). The diameter of the input receptive fields are different in each network, the field diameter in the one network being twice the diameter of inputs in the other network. As fine stripes produce significantly larger contrast modulation within the smaller receptive fields it is possible that only the small field network is activated with low pattern wavelengths. In the smaller receptive fields $\left[\frac{m_o}{m_i}\right]_r$ will reach a maximum with a pattern wavelength of 8° whereas in the larger fields $\left[\frac{m_o}{m_i}\right]_r$ becomes



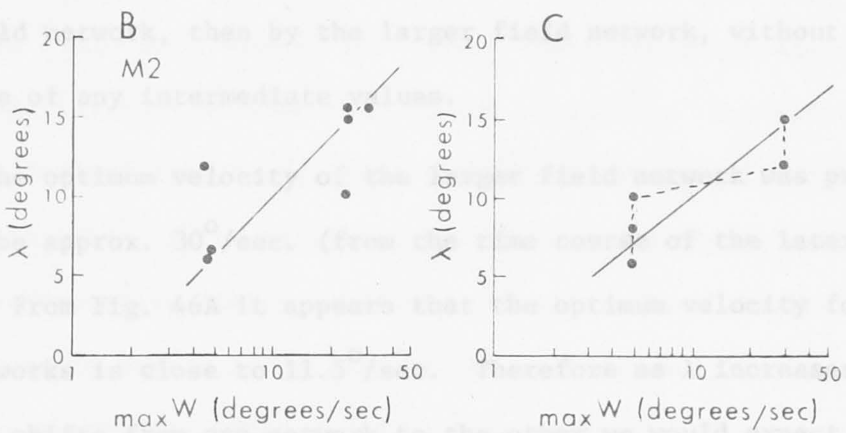


Fig. 46 Dependence of optimum velocity ($_{max}w$) on pattern wavelength (λ). A. Results from 2 M1 neurons indicated by different symbols. B. Dependence of $_{max}w$ of an M2 neuron on λ. In both A and B $_{max}w$ was determined from a plot of constant velocity (in the preferred direction) against p (spikes/second) for each wavelength. 5 movements were averaged to give each point. Optimum velocity ($_{max}w$) was that which elicited the greatest response on a smoothed curve. As the constant velocity curves of M1 neurons are broad and flat some scatter may have been introduced here. C. Theoretical plot (dashed line) of optimum velocity during a switch from one ideal asymmetric network to another network with a different optimal velocity (see text for explanation).

maximal with pattern wavelengths of 15.5^o. By using patterns with wavelengths, from say $6 - 15^o$, it may be possible to demonstrate a switch from function of the small field network only, to function of both networks.

3). The larger field network mediates the sharp velocity peak, whereas the smaller field network broadens the frequency response. When both networks are equally activated the peak of the larger field network should determine the optimum velocity and dominate on the $_{max}w, \lambda$ plot. Therefore as wavelength increases the optimum velocity will be determined first by the small field network, then by the larger field network, without the appearance of any intermediate values.

The optimum velocity of the larger field network was previously found to be approx. 30°/sec. (from the time course of the lateral interaction). From Fig. 46A it appears that the optimum velocity for the small field networks is close to 11.5^o/sec. Therefore as λ increases and dominance shifts from one network to the other we would expect a sudden jump from $_{max}w \doteqdot 11.5^o$/sec. to $_{max}w \doteqdot 30^o$/sec. without the appearance of any intermediate values. This is precisely what is seen in Fig. 46B. There is a cluster of points about $_{max}w \doteqdot 5^o$/sec. and another about $_{max}w \doteqdot 25 - 30^o$/sec. with no intermediates. The shift occurs in the region $\lambda = 10 - 12^o$.

A theoretical plot of two asymmetric networks is shown in Fig. 46C. Here the two ideal networks are represented by two lines $_{max}w = 5$ and $_{max}w = 30$ and a shift from one to the other occurs between $\lambda = 10,12$. The w on λ regression line has a slope $\frac{w}{\lambda} = 2.0$ and this agrees well with the slope ($\frac{w}{\lambda} = 1.8$) of the experimental plot. We have already proven that the M1 neuron receives inputs from asymmetric networks. The close agreement here between predicted and experimental results indicates that the M2 neuron also receives inputs from only asymmetric networks. This means that there are two excitatory and two inhibitory Barlow & Levick network

supplying the M2 neuron, each network responsible for one peak on the plot of spatial interactions of the M2 neuron (Fig. 39). The inputs to the M2 are summarised in Fig. 48.

Conclusion

We can now summarise in detail the inputs and properties of the locust optomotor neurons and compare these with the predictions in Chap. 1. The M1 neuron (Fig. 47) receives inputs from only one type of neuron which, from M1 edge responses, must be ON cells. Their receptive fields have a diameter slightly smaller than that of the receptors. The lateral interactions are derived from every fifth ommatidium along a horizontal row. The separation in space of the fields of the interacting inputs coupled with their narrow receptive fields makes them ideally suited for the detection of tiny movements over a large area of the eye, as would be caused by the insect's own movements. They would be less responsive to movements over only a small part of the eye. This distinction between external and the animal's own movements is increased further by the high threshold of the type 1 neurons which require stimulation of many omma's to elicit a response (c. 80 for the B1 neuron).

The direction analysis is carried out by means of asymmetric connections between the inputs as predicted in Chap. 1. A network with excitatory interactions boosts the response to movements in the preferred direction while an inhibitory network reduces the discharge to movements in the null direction. Several mechanisms allow good response to a broad range of velocities and oscillation frequencies. The lateral interactions have a short latency and are short lasting. These allow responses to faster movements. The good responses to slower movements which were postulated in Chap. 1 are caused by a selective facilitation at the M1 neuron which allows the firing rate to build up over the several seconds of a very

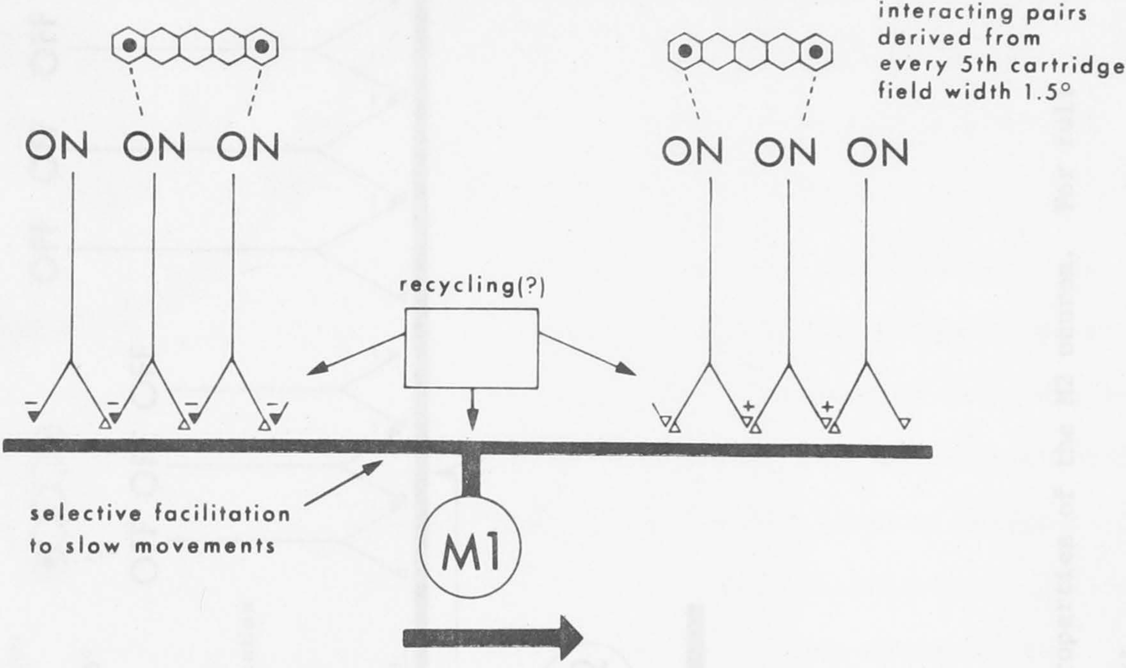


Fig. 47 Summary of input properties of the M1 neuron. See text for full explanation. Receptive fields of interacting inputs are drawn with respect to the ommatidial array. Open triangles represent excitatory synapses, closed triangles represent inhibitory synapses. Neurons are drawn so that their profiles are symmetrical to coincide with known neuron profiles. Although inputs from every 5th omma only are shown, all ommatidia contribute.

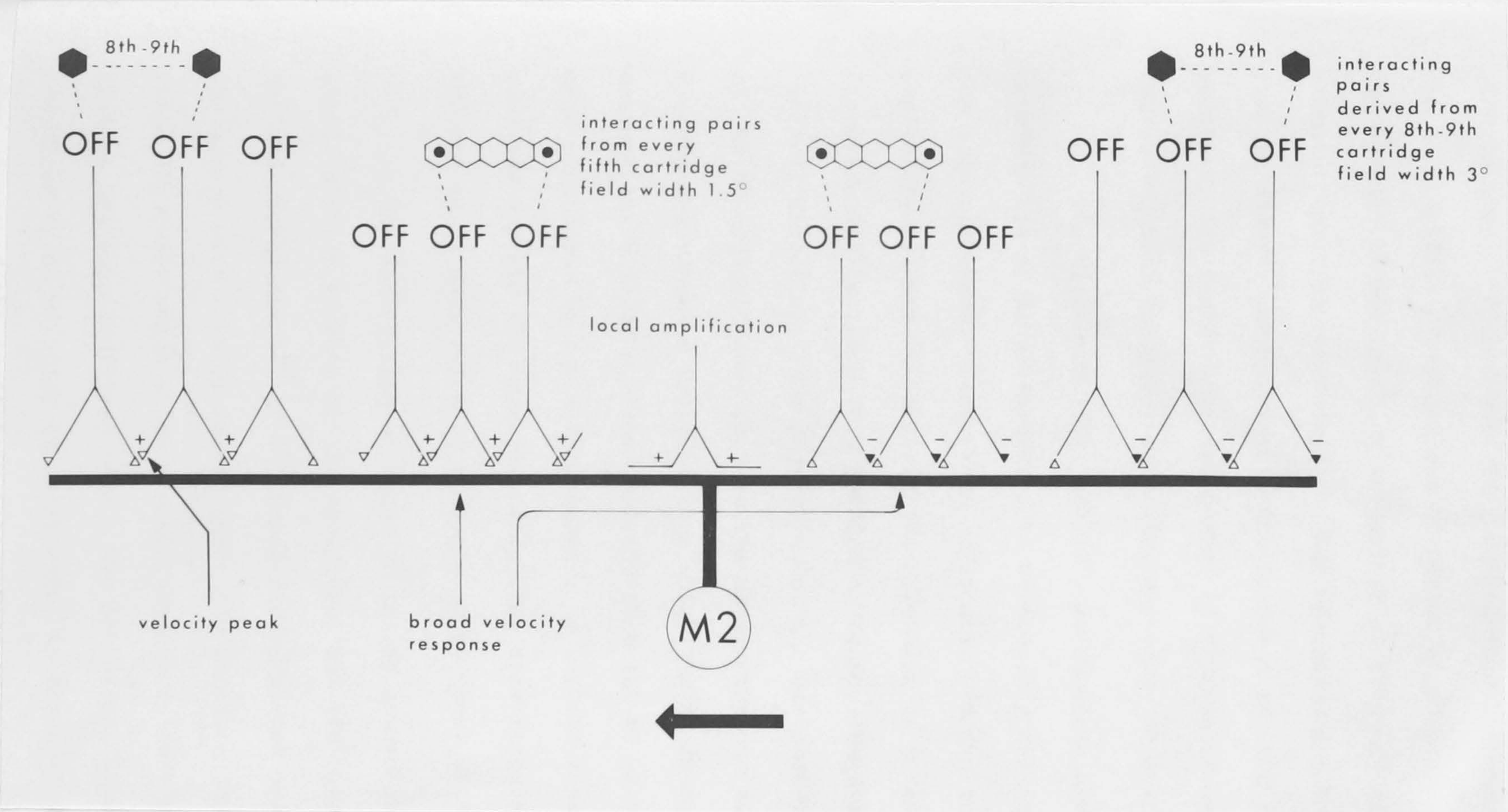


Fig. 48 Summary of input properties of the M2 neuron. For full explanation see text.

slow movement. Also a recycling or reverberating mechanism could maintain the excitability of either the M1 neuron or the inputs for long periods in the absence of any opposing stimuli (i.e. presence of other visual stimulation or new movements). This mechanism may be the basis of optokinetic memory. The flat velocity response and the regularly increasing response with increase in the number of stimulated ommatidia make the M1 neuron an ideal magnitude coder for an optomotor system.

The M2 neuron (Fig. 48) is more complex than the M1 neuron. It receives two types of inputs, both necessarily OFF cells as determined by the edge responses. Both types of inputs form two asymmetric networks, an excitatory network to increase the discharge to movements in the preferred direction and an inhibitory network to reduce the discharge to movements in the null direction. The properties of the one network are similar to those of the M1 neuron; they improve the M2 response to small movements and broaden the range of velocities to which the M2 responds. However this M2 network has a lower optimum velocity than the M1 network and also responds more vigorously to smaller movements. A localised excitation or facilitation may explain the edge reversal, the large response to small movements, and the early saturation of response as movement amplitude increases.

The second type of input to the M2 neuron has a larger receptive field, similar to that of the receptors, and the interacting inputs are derived from every 8th of 9th ommatidium. It was predicted in Chap. 1 that the neuron with back preferred direction receives inputs from larger field OFF cells which allow a good response to fast movements. This prediction has been confirmed here. The inhibitory interaction is long lasting and there is no velocity discrimination in the null direction whereas the time course of the excitatory interaction is such that a sharp velocity peak is formed for movements in the preferred direction. The velocity discrimination of the larger field inputs is superimposed on the activity of the

small field network when both the excitatory networks are activated. The activity of both systems explains the good response when much of the eye is blinded (Chap. 1). The combination of the two input systems allows a velocity enhanced firing rate after an early saturation to increase in the amount of stimulation generated by the moving pattern. Thus the M2 neuron can code for velocity of a movement almost regardless of the complexity of the stimulating pattern.

The electrophysiological experiments (Chaps. 2 and 3) have confirmed nearly all the predictions from the behavioural experiments (Chap. 1). The neuron recordings have confirmed the essential principles of the behavioural model and have revealed a further complexity and multiplicity of neuronal mechanisms. The behavioural predictions and the electrophysiological results differ in only one respect. Whereas behavioural experiments suggested that the receptive fields of the inputs to the directional neurons were derived from many ommatidia the experiments in Chap. 3 demonstrate clearly that these receptive fields are derived from only one ommatidium and that the interaction between the neurons can be described in terms of interacting facet or cartridge pairs.

One reason that large receptive fields were postulated was to explain the need to stimulate large number of ommatidia to elicit an optomotor response. The simple alternative is that summation from a large number of interacting facet pairs is required before the optomotor neuron responds. However the major reason for inferring large field cells was that the arrangement of viewing facets, and thus the number of interacting pairs, made no difference to the ability to detect direction of a horizontal movement (Table 1, Chap. 1). An explanation which fits both behavioural and electrophysiological data is that each horizontal movement is analysed by neurons with horizontal and vertical preferred directions as in the fly, where illumination of two receptors to simulate a vertical movement,

produces a yawing optomotor response (Kirschfeld, 1972). Only the vertical and horizontal distribution of reacting facet pairs shifts with a change in facet arrangement. (i.e. there are more pairs able to act along the horizontal axis in a horizontally arranged viewing area) but the total number of facet pairs remains constant for each size viewing area regardless of its arrangement. Thus neurons with perpendicular preferred directions, simultaneously analysing the direction of each movement, receive a total input dependent on only the direction of movement not on the arrangement of the viewing area.

CHAPTER 4 Nonoptomotor motion detecting neurons

Some neurons must provide information on the movements of objects within the visual field, in contrast to the optomotor neurons which detect only the animal's movements. Unlike the optomotor neurons which respond optimally to stimulation of the entire eye, the neurons detecting external movements must respond when only a small part of the eye is stimulated. Well known examples of such external movement detectors are the DMD fibres which respond preferentially to movements of a small dark object but fail to respond or are even inhibited by movements of the whole visual field (Palka, 1967, 1969; Rowell, 1971a).

This chapter describes several neuron types which appear suited for the detection of external movements as they respond well to movements of a small spot and, in some cases, are unresponsive to movements of a striped pattern. One type responds only to movements of a spot or an edge but, unlike the DMD neuron, this type shows directional selectivity. The other type described here are small field motion detectors which have no true directional selectivity but may give a greater discharge to movements in both directions along a particular axis. The existence of these various types of motion detecting neurons, which differ considerably from the optomotor neurons, supplies evidence that the different direction detecting behaviours, tracking and stabilising are mediated by different neurons.

Neurons with directional selectivity

Directionally selective neurons which respond only to very small amounts of stimulation were recorded in locust optic lobe and circumoe-sophageal connectives. One neuron, found in the circumoesophageal connectives, responded only to a small black or white spot (dia. 10°) moving

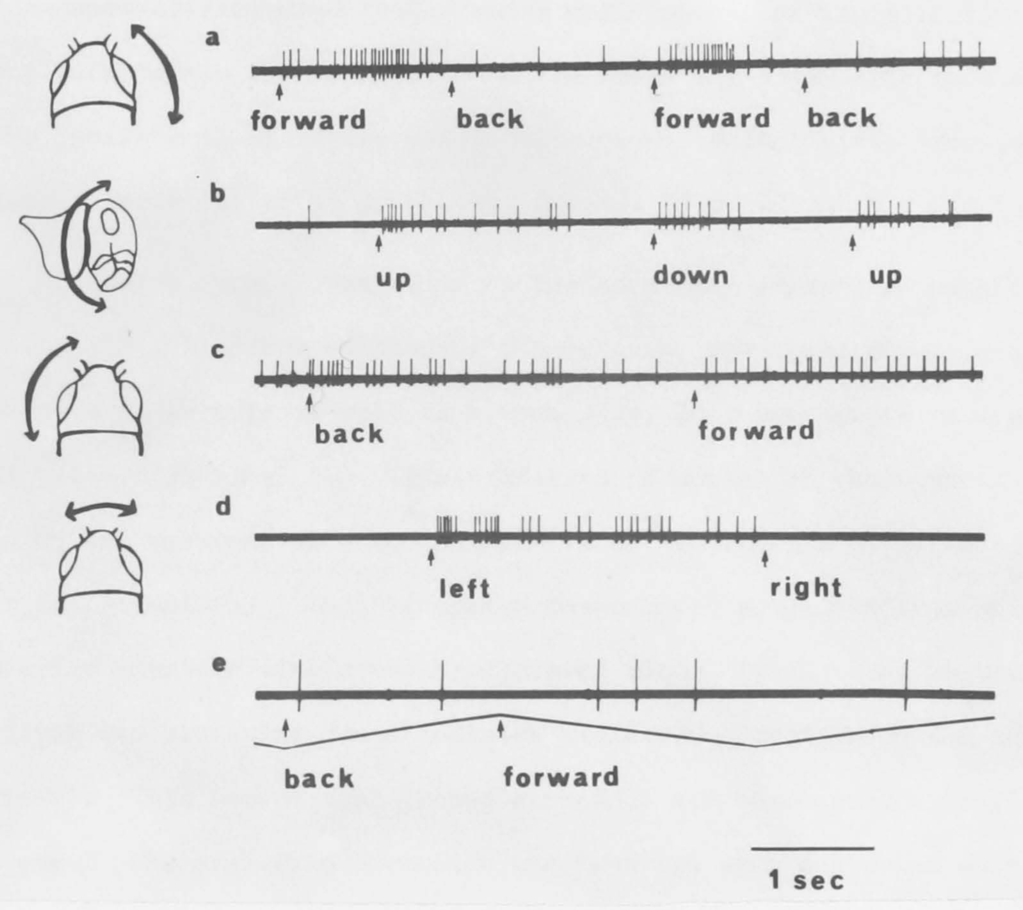


Fig. 49 A directionally sensitive fibre in the locust circumoesophageal connective. This neuron fires strongly to movements of a small spot forward over the contralateral eye (a). It does not fire to movement in the opposite direction. There is little spontaneous firing. Dorso-ventral movements over the contralateral eye (b) cause smaller responses equal for either direction of movement. The neuron responds to movement over the ipsilateral eye (c) but without directional sensitivity. The binocular zone (d) is dominated by the contralateral eye. Oscillating movements of a striped pattern (e) evoke no response, indicating that this type of fibre is not involved in the optomotor response.

forward over the contralateral (the right) eye (Kien, 1973b). This unit had no spontaneous activity and therefore no null inhibition was elicited by a movement back across the right eye. While there was a response to movements over the ipsilateral eye there was no directional selectivity. Movement of a striped pattern failed to evoke any response (Fig. 49).

A neuron type, found close to the optomotor neurons in both the optic lobe and the circumoesophageal connectives, responded directionally to movements of an edge as well as a spot (dia. 10°) but not to movements of a single stripe (Fig. 50). (The preferred direction of these units is defined by the response to a moving spot which, unlike the edge, is a symmetrical stimulus.) The lobe neuron responded to movements from anterior to posterior anywhere within the ipsilateral visual field, that in the connectives was binocular (anticlockwise preferred direction in the left connective). This neuron type showed anomalous responses to the single moving edge. The preferred direction was reversed when the white anterior edge was used, the reversals being more marked than those of the optomotor neurons (Figs. 24 and 50).

Two responses verify the edge reversal as a genuine motion response. Firstly, the neurons respond to light ON, yet the movement of the white anterior edge to which the neurons respond causes a decrease in light. Therefore the neurons are not responding to an overall change in light intensity. Secondly, the large response to movements of a small spot anywhere within the receptive field show that the neuron is a genuine motion detector as the intensity change caused by the spot is negligible in such a large receptive field.

The reversal of the lobe neuron to the white anterior edge indicates that this neuron receives inputs from a network similar to those supplying the optomotor neurons. That is, the neuron must receive inputs from an asymmetric network built up from OFF units (the neuron responds to

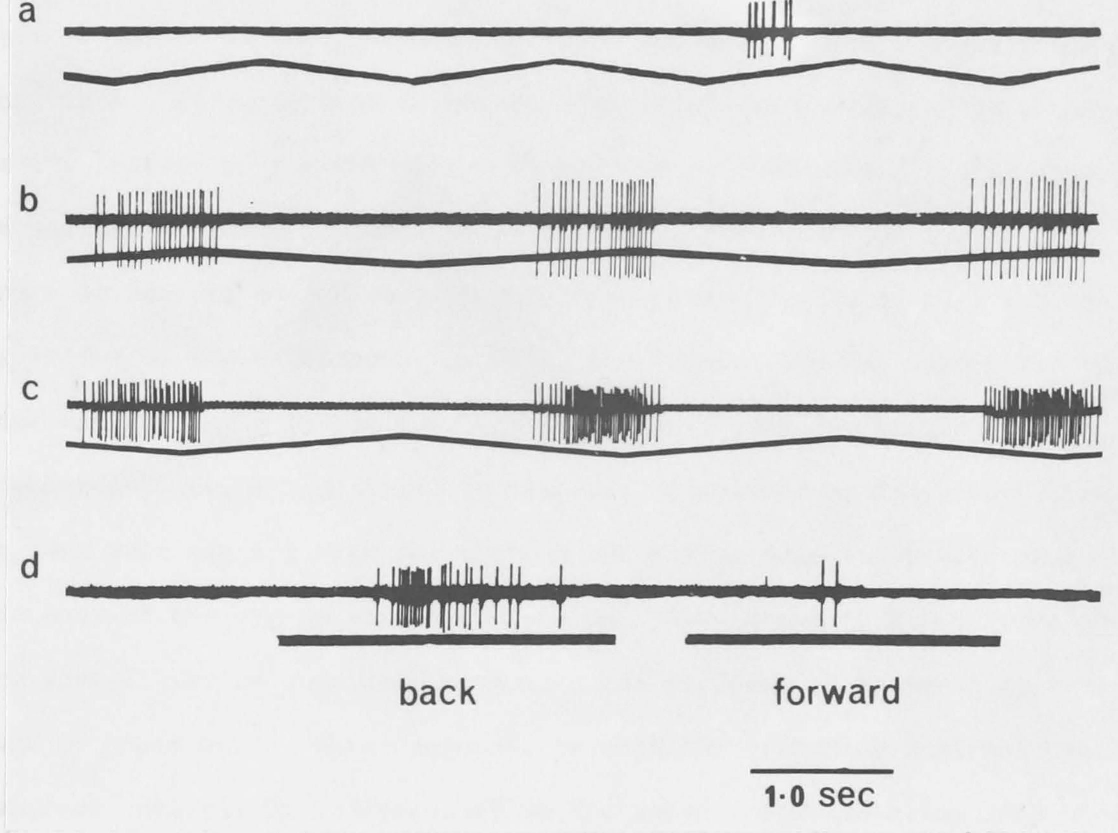


Fig. 50 A neuron in the optic lobe with back preferred direction which responded to movements of an edge and a small spot. The preferred direction is defined by the responses to the spot as in (d) where responses to movements of the hand held 10° black spot are shown. The neuron is unresponsive to movements of a single stripe (a) but responds well to movements of the white anterior edge (b). There is a reversal of preferred direction when the black anterior edge is used (c). A similar response is seen in the large neuron in Fig. 24. Lower trace in all records indicates stimulus movement: (a-c) upward deflection represents anterior to posterior movements (back); (d) bars represent duration of movements of the hand held spot.

edge movements causing decrease in light). Different integration of the input or output of this network can imbue the neuron with its particular properties. An excitation-dependent inhibition was postulated to account for the failure of the DMD neuron to respond to movements of large objects and striped patterns (Palka, 1967) and such a mechanism applied to the inputs or outputs of a direction detecting network would account for the properties of these neurons. As well, one cannot rule out inhibition by a neuron responding to stripes. It is unlikely that the single stripe, to which the neuron had failed to respond, stimulated an inhibitory area not seen when testing with the spot as the moving edge stimulates much the same area of the eye as the single stripe. Also there is no evidence that form specificity is required to explain the response of a neuron to movements of spots only. This response, as with the optomotor neurons, can be explained entirely by a dependence on the amount of stimulation generated by the moving object.

Both neuron types, that responding to the spot only and that responding to the spot and the edge, are ideally suited for the detection of a small external movement but are insensitive to the visual stimulation caused by the animal's movements.

Nondirectional neurons in the medulla

The direction detecting networks must lie in the medulla as this is the first synaptic area where directionally selective neurons are found (Bishop & Keehn, 1967; Bishop et al., 1968; Swihart, 1968; Northrop & Guignon, 1970; Mimura, 1971). However, a brief search in the medulla failed to find either the optomotor neurons, M1 and 2, or their inputs as defined in Chap. 3 (i.e. ON or OFF cells with a receptive field diameter of 1.5 - 3.0^{o}). Instead recordings were obtained from a variety of nondirectional motion detecting neurons which in many ways resembled those

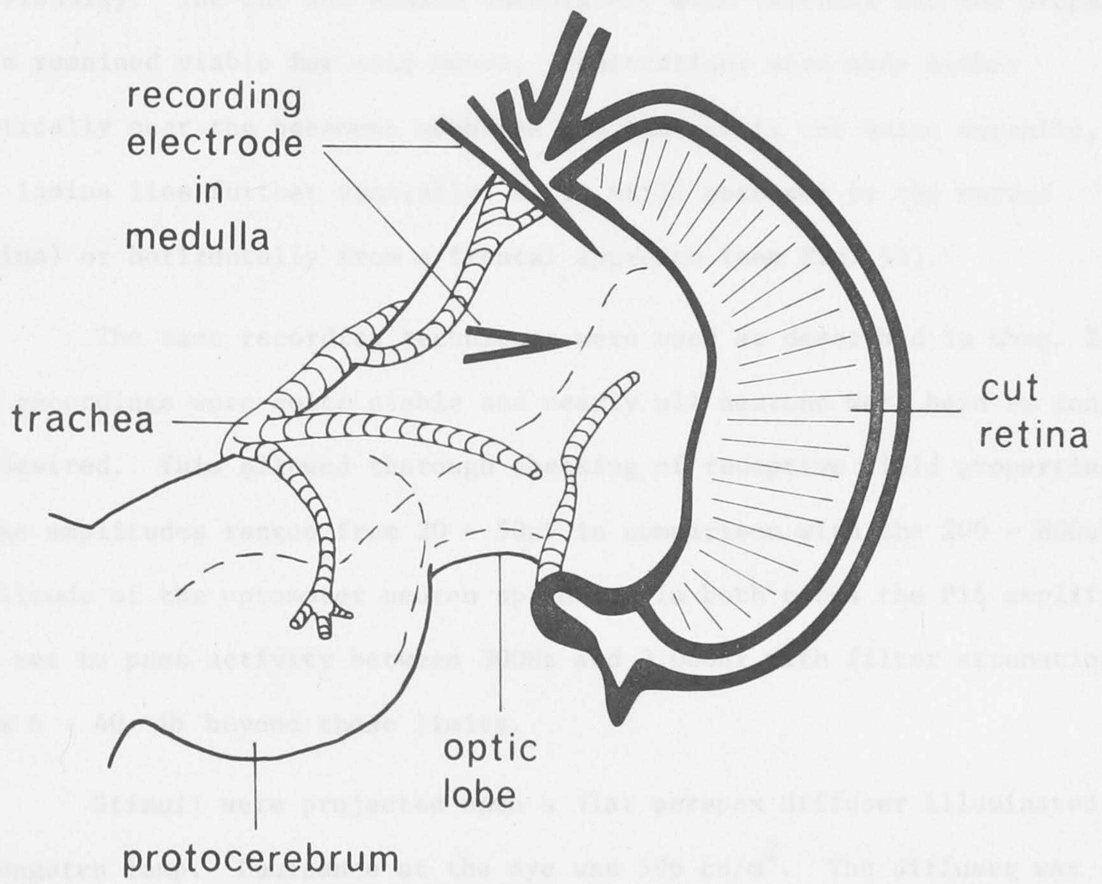


Fig. 51 Dorsal view of the preparation used for recording in the medulla. Both electrode approaches are shown. Penetrations were made within the area bordered laterally by the two tracheae. Note that from this angle the lamina is still obscured beneath the curving retina.

found in the fly medulla by Mimura (1971).

The preparation is shown in Fig. 51. The curve of the eye obscures the lamina and anterior medualla from view from most angles. Thus a sliver was removed from the top of the eye so that the electrode could be positioned visually. The cut was sealed immediately with vaseline and the preparation remained viable for many hours. Penetrations were made either vertically near the basement membrane (as the eye is cut quite dorsally, the lamina lies further ventrally and is still obscured by the curved retina) or horizontally from a frontal approach (see Fig. 51).

The same recording techniques were used as described in Chap. 2. The recordings were quite stable and nearly all neurons were held as long as desired. This allowed thorough checking of receptive field properties. Spike amplitudes ranged from 20 - 50μV in comparison with the 200 - 800μV amplitude of the optomotor neuron spikes. In both cases the P16 amplifier was set to pass activity between 300Hz and 3,000Hz with filter attenation from 6 - 40 db beyond these limits.

Stimuli were projected onto a flat perspex diffuser illuminated by a tungsten lamp. Luminance at the eye was 596 cd/m^2. The diffuser was centred on the eye centre and was placed 1cm from the eye. For receptive field plotting a 2 axis co-ordinate system was marked on the back of the diffuser so that the position of a stimulus relative to the eye centre was given by 2 co-ordinates. These were geometrically converted to angular distances from the head centre so that final receptive field plots were directly comparable to those of the optomotor neurons (Figs. 29 and 30). Receptive fields were qualitatively plotted with a hand held 10° spot. Each border on the receptive field plots marks the disappearance of the response or an abrupt change in its character. Triangular oscillations of stripe edge and spot were provided as before.

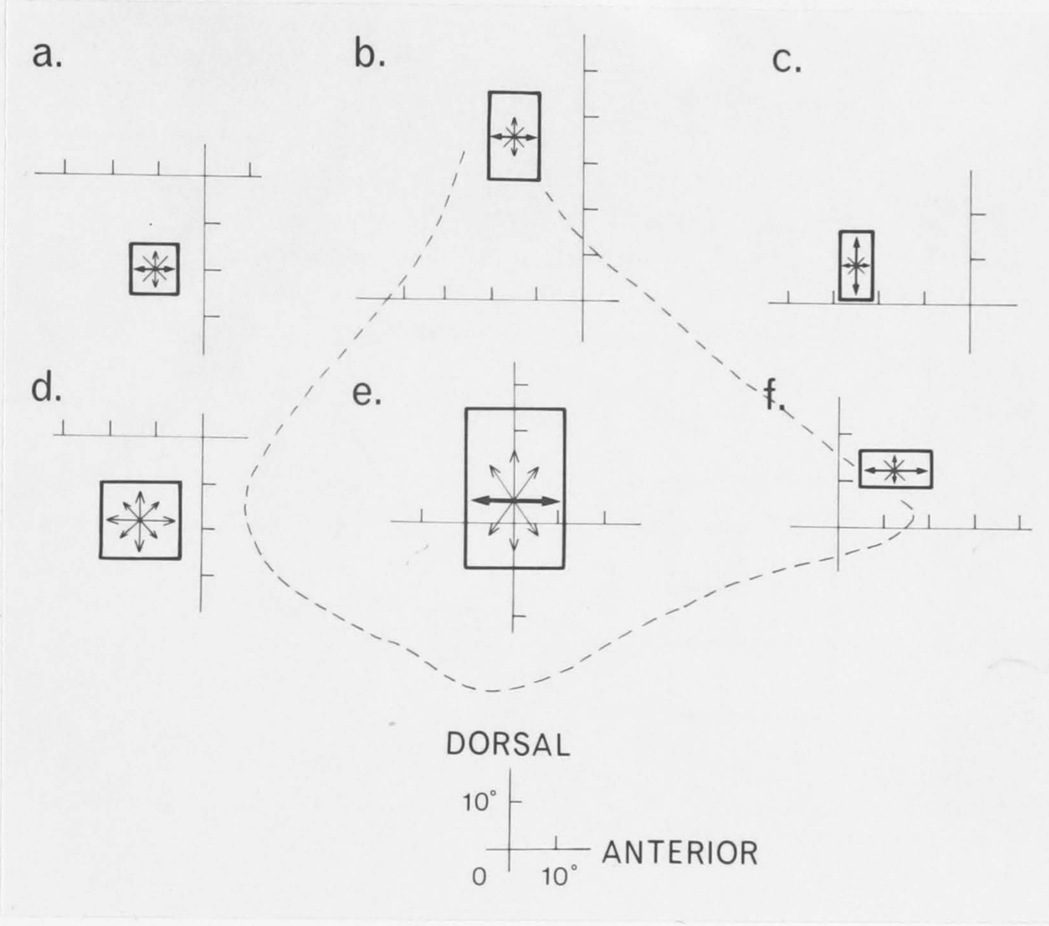


Fig. 52 Small homogeneous receptive fields of some nondirectionally sensitive motion detectors. All fields are plotted with respect to the head axes as in Figs. 29 and 30, with the intersection of axes in each plot representing the intersection of head axes. Only (e) is shown correctly positioned within the total visual field of the left eye (dashed line). The outline of the visual field provides a comparison of the receptive field sizes to the total eye field. Arrows within each field mark the direction of motion to which there was a response. Note that in (a) and (b) there was a stronger response to movements along the horizontal axis.

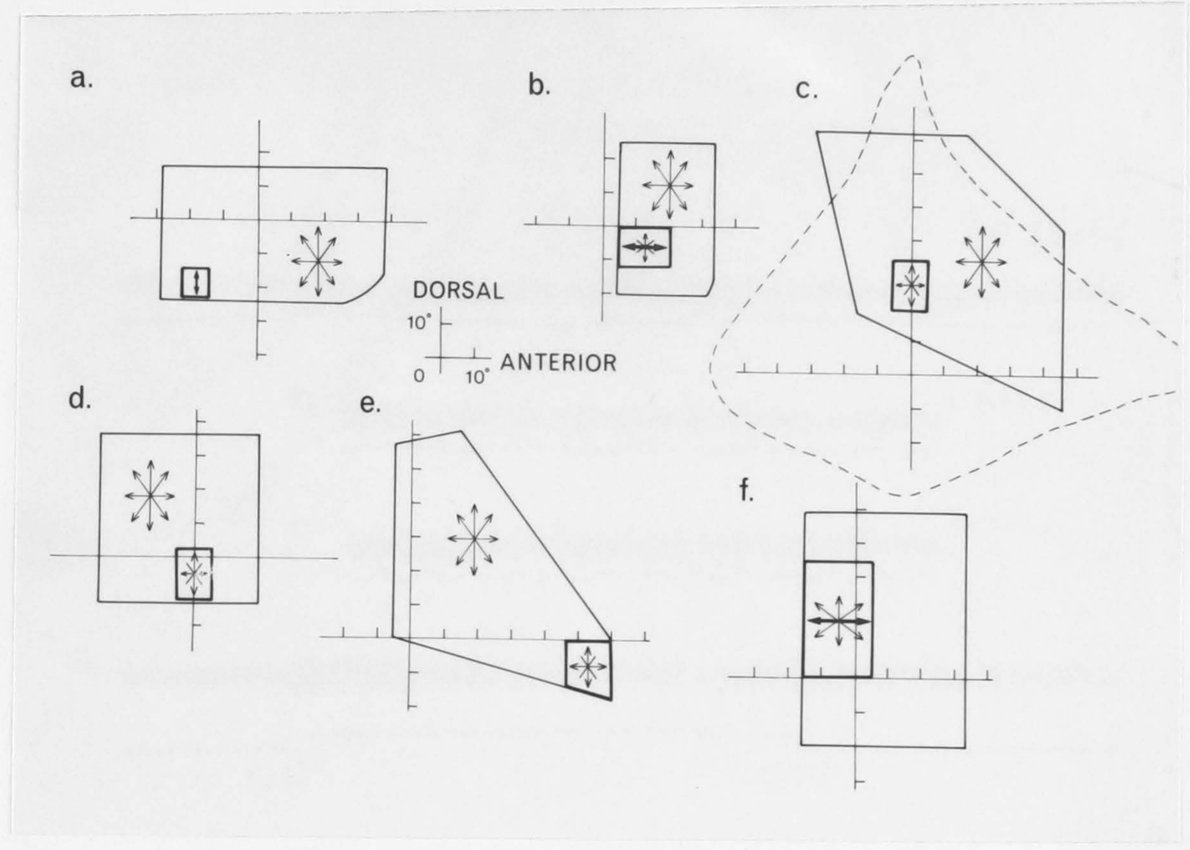


Fig. 53 Receptive fields of nondirectional motion detectors still falling within the first group because of the small size of their maximally excitable area (heavy line in each plot). Fields are drawn as in Fig. 52. All these neurons showed a strong response in the maximally excitable area and a weak response throughout the remainder of the receptive field. Note the preference for horizontal movements in (b) and (c) which is not shown in the surround. (a) was the only field in this group which showed a preference for vertical movements.

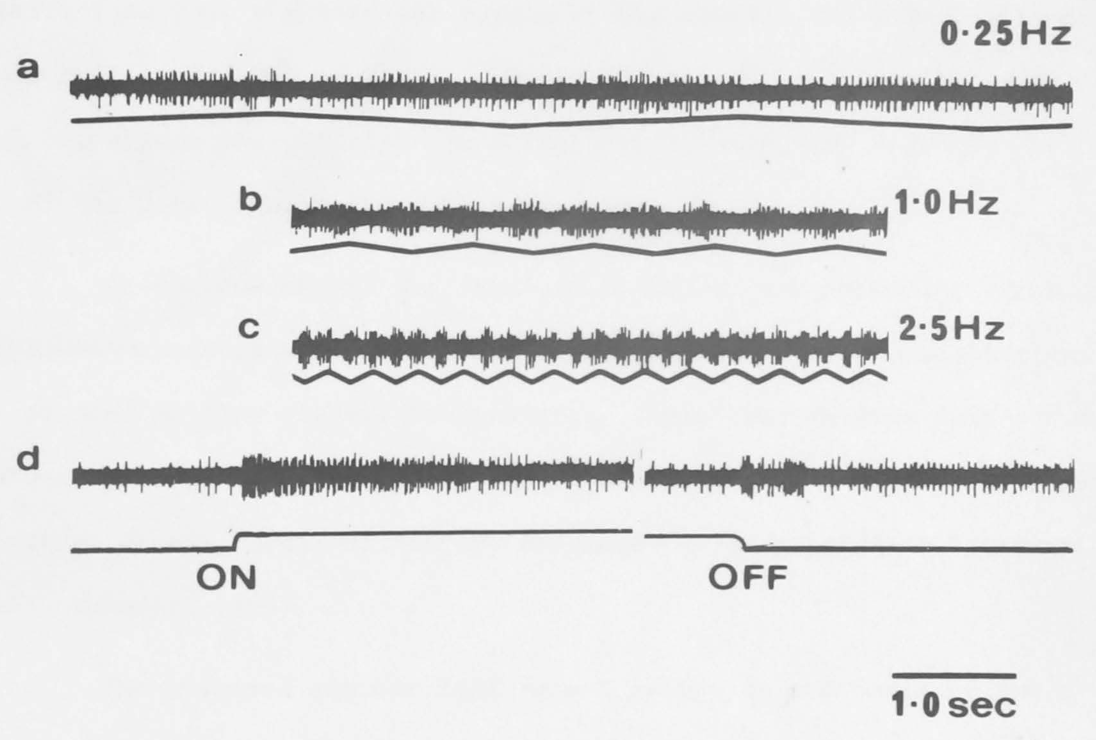


Fig. 54 Responses of a small field neuron, (a-c), to a stripe pattern oscillating at different frequencies (movement amplitude 15.4^{o}, pattern repeat period 15.8^{o}, stimulus trace as in previous records). (d) responses to light ON and OFF. Here stimulus trace is the output from a monitoring photocell. Note the greater response to light ON than to pattern movements.

Motion detectors with differing properties and receptivefield sizes were found in all examined areas of the medulla. There was no precise correlation between recording position and unit properties but vertical penetrations near the anterior margin of the medulla did reveal only small field cells (dia. 20° or less). Neurons with both small and large fields were found more posteriorly. No directionally selective neurons, including the M1 and 2 neurons, were recorded.

As the search was for possible inputs to the optomotor system only those units were examined which responded to slow (0.25Hz) oscillations of the striped pattern without habituating. These requirements rule out any neurons which could belong to the group consisting of 'novelty' detectors (Horridge et al., 1965) or jittery movement fibres (Wiersma & Yamaguchi, 1966; Swihart, 1969).

The examined neurons fall into 3 groups on the basis of their receptivefield size. The first group contains units with small receptive fields (Fig. 52). Some fields had a small strongly excitatory area with a large surround in which the neuron could be weakly excited (Fig. 53). As shown in Figs. 52 and 53 many of the neurons were nondirectional motion detectors but some showed a preference for movements along one axis which was usually the antero-posterior (horizontal) axis. This preference was not seen in the surround areas. Movements of a single stripe, spot or edge produced responses similar to those evoked by pattern movement. Neurons with very small receptive fields showed equal responses to these stimuli, neurons with larger receptive fields gave a smaller response to these simple stimuli. The one neuron tested for response to very slow oscillations of the pattern responded to an oscillation frequency of 0.05Hz with the same discharge as evoked by a pattern oscillation of 0.25Hz. The upper frequency limit where the neurons still responded reliably was 2.5 - 5.0Hz (Fig. 54). The neurons could follow faster oscillations for only 2 - 5

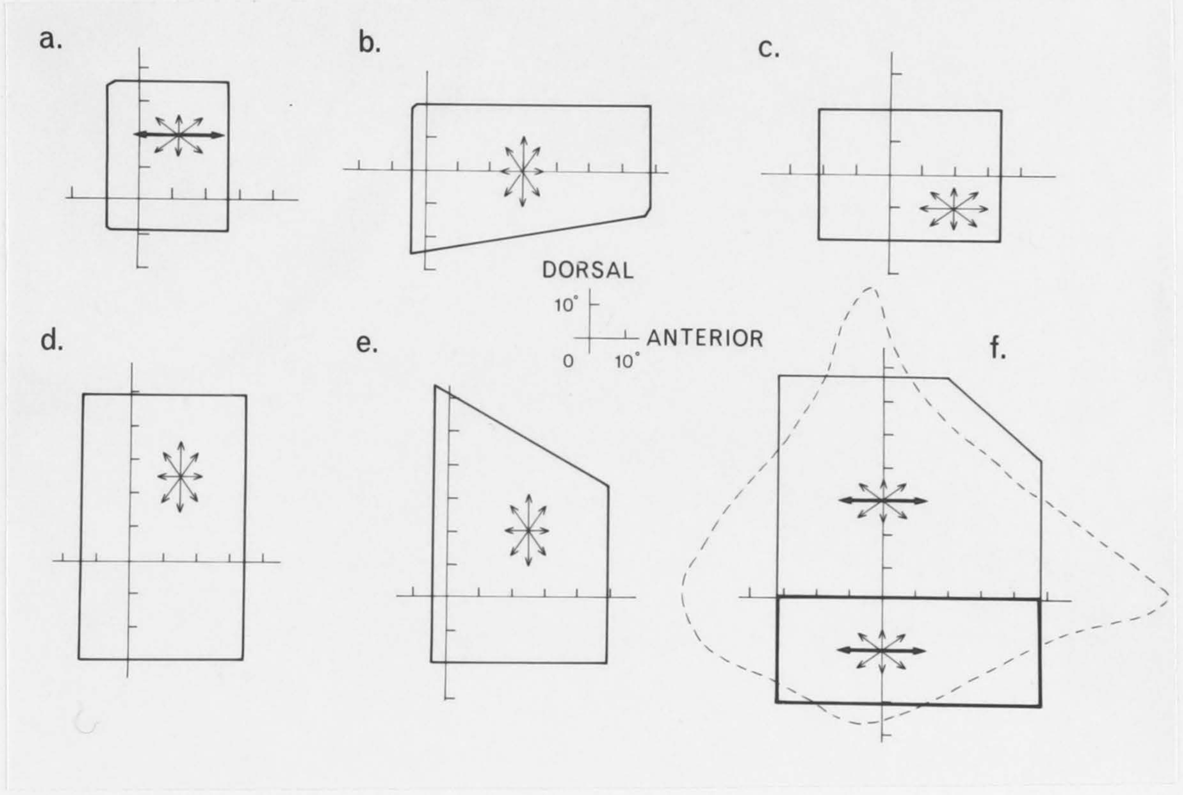
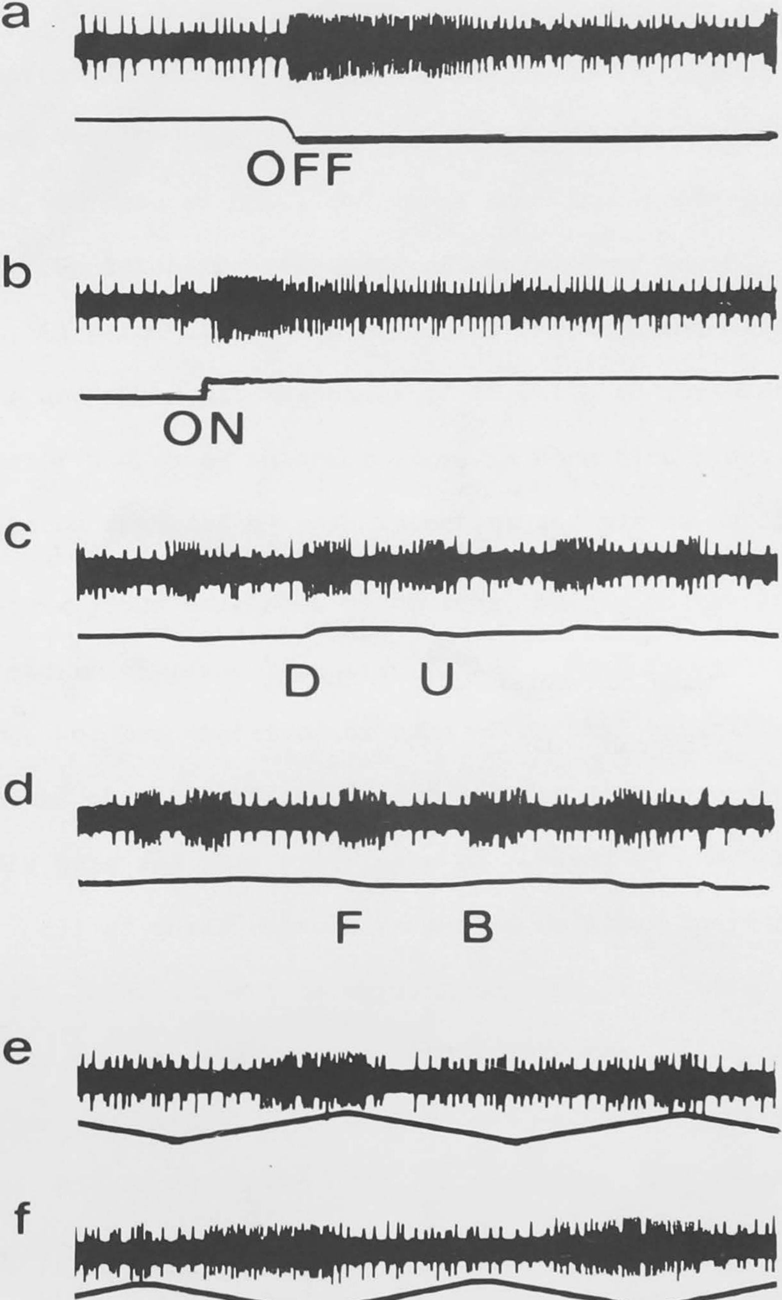


Fig. 55 Medium sized receptive fields of some nondirectional motion detectors. Plotted as in Figs. 52 and 53. The whole visual field (dashed line) is given for comparison with field sizes. The neuron in (f) responded well in the area marked by the heavy line. Only a weak response could be elicited in the remainder of the receptive field. Note the preference for horizontal movement in (a) and (f).

Fig. 56 Responses of an ON-OFF neuron with medium sized receptive field to (a) light OFF, (b) light ON, (c) & (d) movements of a hand held 10° black spot. Stimulus mark represents spot movements as monitored by a photocell: B. back, F. forward, U. up, D. down. The response to the spot movements show that the neuron must be detecting motion as well as intensity changes. (e) response to oscillations of the black anterior edge, and (f) the white anterior edge. Although this unit is motion detecting, its responses to edge movements can be related to intensity changes. Light OFF produces a greater response than light ON and edge movements causing a decrease of light elicit the greatest response. All other neurons showed edge responses similar to those in Fig. 58.


a
OFF
b
ON
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D
U
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cycles and then the response gradually disappeared. With slower oscillations the response remained stable for more than 50 cycles.

The stimulus which elicited the greatest discharge in all these neurons was not stripe movement but a gross change in light intensity (Fig. 54). 5 of 9 units responded to light ON, 4 were ON-OFF units. There was no sustained response to changes in light intensity, the steady state discharge being the same in the light as in the dark in all but one unit. However strong, the intensity responses cannot account for all the movement responses, in particular the preferences for movements along a particular axis and the equal responses of ON units to movements of both the black anterior and white anterior edges in both directions. Therefore the neurons must be regarded as both intensity and motion sensitive.

The second group consisted of neurons, mostly in the posterior medulla, with medium to large receptive fields. Most receptive fields were homogeneous but one contained an area of maximal excitation (Fig. 55). Two of the neurons showed a slight preference for movements along the antero-posterior axis and this preference was shared by the weakly responding area also. All of these neurons responded to gross increase and decrease of light intensity but to varying degrees, i.e. some neurons showed a stronger ON than OFF response and vice versa. Although the ON or OFF discharges are large, these neurons are definitely motion detectors as they respond well to movements of a 10° spot (Fig. 56) which would cause a negligible intensity change within a large receptive field. In only one neuron was the response to the single edge related to intensity changes (Fig. 56). These neurons with their large receptive fields showed smaller responses to the single stripe edge, edge and spot stimuli than to the striped pattern. They responded better to faster oscillations, the spike frequency increasing from 11.5 - 16 spikes/sec. for movements at 0.25Hz to 12 - 22.5 spikes/sec. for movements at 1.0Hz, a mean increase

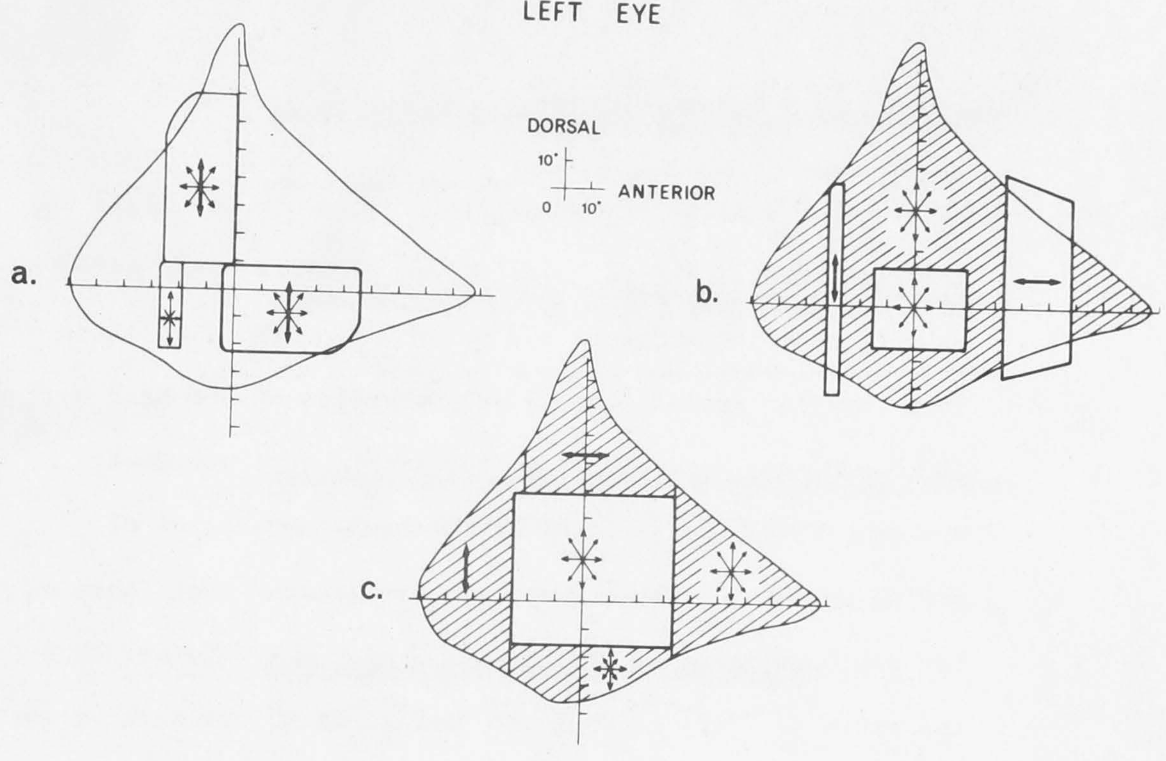
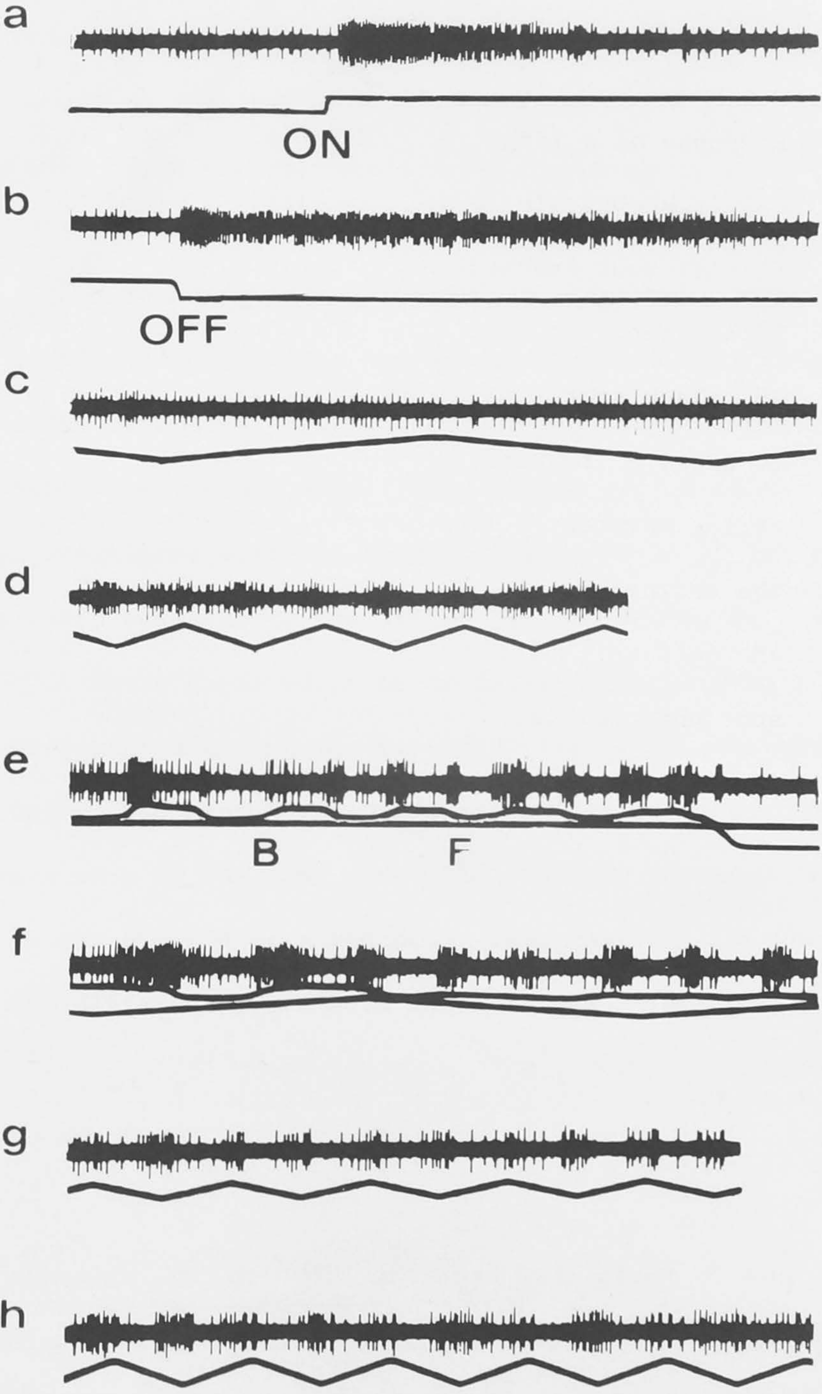


Fig. 57 Composite receptive fields of 3 neurons. Plotted as before. (a) receptive field covers a large part of the visual field. There is one maximally excitable area (thickest line) and 2 areas where a weak response could be elicited. Thin line indicates weakest response. In (b) and (c) responses could be elicited anywhere in the visual field (hatched areas) but these responses were weak. Maximal responses were elicited in unhatched areas. Note the different preferred axes of movement in the different areas.

Fig. 58 Response of a large receptive field neuron to (a) light ON, (b) light OFF, (c) & (d) oscillation of the striped pattern at different frequencies: c. 0.25Hz, d. 1.0Hz (amplitude 15.4^{o}, repeat period 15.8^{o}), (e) movements of the hand held 10° black spot. Middle trace represents spot movement: B. back, F. forward; lower trace shows the absence of stripe movement. These responses are greater than those of the stripe pattern as the hand held spot moved faster than the pattern. (f) response to simultaneous movements of the spot and oscillation of the single black stripe in a different area of the receptive field. Note the response is to the spot which is moving faster than the stripe. (g) response to oscillations of the black anterior edge and (h) the white anterior edge. These edge responses are of the type shown by nearly all the nondirectional motion detectors. Spike counts on (d), (g) and (h) show that the response to stripes is slightly greater than that to the moving edge.


a
ON
b
OFF
c
d
e
B
F
f
g
h
1·0 sec

of 1.4 times (5 neurons). This result is consistent with findings in fly (Mimura, 1971) and rabbit (Oyster et al., 1972) where neurons with larger receptive fields tend to respond better to faster movements.

The third group consists of three neurons whose receptive fields covered most or all of the ipsilateral visual field. Two neurons had composite fields with different preferred axes of motion in different areas (Fig. 57). All these neurons were of the ON-OFF type, with no sustained responses to changes in background illumination. They were sensitive to oscillation frequency, an increase from 0.25Hz to 1.0Hz almost doubling the spike frequency. These neurons, like all the others, responded equally to movements of either edge. They showed only slightly reduced responses when stimulated with the single stripe or the 10° spot in comparison to their response to the stripe pattern moving at the same speed (Fig. 58). There appeared to be no interaction between 2 simultaneous movements in different areas of the receptive field. If the movements were at different speeds the neuron responded mainly to the faster one (Fig. 58), if the movements were at the same speed the response appeared to be the sum of responses to the individual movements. This applies also when the movements in the different areas were in different directions.

The misnomer 'ON' or 'OFF' unit has been given to many neurons showing complex properties apart from their responses to intensity changes. Small field ON units have been previously recorded in the medulla of several insects (locust, Burtt & Catton, 1960; Horridge et al., 1965; butterfly, Swihart, 1968, 1969; fly, McCann & Dill, 1969; Mimura, 1971). While in many cases their only reported response was to changes in light intensity, in two cases the small field ON units have been shown to

possess other properties. The small field nondirectional motion detectors of Mimura (1971) in the fly are small field ON units. Similarly in the fly, small field units which respond best to illumination of a pattern with a particular orientation (McCann & Dill, 1969) may be classified as small field ON units. Also the movement responses of the small field ON units found here cannot be explained entirely in terms of intensity changes. The preference for movement along one axis suggests that the inputs to these cells may be connected along one axis before reaching the cell. Perhaps, as in the fly motion detectors, the response to movement along a particular axis is enhanced by excitatory collaterals between inputs (Mimura, 1972).

Many neurons with medium to large receptive fields, apparently responding only to light ON or ON-OFF can be found easily in a variety of arthropods, e.g. ON-OFF units in the optic tract of the crab *Podopthalmus*, with receptive fields varying from dia. 15 - 45° (Waterman, Wiersma & Bush, 1964); ON units in Limulus with fields covering more than $\frac{1}{2}$ the field of one eye (Snodderly, 1971); fly ON or ON-OFF units with field diameters up to 45° (Bishop et al., 1967); locust ON or ON-OFF units with fields ranging up to whole eye fields (Burtt & Catton, 1956; Horridge et al., 1965); moth optic lobe (Ishikawa, 1962), moth protocerebrum (Blest & Collett, 1965), and cricket protocerebrum (Dingle & Fox, 1966). The ubiquity of these neurons with the same apparent function of measuring changes in light intensity, in the otherwise highly economical visual system is more likely to be due to a lack of subtlety of testing than a real redundance. Although the neurons may show a large discharge to change in light intensity, they may also possess a variety of other properties such as the motion detection described here. As we know neither the connections nor the function of these units we cannot know which response property is used by the animal under normal circumstances.

At present very few hypotheses can be made concerning the input to both the directional and nondirectional neurons. The directional neurons may receive inputs from the same neuron type which supplies the optomotor neurons. However the interacting inputs may be derived from cartridges closer than those in the optomotor networks to allow further discrimination between object and body movement. The lack of symmetry of the receptive fields of the nondirectional motion detectors suggests that the recordings may be derived from those elements of the medulla which do not occur regularly in each cartridge (Campos-Ortega & Strausfeld, 1972).

The function of both types of neurons is not yet determined. Both major types described here, directional and nondirectional, must be part of that system which informs the animal of the direction and speed of a movement in the environment. The directional neurons distinguish between object and body movement but provide no information on the location of the stimulus within the receptive field. The motion detectors with small to medium sized receptive fields may convey precisely this information. The use of small field motion detecting neurons to determine an object's position has already been suggested in the lobster (Wiersma & York, 1972) where the 'seeing fibres' are thought to provide the visual information to guide the antenna in the antennal pointing reflex. A function for cells with composite receptive fields was suggested by Mimura (1971) who postulated that these neurons may provide a means of tracking an object rotating about the body, as could occur during flight.

DISCUSSION An overview of the optomotor system

I have described the neuronal integration processes within the locust optomotor system (Chap. 2), concentrating particularly on the mechanism of directional selectivity (Chaps. 1 & 3). Yet the visual analysis of direction of a movement is only one step in a complex system. In this system several modalities provide information on the animal's head movements in order to distinguish these movements from any external movements and to stabilise the head with respect to the environment. The following review summarises what is known, in both vertebrates and invertebrates, of how visual information is used to stabilise the eyes or head. Also discussed is the relation between the tracking or smooth pursuit movements with which the eyes follow a moving object and the compensatory reflex which tends to keep the eyes stationary with respect to the visual background.

Inputs to the directional neurons in insects

We are hampered in a histological demonstration of neurons synapsing with optomotor neurons by an ignorance of precisely which are the optomotor neurons, and a lack of knowledge of the connections between neurons in many neuropile areas. Evidence from 2 electrode mapping experiments in the fly (Bishop et al., 1968; McCann & Dill, 1969) and the moth (Collett, 1970, 1971) and lesions marking recording position in the fly (Bishop & Keehn, 1967) indicate that the directional neurons are tangential fibres arising in the medulla. Similarly, in the locust, the major fibre tract in the area where the optomotor neurons were recorded (Chaps. 2 & 3) was Cuccatti's bundle which contains the axons of the medullary tangential fibres (Power, 1943; Strausfeld, 1970; Strausfeld & Blest, 1970). By

correlating electrode mapping results with the Golgi profiles of the tangential neurons (Strausfeld & Blest, 1970) Collett (1970) has tentatively identified as efferent neurons to the medulla, M:tan 1 and M:tan 2, the two large tangential fibres whose branches spread across the entire anterior surface of the medulla. It is not known which of the other tangential fibres are the monocular optomotor neurons. Their morphology provides no clues; all could equally well be large field motion detectors as the main branch of each neuron runs the length of the medulla giving off fine branches at regular intervals. Although these branches terminate in a layer of the medulla specific for each type of tangential (e.g. the M:tan 3 tangentials send fine branches to every medullary cartridge) (Strausfeld, 1970; Strausfeld & Blest, 1970), we cannot postulate the function of a tangential from the particular termination of its branches. Detailed descriptions of medullary structure have been restricted to the components entering the medulla cartridge from the retina and lamina (Trujillo-Cenoz, 1969; Campos-Ortega & Strausfeld, 1972a; Strausfeld & Campos-Ortega, 1972) and many of the 46 profiles in each medullary cartridge have not been identified (Campos-Ortega & Strausfeld, 1972). Nothing is known of the location of the synapses of the medullary cells in each cartridge or of intercartridge connections.

The present physiological knowledge is also far from complete. No medullary neuron has been identified by intracellular dye marking. Only two of the lamina inputs to each medullary cartridge, the 2nd order L1 and L2 neurons, have been examined (fly, Autrum, Zettler & Järvilehto, 1970; Järvilehto & Zettler, 1973; dragonfly, Laughlin, 1973; bee, Menzel, in preparation). Another neuron which has been recorded from and identified on only one occasion is the 'centrifugal' fibre (Trujillo-Cenoz & Melamed, 1970) which synapses with the retinula axons in the lamina and the L2 ending in the medulla. The recordings indicate that this is not a centrifugal fibre but is, in fact, a centripetal fibre conducting from the lamina

to the medulla (Järvilehto & Zettler, 1973).

Both the lamina monopolars and the 'centrifugal' fibre show slow hyperpolarising potentials with peak and plateau to light stimulation. As light intensity increases the negative plateau diminishes and a positive peak appears at light OFF. At high intensities the response consists of a negative peak at light ON, a very reduced negative plateau and a large positive peak at light OFF (Autrum et al., 1970; Laughlin, 1973). In dragonfly the receptive fields of the lamina monopolars are the same size as those of the receptors (Laughlin, 1973) but in the fly, both monopolars and the 'centrifugal' cell have receptive fields smaller than those of the receptors, indicating the existence of a lateral inhibition between these 2nd order neurons (Järvilehto & Zettler, 1973; Zettler & Järvilehto, 1973).

Two unidentified spiking neurons have been recorded between lamina and medulla in the fly (Arnett, 1972) and one has been implicated as an input to directional neurons (Mimura, 1972; McCann, 1973). This neuron shows a sustained response to light ON in a portion of its receptive field equivalent to that of one lamina cartridge, and is flanked on either side by areas, also equivalent to one cartridge field, where the neuron responds to light OFF. This unit is thought to receive excitatory input from one cartridge (though whether from lamina or medullary cartridge is not clear) and lateral inhibition from the neighbouring cartridges. At light OFF release of the inhibition generated in these cartridges causes the rebound firing which constitutes the OFF response (Arnett, 1972). The precise relationship of this neuron to the lamina monopolars, the neurons in the medullary cartridge or the directionally selective neurons is not known.

The two spiking neurons, an ON-OFF unit and the sustaining unit described above, recorded between lamina and medulla (Arnett, 1972) certainly demonstrate that information about transient changes in light intensity and about changes in light intensity levels have been extracted either

directly from the lamina cells or via medullary neurons. But, until the responses of the remaining lamina monopolars and the neurons in the medullary cartridge are determined it is useless to speculate how this information is extracted from the graded potentials in the lamina neurons and how it is passed to the motion detecting neurons.

In this context, however, it is worthwhile to compare the insect optic lobe with the vertebrate retina where information is also carried by graded potentials in several neurons types (Dowling, 1970). Amacrine cells respond only to changes in light intensity with a depolarising transient to light ON and light OFF. Similarly, those ganglion cells which receive inputs mainly from amacrine cells respond to changes in light intensity with a depolarising transient on which a short burst of spikes may be superimposed (Kaneko, 1971; Werblin, 1970). On the other hand, information on the level of light intensity is provided by the bipolar cells with their maintained de- or hyperpolarisations during illumination. Ganglion cells which receive inputs mainly from bipolar cells can sustain spiking during the entire period of stimulation of their receptive field centres (Dowling, 1970; Werblin, 1972). As the responses of the insect lamina monopolar cells, with their transients, resemble the amacrine responses and the plateau resembles the maintained responses of the bipolar cells, the method of integration in insects may be slightly different.

The importance of the inhibitory surround in determining the properties of visual neurons cannot be overemphasised. In the vertebrate retina both bipolar and ganglion cells possess antagonistic surrounds. In the ganglion cells these surrounds sharpen the responses of the receptive field centre to contrast (e.g. ON centre, OFF surround, Werblin, 1972), colour (red centre, green surround, Daw, 1972) and motion sensitivity (inhibitory processes around the field centre, Henn & Grüsser, 1969). Similar surround mechanisms occur in the insect visual system. For instance

Arnett's (1972) sustaining unit is an ON centre cell with an antagonistic surround along one axis.

A simple variation in the parameters of these lateral inhibitory mechanisms may account for the different optomotor edge responses on different insects. The reversed edge responses of the locust and the female Pieris are caused by the directional neurons receiving inputs from either ON cells or OFF cells but not from both, while in insects showing no edge reversals, the directional neurons must receive inputs from both ON and OFF cells or from ON-OFF cells. A neuron such as the Arnett cell becomes an ON-OFF cell through the responses of the inhibitory surround which are caused by rebound firing after the release of inhibition. If there is no rebound firing this neuron becomes an ON cell whose silent antagonistic surround can be demonstrated only by simultaneous stimulation of centre and surround. This type of ON cell is exactly the type predicted to supply inputs to the M1 neuron in the locust (Chap. 3). It is possible that either ON centre or OFF centre neurons supply the directional neurons in all insects. In some insects the presence of rebound firing after the release from inhibition from the surround transforms these neurons into ON-OFF neurons, while the absence of rebound firing in the comparable neurons of other insects leaves each directional neuron receiving inputs only from ON or OFF neurons. A consequence of this suggestion is that the differences between male and female Pieris could be caused simply by a difference in neuron activity rather than by a morphological difference.

Mechanisms subserving directional selectivity

Although most animals with well developed visual systems are able to detect the direction of a movement the neuronal mechanisms of directional selectivity have been examined in detail only in vertebrates and insects. The difficulty of recording or the complex properties of the easily recorded

directional neurons have so far prevented analyses in other animals.

Directionally selective neurons in the retina were first described by Barlow & Hill (1963) in the rabbit. The mechanism by which directional selectivity is created was then analysed in the rabbit by Barlow & Levick (1965) who postulated the asymmetric networks shown in Fig. 1A. Of these two networks, the inhibitory model showed a close fit with the properties of the directionally selective neurons. In this model excitation in input A inhibits the neighbouring input on one side, input B. Movement from A to B results in input B being unable to respond when the moving stimulus reaches its receptive field. On the other hand, movement from B to A allows both inputs to fire normally. It was originally thought that the inputs were bipolar cells and the horizontal cells conducted the information laterally (Barlow & Levick, 1965; Michael, 1968). More recent studies of the responses of the retinal neurons suggest that the lateral interactions are mediated by the amacrine cells (Dowling, 1970).

The basic mechanism proposed by Barlow & Levick, has been confirmed in the squirrel (Michael, 1968). The similar responses of the directionally selective neurons recorded in other vertebrates (fish, Daw & Beauchamp, 1972; chick, Miles, 1972; mudpuppy, Werblin, 1970) and the similar anatomy of their retinae suggest that probably all vertebrates use this asymmetric network to create directional selectivity. Furthermore, similar asymmetric networks exist in the locust optomotor system (Chaps. 1-3) and supply some fly neurons (Mimura, 1972). As the fly and the locust are far removed from the vertebrates in evolutionary terms and yet show the same mechanism of directional selectivity, it is plausible that the asymmetric network is the universal biological method for analysing direction. Certainly, the basic network can be varied sufficiently to account for the differences in the properties of the directionally selective neurons recorded in both vertebrates and invertebrates and further flexibility can be created by the

addition of extra networks all connecting to the same neuron. Indeed the M1 and 2 neurons show that these methods are used to alter the responses of directional neurons and that neurons with different properties do not utilise different methods of direction analysis. For example, the M2 neuron receives inputs from 4 asymmetric networks; two mediate the responses to small movements while only one is responsible for the conspicuous velocity peak. The method of altering neuron properties by increasing the number of input networks is analogous to a computer whose output is more easily altered by the re-running the same programme, in which only one or two parameters are altered, rather than by rewriting the entire programme.

Only slight variations in the inputs or the interconnections between networks account for the major differences in insect optomotor behaviours. It has already been described how the anomalous edge responses of the locust and female _Pieris_ are abolished if the inputs to each directional neuron respond to both increases and decreases of light. Asymmetric networks can also account for the behaviour responsible for the formulation of the basic multiplicative rules (A+.B+=A-.B-, A+.B-=A-.B+ ≠ A+.B+) (Reichardt, 1961, 1969). The model in Fig. 59 was proposed by Collett & Blest (1966) as a neuronal network whose output complied with the multiplicative rules. This model consists of an asymmetric network receiving inputs from ON cells, a network receiving inputs from OFF cells and inhibitory interconnections between ON and OFF neurons. The countermovements, elicited when the illumination of one ommatidium is increased while the illumination on the neighbouring ommatidium is decreased (A+.B- and A-.B+), are explained by rebound firing after the release of inhibition. There is no direct evidence for this model. However, certain features such as the inhibitory connections between ON and OFF systems and the rebound firing after release of inhibition are combined in the responses of the sustaining unit (Arnett, 1971) implicated in motion detection in the fly (Mimura, 1972; McCann,

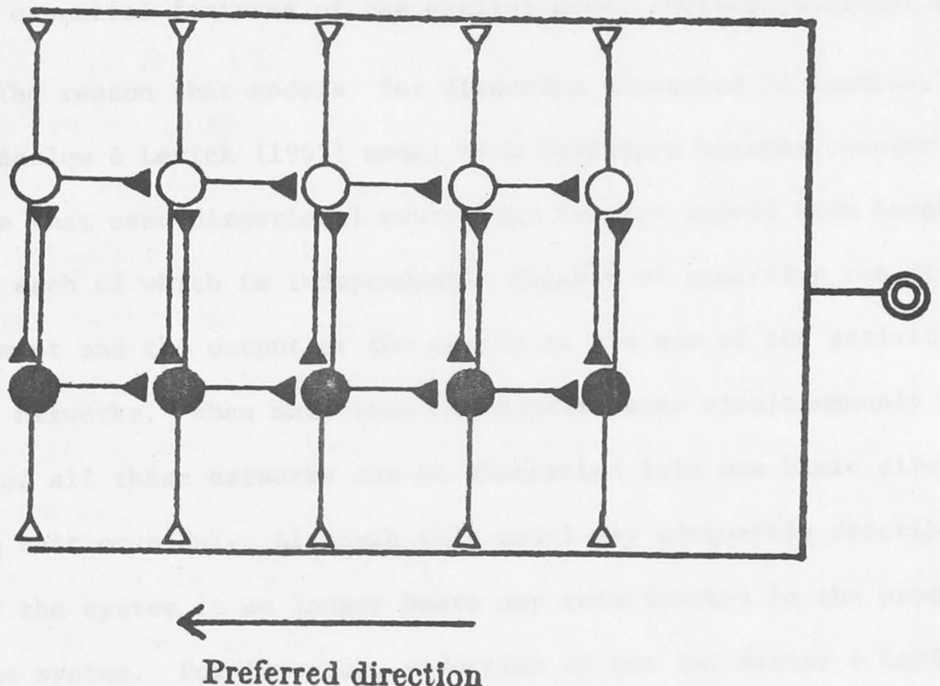


Fig. 59 A model of a neuronal network for directional selectivity proposed by Collett & Blest (1966). Open circles represent ON cells, closed circles are OFF cells. Open triangles are excitatory synapses, closed triangles are inhibitory synapses. ON and OFF neurons connect to the same directionally selective neuron whose preferred direction is from right to left.

1973). That these units form an asymmetric network has been tentatively suggested by Mimura (1972) on the basis of the spread of excitation in the preferred direction when two light spots are used. Such a network reproduces the essential features of the earlier model (Collett & Blest, 1966).

The reason that models for direction detection in insects, other than the Barlow & Levick (1965) model were developed becomes clearer when we realise that each directional neuron may receive inputs from several networks, each of which is independently capable of analysing the direction of a movement and the output of the neuron is the sum of the activity in all these networks. When more than one network acts simultaneously the activity of all these networks can be abstracted into one basic direction detecting unit or model. Although this model may adequately describe the output of the system, it no longer bears any relationship to the processes within the system. For instance, reduction of the two Barlow & Levick networks supplying the M1 neuron into their simplest form results in a basic unit providing inhibition in one direction and excitation in the other. Apart from the fact that the inputs respond not to steady light flux but only to increases in illumination, this abstracted unit resembles the multiplicative model (Reichardt, 1961) in many ways. Also, the model in Fig. 59 (Collett & Blest, 1966) shows that two separate asymmetric networks can reproduce the behaviour of the multiplicative model. Thus, any symmetrical model may be an abstract of the activity of several asymmetric networks which all connect to the same neuron. Therefore it is possible that all insects use the same Barlow & Levick networks as the vertebrates but their different arrangement, such as the convergence of several networks onto one neuron, has resulted in the erroneous belief that insects employ a different mechanism to create directional selectivity.

Although they utilise the same mode of direction analysis, there are slight differences between the individual networks in insects and

vertebrates. First in the locust, information from the whole visual field is supplied to a single directionally selective neuron while in the vertebrate retina the directionally selective ganglion cells have very small receptive fields. Their diameters are less than 4° in the rabbit, squirrel and chick (Barlow, Hill & Levick, 1964; Michael, 1968; Miles, 1972) and less than 8° in the goldfish (Daw & Beauchamp, 1972). Another difference between insects and vertebrates is the spacing of the interacting inputs. In insects these are quite widely separated, the visual angle between inputs being between approximately 6 and 15° in the locust (Chap. 3) and $5.2 - 6.0^{o}$ in the fly (Braitenberg, 1970; Kirschfeld, 1972). In vertebrates it is thought that the interacting inputs are neighbouring bipolar cells and their experimentally determined separation is 12-24' of arc (Barlow & Levick, 1965). The differences between insects and vertebrates may be the result of the different number of neurons in each nervous system. A large field optomotor neuron becomes more efficient at detecting only the animal's motion if its input already shows some form of selectivity which reduces the response to motion of an object within the visual field. Spacing the inputs provides clear information of the animal's movements where the whole visual field moves across the retina but will decrease the response to movements of small objects within the external environment (Chap. 3). Such a preliminary filtering is required where directional analysis for the whole visual field occurs in one step. In the vertebrate, the distinction between eye and object movement must be made by summing the responses of numerous small field directional neurons which can be recorded in many areas of the retina (Barlow et al., 1964).

Insect optomotor neurons do not possess the inhibitory surrounds (Chap. 2; McCann & Dill, 1969) which are present in directionally selective neurons in vertebrates (Barlow et al., 1964; Michael, 1968; Werblin, 1970; Miles, 1972). The role of the inhibitory surround in direction integration in the vertebrate retina is not yet known. In the rabbit, comparison of responses elicited by stimulation of only the directionally selective

centre with those elicited by stimulation of both centre and surround, revealed that the inhibitory surround depressed the initial transient of the response but did not usually reduce the discharge to a maintained movement. The only appreciable effect of surround stimulation on the maintained response was to reduce further the response to slow movements of those neurons whose centre already gave a greater response to faster movement (Oyster, Takahashi & Collewijn, 1972). The attractive hypothesis that the surround may sharpen velocity responses has not yet been tested in these directional neurons. In the chick, results from using bars or spots to stimulate the cell suggest that the surround may sharpen the directional selectivity of some neurons (Miles, 1972).

An unknown feature of both vertebrate and invertebrate direction detecting networks is the nature of the lateral interaction. In the inhibitory networks in Figs. 1A, 47, 48 and 59 each ON or OFF cell excites the direction selective neuron but inhibits its neighbour on one side. Either the neuron is capable of exerting two different effects at its endings or the lateral interaction is mediated by a separate neuron. It is no longer valid to exclude the possibility of the one neuron mediating both excitation and inhibition since experiments with Aplysia have clearly demonstrated that excitation, inhibition or even both actions are mediated on the follower cells by the same neuron (Blankenship, Wachtel & Kandel, 1971). Therefore both possibilities must be considered. In the vertebrate retina it has been necessary to assume that inhibition and excitation are mediated by the same cell. In a neuron circuit designed to fit the responses of retinal neurons and their known synaptic arrangements to the motion detecting model, Dowling (1970) has had to propose that one amacrine neuron provides an excitatory input to a ganglion cell and an inhibitory input to another amacrine cell. However the capability of visual interneurons in the vertebrate retina and insect lobes to mediate both excitatory and

inhibitory reactions remains to be conclusively demonstrated.

The anatomical pathways of optomotor systems

No optomotor system has been described completely from visual inputs to behavioural output. Motor outputs in some crustaceans and vertebrates have been analysed in detail (Horridge & Sandeman, 1964; Burrows & Horridge, 1968a,b; York, Wiersma & Yanagisawa, 1972; Robinson, 1972; Henn & Cohen, 1973) but in crustaceans little is known of the sensory interneurons and in the vertebrates the anatomical pathway of the optomotor system is not completely understood. In insects the relationship between sensory and motor neurons and the precise contribution of each motoneuron to a head movement are not clear although the sensory interneurons have been analysed in detail (e.g. Chaps. 2 and 3).

The sensory pathways in the insect optomotor system appear extremely simple. Each monocular directionally selective neuron originates in the medulla which is the second synaptic region of the optic neuropile (see above). The neuron passes to the protocerebrum where it combines with neurons from the other optic lobe to supply an input to a now binocular directionally selective neuron. Some of the binocular neurons return efferently to the optic lobes while other similar neurons pass to the ventral cord to reach the ganglia containing the appropriate motoneurons (Chap. 2; Bishop et al., 1968; McCann & Dill, 1969; Collett, 1970, 1971). There are cross inhibitory interactions between the directional neurons within each optic lobe, the directional neurons from both optic lobes and the binocular neurons (Chap. 2; Collett & Blest, 1966; Collett, 1971; McCann & Foster, 1971). These interactions may serve to sharpen directional selectivity (Levick et al., 1969) or coding of the number of ommatidia stimulated by each movement (Chap. 2). Information from these neurons must pass to the suboesophageal and thoracic ganglia where it can activate the

motoneurons involved in optomotor behaviour. The destination of optomotor neurons within the thoracic ganglia is completely unknown. The neurons may project to interneurons or they may synapse directly with the motoneurons. In the locust 205 motoneurons are involved in co-ordinating the activity of 32 muscles which move the head (Shepheard, 1973) and therefore the distribution of optomotor information must be extremely complex to allow all the muscles to produce a smooth following movement.

In crustacea both the anatomy and the function of the motoneurons innervating the eyecup muscles have been thoroughly examined (Burrows & Horridge, 1968b; Sandeman & Okajima, 1973) but nothing is known of the course of the sensory interneurons which supply the stimulus for eye movement.

The destination of the directionally selective neurons originating in the vertebrate retina is not known with any certainty. Fibre tracts pass from the retina via a relay to the visual cortex, and to the superior colliculus which also receives innervation from the visual cortex. Lesion and stimulation studies have shown that the superior colliculus plays an important part in mediating eye movements (Schiller, 1972) and many of the units in the colliculus are directionally selective (Gordon, 1973). There is no direct connection from the colliculus to the motor nuclei of the eye muscles and electrical stimulation of different brain regions has shown that the neuron circuit passes first through certain regions of the pontine reticular formation. These areas are directly connected to the motor nuclei (Cohen & Komatsuzaki, 1972).

Direction analysis by the optomotor system

The accurate following that can be observed during optomotor stimulation in different directions emphasises that the output from the directionally selective neurons must contain precise information on the direction of

any movement. However the individual neurons respond to movements whose directions are distributed about the preferred direction. The directional selectivity varies in different animals but most neurons give a small discharge to movements at 90° to the preferred-null axis (Chap. 2; Oyster, 1968; Bishop et al., 1968; Northrop & Guignon, 1970; Miles, 1972). This spread of directionality is advantageous as it increases the number of directions of movement to which the neuron can respond with p - n greater than zero, for if a neuron responds only to movements precisely in the preferred direction it gives no information on movements in any other direction. The neurons which respond to a broad range of directions can effectively perform a vector analysis by giving a smaller response as the direction of movement diverges from the preferred direction. If the preferred directions of several neurons are arranged around 360° their relative firing defines the direction of any motion.

In some vertebrates the preferred directions of the visual neurons are aligned with the line of action of the various eye muscles. For instance, in the rabbit the preferred directions of the ON-OFF directional neurons fall into 4 groups at approximately 90° to each other, coinciding with the lines of action of the four rectus muscles. The preferred directions of the ON type neurons lie in 3 groups at approximately 60° to each other. These neurons could still activate three of the four rectus muscles (Oyster, 1968). Summing the actions of these muscles sums all the vector components of the movement as detected by the directionally selective neurons causing the eye to follow the stimulus movement accurately. Thus in these vertebrates there is no complex central mechanism for integrating the direction of stimulus movement; this analysis is performed by means of the appropriate connections of the directionally selective neurons.

In insects the optomotor reflex must move, not the eyes, but the whole head which is supported in a complex fashion on the neck. Although

the directionally selective neurons have horizontal or vertical preferred directions, few of the neck muscles have these lines of action. For example, the locust, unlike the crab with its 9 eye muscles (Burrows & Horridge, 1968a), has 16 pairs of muscles to move the head. Only one pair contributes a pure yaw movement, the others all contributing a mixture of yaw and roll (Shepheard, 1969). It is most probable that each neuron connects either indirectly, via interneurons, or directly to a large number of motoneurons whose muscles can contribute to a movement in the preferred direction of that neuron. The vector summing would then be performed in two stages; the action of each muscle must be the sum of its vector inputs and the head movement is the sum of the actions of all the muscles. The same two stages of vector summing would occur in all insects regardless of whether the preferred directions of the neurons fall into 3 groups as in locust (Chap. 2; forward, up, back) or into 4 groups (up, down, forward and back) as in fly, moth and butterfly (Collett & Blest, 1966; Swihart, 1968; Bishop et al., 1968; McCann & Dill, 1969).

In some insects, the moth (Collett & Blest, 1966; Collett, 1970), the fly (McCann & Foster, 1971) and the beetle (Frantsevich & Makrushkov, 1970), directionally selective neurons have been recorded in the ventral cord below the suboesophageal ganglion and in the thoracic ganglia. Presumably these neurons mediate the optomotor steering of flight (Götz, 1968, 1972) and walking (Reichardt, 1961). The same stages of vector summation as for head movement probably occur although again the precise neuronal mechanisms are unknown. The mechanism of connecting neurons to muscles with similar lines of action is the simplest method of directional analysis and is probably widespread.

Velocity coding by the optomotor system

Studies of optomotor behaviour in vertebrates and crustacea show

that the optomotor system acts as a velocity correcting servo. Simple closed loop experiments (where the stimulated eye is free to move) or open loop experiments (where the seeing eye is clamped and a blinded eye is free to move) have demonstrated that the output of the system is the velocity of eye movement. The eye velocity approaches, but never reaches, that of the stimulus and the input to the system is the difference between the stimulus speed and the eye speed, i.e. the slip speed (Horridge & Sandeman, 1964; Collewijn, 1969; Koerner & Schiller, 1972).

It has previously been thought that absolute velocity could be determined in the central nervous system by a discrimination using two or more neurons with overlapping velocity-response functions (e.g. Bishop & Kaiser, 1970) in much the same way as colour discriminations are made (Menzel, 1973a). However most insects possess only one type of velocity coding neuron, e.g. neurons peaking at velocities of 30°/sec (locust M2, Chap. 2,3), 50-60°/sec (moth, Collett & Blest, 1966), 50-200°/sec (flies, Bishop & Keehn, 1967). (Too little is known of the properties of the bee neuron in Fig. 34 to ascribe to it the function of a velocity coder. At present only one velocity coder has been described for bee, peaking at velocities of 40-150°/sec; Kaiser & Bishop, 1970; Chap. 2). The chick directionally selective neurons show only one type of velocity-response function, the firing rate increases with velocity and has not reached a peak at velocities of 200°/sec (Miles, 1972). In the rabbit two velocity coders have been recorded (Oyster et al., 1972) but only one type would be used under normal conditions (Collewijn & van der Mark, 1972). Therefore the velocity coding must be performed by only one neuron type in most animals and there can be no determination of absolute velocity.

In each neuron different stimulus velocities can elicit the same firing rate if one velocity is less than, and one is greater than, the velocity eliciting the maximum firing rate. Therefore an essential

consequence of any hypothesis that the output of a single velocity coder sets the velocity of eye or head movement is that similar ambiguities, where different stimulus velocities evoke the same eye velocity, should be observed. Indeed, such ambiguities have been demonstrated in crab, rabbit and monkey (Horridge & Sandeman, 1964; Collewijn, 1969; Koerner & Schiller, 1972) and in the locust and the rabbit under open loop conditions the behavioural velocity-response function closely resembles the velocity-response functions of the directional neurons (Oyster et al., 1972; cf Thorson, 1966b with Figs. 27, 43B). For example, with fast stimuli the difference between stimulus and eye velocity increases, thereby increasing the slip speed or effective stimulus but the actual eye velocity decreases. The slip speeds which result in the decreasing eye velocities equal the stimulus speeds which provoke decreasing firing rates in the directionally selective neurons. The close fit of the firing rate of the optomotor neurons under open loop conditions to the observed open loop eye velocity can be expressed as

$$F_o \propto V_o \qquad (1)$$

where F_o is the firing rate of the optomotor neuron in spikes/sec and V_o is the velocity of the eye or head. Equ. 1 must hold true for closed loop conditions also but as the neurons cannot be recorded under closed loop conditions this relationship cannot be verified directly. However, when Collewijn's (1969) data is converted from drum velocity vs eye velocity to slip speed vs eye velocity an agreement is revealed between eye velocity and the neurons' velocity-response functions under open loop conditions.

The poor velocity compensation at high velocities is insignificant under normal circumstances. As has been emphasised repeatedly (Horridge & Sandeman, 1964; Collewijn & van der Mark, 1972; Robinson, 1972) the

optomotor system stabilises the eyes or head against their own movement. The situation where the reflex causes the eye to follow an external movement is thoroughly artificial and is used experimentally only because of its great manipulative convenience. The optomotor system normally functions at the velocities at which the eyes or head move. In the rabbit units contributing the major input to the optomotor system, the ON type units, peak at input velocities of 0.4^{o}/sec (Oyster et al., 1972). Under normal conditions at rest the rabbit's eyes move at a maximum velocity of 1°/sec but most movements are at velocities below 0.5^{o}/sec (Collewijn & van der Mark, 1972). In insects, the optomotor reflex must cope with any turning movement of the head as well as drifts or errors in flight. Correspondingly, we find that the velocity maxima of the optomotor neurons ranges from 30-200°/sec and the insects are unlikely to exceed these high angular velocities during drifts or veering movements during walking or flying. Thus, the one velocity coder in each animal provides sufficient information to allow good compensation for any velocity of movement that would be encountered under normal conditions. Ambiguities can only be demonstrated in artificial conditions.

Once we have established that absolute velocity is not coded but that eye or head velocity closely follows the firing rate of the optomotor interneurons we can consider the nature of the connections between the optomotor interneurons and the motoneurons. Many studies in vertebrates have related the firing rate of the eye muscle motoneurons to an absolute eye position, i.e. each firing rate of the motoneuron determines a specific eye position (Robinson, 1970, 1972). However a recent evaluation of saccadic movements and fixation (Henn & Cohen, 1973) has shown that this is not the case; each eye position must be regarded as a change from the previous position and the new position is determined by the change in firing of the motoneurons, not by the absolute firing rate as in Equ. 2

$$\Delta P \propto \Delta F_m . T \qquad (2)$$

where ΔP is the change in position of the eye, ΔF_m is the change in firing rate of the motoneuron and T is the duration of the movement. Equ. 2 can be rewritten as

$$\Delta F_m \propto \frac{\Delta P}{T} \quad \text{or} \quad \frac{dF_m}{dt} \propto V_o \qquad (3)$$

Substituting from Equ. 1 we have

$$F_o \propto \frac{dF_m}{dt} \propto V_o \quad \text{and} \quad F_m \propto \int F_o \, dt \qquad (4)$$

Equ. 4 means that the motoneuron (or an intermediate neuron) performs an integration on every firing rate of the optomotor interneuron. This preset increase of motoneuron firing rate determines the rate of contraction of the muscle and thereby the eye velocity. When we remember that each sensory neuron probably sends information to the muscle whose line of action coincides with the neuron's preferred direction, we see that the rate of firing of the optomotor neuron determines the rate of movement in the appropriate direction.

A major characteristic of any system is its gain. For the overall optomotor system, gain $(\frac{\text{output}}{\text{input}})$ can be defined as $\frac{\text{eye velocity}}{\text{slip speed}}$. In both vertebrates and invertebrates there is a high gain at low slip speeds (up to 100 in the rabbit and 15 in the crab at 0.001°/sec), and gain falls below 1 as slip speed increases (Horridge & Sandeman, 1964; Collewijn, 1969; Koerner & Schiller, 1972). As the firing rate of the optomotor neurons has a fixed relationship to the firing in the muscle this gain must lie between the stimulus and optomotor neuron. In fact, a plot of gain, as $\frac{F_o}{\text{slip speed}}$,

from the velocity-response functions of rabbit directional neurons given by Oyster et al. (1972) is identical in shape to the plot of gain derived from behavioural studies (Collewijn, 1969). The gain in locust, derived from the velocity-response functions of the M2 neuron (Chaps. 2 & 3) also is high at low stimulus velocities and low at faster speeds. Converting the oscillation frequency in Fig. 43B to angular velocity, we find that at a velocity of 1.5^{o}/sec gain is 23.3; at a velocity of 23°/sec gain is 3.3 and at 154°/sec gain is 0.2. The optomotor system can now be entirely described by

$$G.V_{slip} = F_o, \quad F_o \propto \frac{dF_m}{dt} \propto V_o \qquad (5)$$

where G is the optomotor neuron gain, V_{slip} is the slip speed. The optomotor neuron gain is related to the system gain by a constant.

The advantages of low gain at high slip speeds and high gain at low speeds are clear. When a movement commences the slip speed is high and the low gain causes the eye to move relatively slowly. As the eye compensates the slip speed drops, the gain increases and the eye velocity quickly approaches its maximum for that slip speed. The change in gain causes a rapid adjustment to the correct eye velocity and prevents an initial overshoot. For very slow movements the gain is high even before the eye compensates and one might expect an overshoot. However as shown in Fig. 44 the neurons take some time to reach their maximum firing rate for a low velocity. The consequence is that at the start of a slow movement the initial low firing provokes a slower movement than would occur if the firing rate had reached its maximum immediately. As the eye moves the slip speed falls and the firing rate is now more appropriate to the new slip speed and no overshoot has occurred. Not only does this mechanism explain the almost immediate rise to a constant velocity for low stimulus movements in the

closed loop situation but it also explains the slow rise to a constant velocity in the open loop situation. This rise was previously thought to be due to a double integration at the output (Collewijn, 1969, 1972).

The nature of the integration between F_o and F_m is not yet clear. It is possible that each spike in the optomotor interneuron elicits a burst of spikes in the motoneuron. Close coincidence of these bursts could result in a steady increase of motoneuron spike rate by facilitation. The decay time of the excitation elicited by each optomotor neuron spike may account for some of the long time constants observed in the system (Horridge & Burrows, 1968a). Without a firing maximum in the motoneuron, a long lasting movement would raise the motoneuron firing rate until the neuron was saturated. The firing rate would no longer change and the eye would stop moving. To prevent this instability, vertebrates and crustacea show a fast flick back, a fast movement which returns the eye close to its original position and resets the firing rate of the motoneurons (Horridge & Sandeman, 1964; Collewijn, 1969). Many insects do not show regular flick back or fast phases but they can be induced after a long lasting movement during which the head has moved as far laterally as possible. The next stimulus can evoke a countermovement, returning the head to its normal position whereupon another stimulus evokes a normal following response (observations during experiments in Chap. 1). Very brief saccades observed in fly during optomotor stimulation (Land, 1973) may serve a similar function.

The previous functional models of the optomotor system have contained summing stages, differentiations, limiting stages and double integrating output stages (Robinson, 1972; Collewijn, 1972). The model described here (Equ. 5) where the firing rate of the optomotor neuron sets the rate of change of the firing rate of the motoneuron includes all these stages. The summing stages, differentiators and limiting stages are all combined in the response of the directionally selective neurons. The summing stage

represents the acquisition of information from the whole eye; the differentiators and the limits are contained in the velocity-response function of each neuron. The first of the two integrations which were required to explain the gradual increase in eye velocity to slow movements in the open loop condition, is actually included in the response of the optomotor interneuron. It was described above how the finite rise time of the firing rate of the directional neurons accounted for the behavioural result. The final integrator, responsible for the change in the motoneuron firing rate elicited by a constant input, must reside between optomotor interneuron and motoneuron. This simple reflex arc, monocular neuron-binocular neuron-(interneuron?)-motoneuron is compatible with the anatomy of the invertebrate nervous system. In the vertebrate the reflex arc must contain more neurons as the anatomical connections are more complicated. However the close relationship between the directionally selective neurons and the eye velocity shows that the overall functional simplicity prevails.

The function of the optomotor response in normal behaviour

In animals which move their eyes the optomotor response is a compensating reflex which stabilises the eyes with respect to a visual background. This function can be demonstrated simply by monitoring the eye movements in the dark. The eyes wander about and drift for long periods whereas in the light, against a patterned background, the eyes make fewer excursions and these are smaller and slower (Horridge & Burrows, 1968b; Collewijn & van der Mark, 1972). The direction detecting neurons in the rabbit show a maximum response and an extremely high gain to movements with velocities equal to the normal speed of eye movement or drift (Collewijn, 1969; Collewijn & van der Mark, 1972; Oyster et al., 1972) demonstrating an excellent match of response properties to function. In animals with organs of balance, information on body movements provided by these organs

elicits compensatory eye movements via a simple reflex loop (Highstein, 1973). The compensatory eye movements elicited by organs of balance is beyond the scope of this discussion but it must be remembered that the output of the balance organs interacts with the optomotor output to stabilise the eyes with respect to the visual background when both the eyes and the body are moving. In insects with their fixed eyes, the optomotor response must compensate for head movement. Head tremors and drifts have been recorded from insects left in the dark (Horridge, 1966c) and the optomotor system minimises these in the light.

The optomotor system must function during walking, flying and swimming in all animals. Any deviation from motion in a straight line results in a rotation of the visual environment about the head. This rotation stimulates the optomotor neurons, eliciting a compensatory movement which maintains the motion in a straight line (Götz, 1969, 1972; Wilson & Hoy, 1968). During flight an animal can set its long axis at a certain angle to the horizon and any deviation from this position results in a movement of the horizon relative to the eye. The compensating movement elicited by the optomotor reflex returns the animal to its original setting (Goodman, 1965). Speed can be controlled similarly by monitoring the relative movement of landmarks across the retina (Bastian, 1972).

The requirement for the optomotor system to function at high velocities during turning in flight in insects explains the velocity peak at 30-200°/sec of their optomotor neurons (Chaps. 2 & 3; Collett & Blest, 1966; Bishop & Keehn, 1967) as compared with the 0.5^{o}/sec peak in a non-flying animal (Oyster et al., 1972). Birds, like insects, can turn at high speeds during flight and similarly their directionally selective neurons respond to velocities up to 200°/sec without reaching a maximum (Miles, 1972).

Tracking behaviour and voluntary movements

The optomotor system keeps the animal moving in a constant direction and prevents the eyes from drifting. However if the optomotor system were not overridden no voluntary movement or turning would be possible. Apart from voluntary deviations from a straight course, particular behaviours where it is desirable to suppress the optomotor reflex are saccadic eye movements, scanning eye movements and tracking or smooth pursuit responses.

Tracking or smooth pursuit behaviour provides an excellent example of a behaviour where optomotor compensation must be overcome. The tracking behaviour resembles optomotor behaviour in that the effective stimulus is a velocity error signal which the eye movement tends to reduce. Unlike the optomotor system the error signal is not the velocity of the background relative to the eye but the speed relative to the eye of an object moving against a background. The eye follows the object to reduce the slip speed between object and eye but in the process generates a large slip speed between eye and background. The optomotor response must be overruled or else it would terminate tracking to reduce the slip speed of the background.

Very little is known of the neuronal basis of tracking behaviour. In foveate vertebrates, it seems quite plausible that in the fovea there are many neurons detecting the direction of object movement. Stimulation of these neurons would cause the fovea to follow the object movement in the same way as stimulation of the optomotor neurons elicits as optomotor movement. The simplest scheme is one where these neurons drive the eye against an opposing movement generated by the optomotor neurons, the foveal neurons dominating the response by strength of numbers. That this scheme (hypothesised by Robinson, 1972) may be oversimplified is suggested by the occurrence of neurons in the monkey visual cortex which respond

only to target motion relative to a background but not to target or background movement alone (Bridgeman, 1972).

Neurons, in the moth optic lobe, possibly subserving tracking have a small directional centre and a large inhibitory surround. Movements of large stimuli in the surround in the preferred direction of the field centre suppress the response to target movement across the field centre, while movements of large stimuli across the surround in the null direction may enhance the response to the same target movement. Thus these neurons respond optimally to an object moving against a moving background, precisely the situation which occurs during tracking (Collett, 1971a; 1972). Other directional neurons responding selectively to object movement and not background movement have been reported in the locust (Chap. 4) and in crustacea (Wiersma & Yamaguchi, 1967; Wiersma & Yanagisawa, 1971) but their responses to a target moving against a moving background have not been tested.

The properties of the possible tracking neurons in no way clarify the relationship between tracking and optomotor behaviour. Either tracking and optomotor neurons evoke opposing head torques which are summed to give the final response, or the optomotor reflex is suppressed. There is some evidence for the absence of optomotor responses during other eye movements in crab and fly. In the fly saccadic eye movements occur during optomotor following which starts afresh after each saccade (Land, 1973) with no evidence that there is any optomotor compensation for the rapid eye movement. However, the velocity of the eye during the saccade is 500°/sec (Land, 1973), a speed at which the optomotor neurons no longer fire (Bishop & Keehn, 1967) and the absence of optomotor responses during saccades is caused simply by a failure to stimulate the optomotor neurons.

In the crab, voluntary movement of a seeing eye has no effect on the motion of the other, blinded eye whereas forced movement of the seeing

eye causes reflex compensation of the blinded eye. The failure to compensate during voluntary movements is not due to efferent copy or any simple sensory mechanism (Horridge & Burrows, 1968c). Similarly, in the locust voluntary movements of the legs across the eye fail to dishabituate the DMD neuron while almost identical movements of external objects cause complete dishabituation (Rowell, 1971c). Therefore it appears that, at least in some cases, voluntary movements suppress responses in visual neurons by a mechanism which is at present unknown. It is possible that there is a switch within the optomotor system similar to the arousal switch in the suboesophageal ganglion which is described in Part II.

Conclusion

This review has described briefly what is currently known of optomotor systems. No animal has provided information on the optomotor system in its entirety; some, such as the locust, provide information on the nature of sensory integration in the optomotor system (Chaps. 1-3) whereas others, such as the crab, provide detailed information on a relatively simple motor output. The picture that emerges from a comparison of data from different animals shows a remarkable uniformity of both function and neural wiring in all optomotor systems. These systems can be described as simple reflex arcs whose response properties are exquisitely matched to the behaviour of the animal.

The mode of interaction of optomotor behaviour with other more complex behaviours, such as smooth pursuit, is still unknown. Also unknown are all the causes of variability in the expression of the reflex. Part II deals with the problem of modulation of the optomotor response by different ongoing behaviours and relates variations of response to changes in the animal's behavioural excitability.

PART II

CHAPTER 5 The Optomotor Response and Arousal State

Introduction

'Arousing' stimuli, such as sharp flicks of the striped drum (Horridge, 1966a,c) or weak electrical stimulation of head parts (Burrows & Horridge, 1968c) improve the optomotor performance of an animal which has not been responding to steady movements of the drum. Also, the firing rate of motoneurons activated during optomotor responses in crabs and crayfish more than doubles as the animal becomes more 'excited' (Wiersma & Oberjat, 1968; Wiersma & Fiore, 1971). These improvements in optomotor behaviour in crabs, crayfish and locusts all coincide with 'excited' state. This state has always been defined by the occurrence or increase of spontaneous locomotor or mouthpart movements or increases in respiration rate and respiratory movements (Wiersma & Yamaguchi, 1967; Rowell, 1971b). 'Excited state' seems to be equivalent to the concept of arousal which is widely accepted for vertebrates (Lindsley, 1951). Therefore, I will refer only to arousal level, which is the position on the arousal continuum at any time.

In vertebrates, especially mammals, differing levels of arousal are easily distinguished. For example, an alert mammal sits up and moves its body or eyes frequently; a nonalert animal may lie down but will have its eyes open. When less alert, the animal falls asleep (Walsh & Cordeau, 1965; Malcolm, Bruce & Burke, 1970). A variety of neurophysiological changes have been found to be correlated with these changes in behavioural state, e.g. the elctrocorticogram and gross hippocampal activity (Walsh & Cordeau, 1965) and these can now be used as precise indicators or measures of the animal's arousal level, even in cases where the animal is restrained

and cannot behave freely.

No generalised physiological indicator of arousal level has been defined for invertebrates. The responses of some neurons in the crayfish (Arechiga & Wiersma, 1969a) and locust (DMD neuron Rowell, 1971a,b) which change with arousal level are not useful as a general arousal indicator as the measurements can be quite complex. In crustacea one useful and easily measured indicator is heart rate which decreases as excited state increases (Larimer, 1964). This finding has not been confirmed in other arthropod groups. Respiration rate may also be a useful measure but a detailed correlation of respiration with behaviour is required before this can be reliably used. This means that for the time being, behavioural description coupled with description of changes in muscle activity are the only definitions of arousal state or excitement that can be used for invertebrates.

A major function or result of increased arousal in mammals is an improvement of sensory and motor transmission (Grossman, 1967). In invertebrates the known effects of 'arousing' stimuli on optomotor performance suggest that increase in arousal may function in a similar way and improve reflex responsiveness. Conversely experiments to be described in this section show that decreased reflex responsiveness results from a low arousal level and the experiments demonstrate the existence of a visual arousing system. This system appears to be the visual aspect of a general nonspecific arousal system in the locust which, as Rowell suggested (1971b,c), is completely comparable in function to the vertebrate reticular arousing system.

Optomotor head movements in different states of arousal

The optomotor performance of a locust held in a striped drum improves after stimulation which causes behavioural arousal (Horridge,

1966c). This finding implies that the optomotor performance improves with increasing level of arousal. Conversely, the performance should decrease with a decrease in arousal. The following experiments demonstrate that this is so.

A locust, intact but for the removal of the metathoracic legs, was held by the thorax and the coxae of all legs. Usually the head, prothorax and thorax were waxed together. In some experiments the head was left free but this was found to make little difference to the results. Myograms were recorded with fine insulated copper wires (dia. 0.1mm) bared only at the tips. These wires were inserted through small holes drilled in the cuticle and were waxed in place. AC coupled recordings were made differentially (Devices 3160 amplifiers) between the wire and a stainless steel pin inserted deep into the abdomen. Wire positions were verified visually after each experiment. The neck was opened with the wires firmly waxed in place and the tissue was fixed in alcoholic Bouin's solution for 1 hour to allow easier identification of the individual muscles. The wire position relative to the muscle could be seen quite clearly.

The neck muscles have been described and numbered by Misra (1946) and their innervation and participation in the optomotor response has been described in detail by Shepheard (1969, 1973). The muscles studied here were muscles 50 and 51 on either or both sides. These muscles receive the same excitatory innervation from the suboesophageal ganglion and myograms from the two muscles are very similar. These muscles (mainly 51 which is much larger) are the muscles which turn the head horizontally and are involved in responses to horizontal movements of a pattern. Although many other muscles participate in this movement, they contribute varying amounts of roll.

The locusts became very quiet when left, restrained, in the dark for several hours; all voluntary movements ceased and no muscle activity

was recorded. Occasionally, however, there were sudden short periods of muscle activity together with random leg and abdomen movements. This activity was followed by complete quiescence. These sudden changes in activity are similar to those seen in the locust leg muscles (Hoyle, 1964) and in the DMD neuron whose responsiveness decreases in the dark but can be restored after a period of illumination (Rowell & Horn, 1968). As the DMD behaviour was correlated with arousal changes, the similar behaviour here is also most likely correlated with arousal changes. In the dark, as the animal becomes quieter the arousal or excited state declines. The sudden waves of movement represent spontaneous increases in arousal from this low nonexcited level.

The optomotor response was examined during the different levels of arousal (as indicated by the animal's activity). Movements of a small lamp (torch bulb 2.5V, 0.3 Amp) were used to evoke optomotor responses. This stimulus was not as effective as the oscillating striped pattern but could be better used in the dark and while the background illumination was altered. In normal room light (61.5 cd/m^2) when the lamp was moved around the head, either the animal moved if its head was free or there was an increase in the activity of the appropriate muscles. That is, a clockwise movement about the animal caused an increase in the potentials recorded in the right muscle 50, 51 and a decrease in the left. Anticlockwise movement produced the reverse effect (Fig. 60a,b). When the animal had been left in the dark for a ½ hour or longer the same movement of the lamp (after the initial ON response had ceased - see below) failed to elicit these regular optomotor patterns. Instead the lamp movements provoked a large burst of muscle activity simultaneously on both sides (Fig. 60e,f), and often evoked random leg and abdomen movements which lasted some minutes. This activity was similar to that during spontaneous arousal. This large nonspecific response was only obtained reliably after at least a ½ hour in the dark.

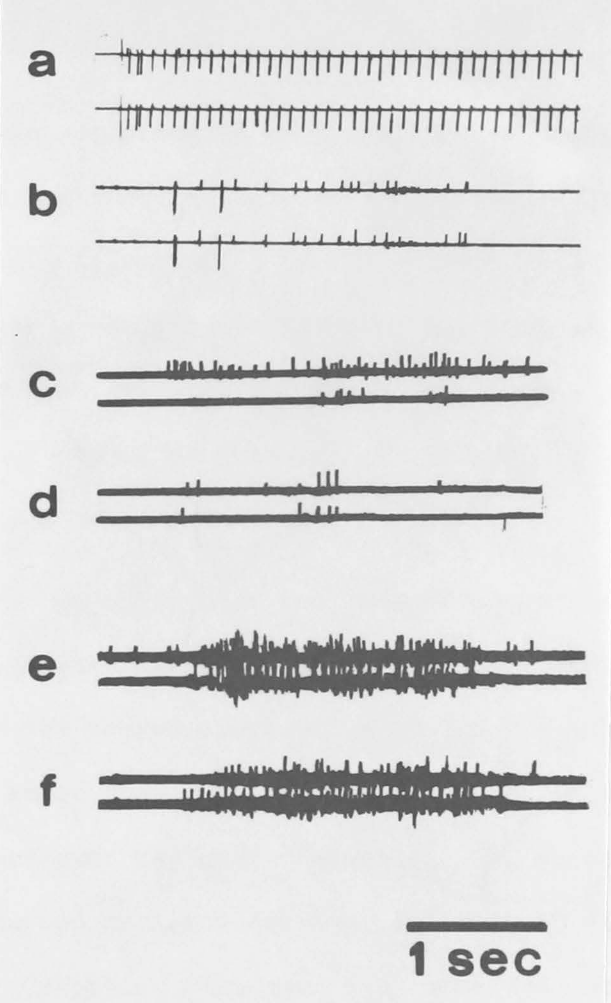


Fig. 60 Neck muscle responses of a locust, with its head fixed, to movements of a small lamp with different background illuminations. (a,b) bright room light (61.5 cd/m^2), top trace shows activity from left muscle 50, lower from left 51. (a) lamp moves anticlockwise (to the left); (b) lamp moves clockwise (to the right). (c,d) dim light (26.6 cd/m^2), top trace shows left muscle 51, lower is from right muscle 51. (c) anticlockwise movement, (d) clockwise movement. (e,f) recordings as in (c) and (d). Lamp moves in an otherwise dark room, anticlockwise (e) and clockwise (f). Note the simultaneous discharges on both sides in the dark and the lack of directional response on the right side in lim light. In bright light there is a large response on the left side to movements to the left; movements to the right reduce this considerably.

The continuous presence of an illuminated background containing contrasting areas improved the optomotor response. This background could be provided by a dim illumination of the laboratory (26.6 cd/m^2)* so that both eyes could see a variety of objects. Now some directionality of response could be seen (Fig. 60c) although the responses were not as clear as those seen using normal room light. There were no large bursts of activity simultaneously on both sides.

It is most unlikely that the loss of optomotor responses in the animals left in the dark is due to peripheral dark adaptation. Firstly, the loss of optomotor responses requires at least a ½ hour in the dark whereas retinula cells show most change in adaptation in the first 3 minutes and a slight change over the next 3 minutes. The mitochondrial movement from the light adapted position develops fully in 15 minutes (Tunstall & Horridge, 1967). Optomotor responses have been demonstrated at light levels low enough to cause considerable dark adaptation in the locust (Thorson, 1966a), in dark adapted bees (Kunze, 1961) and flies (McCann & Foster, 1973). The responses are reduced in all cases at low light levels but a clearly directional response is still obtainable. It must be remembered also that the lamp intensity did not change in the experiments here but the contrast between it and the background increased as the background became darker. This would make the lamp an equally or more effective stimulus in the dark than in the dim light as the optomotor reaction shows a greater dependency on contrast than overall illumination (Kunze, 1961; Thorson, 1966a).

It is also unlikely that the irregular bursts of activity evoked by the lamp in an otherwise dark environment should result from an instability due to lack of visual background. The optomotor response is itself the visual response that stabilises the head or eye (Horridge & Sandeman, 1964; Collewijn, 1969). The stimulus is sufficient to excite

*All given luminances are the luminances of white paper surface measured with meter at the position of the eye.

the optomotor neurons in the light. In the dark the lamp should also be an effective stimulus as the contrast between lamp and background is greater. Therefore the responses are not due to failure to excite the optomotor system.

Leaving the animal in the dark for long periods has two clear effects; there is no light induced excitation in the ocelli and arousal level drops. In flying Schistocerca ocellar occlusion reduces the steering efficiency of the optomotor response (Goodman, 1965) but ocellar occlusion had no apparent effect on the Chortoicetes optomotor preparations used here (Chap. 1). Therefore, the change in arousal that occurs after the animal is left in the dark for some time must be the factor which changes the response. The previously reported effects of arousing stimuli in crabs, crayfish and locusts (Horridge, 1966a,c; Burrows & Horridge, 1968c; Wiersma & Oberjat, 1968; Wiersma & Fiore, 1971) have been to increase the firing rate of the optomotor motor neurons and improve the optomotor performance. The results here show that decreased arousal reduces optomotor performance and that if the arousal level of the animal is too low no optomotor response can be obtained. Instead the stimulus will evoke large amounts of nonspecific activity.

Transmission of optomotor information to thoracic ganglia

The function of the optomotor response in the normal behaviour of the insect is both to stabilise the head with respect to a visual background after its own movement and to distinguish between movements of the head and movements of objects in the environment (Horridge & Sandeman, 1964; Collewijn, 1969). Thus the optomotor response must be essential in the visual regulation of walking and flight (see Pringle 1968 for review). Optomotor fibres have been found in the ventral cords of flies (McCann &

Foster, 1971), moths (Collett, 1970), butterflies (Swihart, 1969) and beetles (Frantsevich & Makrushkov, 1970). However detailed searches in the locust ventral cord (Horridge et al., 1965; Catton & Chakraborty, 1969, and mine) have failed to reveal any direction sensitive neurons below the suboesophageal ganglion. All these searches have been made in dissected and restrained locusts which differ enormously from the freely behaving animal (Rowell, 1971b). In the experiments reported here a much less restrained preparation for electrophysiology than those previously used was compared with a more restrained behavioural preparation in order to determine the factors responsible for the failure to find directional units in the ventral nerve cord.

It has been suggested (Goodman, 1965) that in the flying locust, optomotor information is used in the maintenance of body position indirectly through proprio- and mechano-receptors activated by head movement. This was tested in the following experiments with walking locust. First, the walking response of the completely intact locust was examined. A locust, with both eyes and all ocelli uncovered, was placed in a deep petri dish lying horizontally in the centre of the optomotor drum used previously (Chap. 1) and was observed from above.

When the drum was turned the locust either moved only its head or changed its body orientation as well, sometimes walking in the direction of drum movement. Both walking and shifts of body orientation in the direction of the stimulus were regarded as following responses (Table 4A). This walking optomotor response is the equivalent of the well known Y maze or ball running behaviour of the beetle (Reichardt, 1961). Next, the head and prothorax were waxed to the thorax making the locust completely rigid from head to metathorax. This animal made stronger positive body and walking movements than when the head was free (Table 4A), demonstrating conclusively that head movement is not necessary for the transmission of optomotor

information and that this information is transmitted directly to the thoracic ganglia. These larger movements when the head is fixed could be expected as the optomotor response is a stabilising reflex which utilises a visual feedback (Horridge & Sandeman, 1964; Collewijn, 1969). In the free animal the head can often move sufficiently to reduce visual stimulation and there is less need for further compensation by moving the body. When the head is fixed all compensation must be made by body movement.

Further evidence that there is direct transmission of optomotor information to thoracic ganglia comes from experiments where the sensory inflow to the pro- and mesothoracic ganglia from the thorax was abnormal. As before, the head and prothorax were firmly waxed to the thorax. The pro- and mesothoracic legs were also completely waxed to the thorax, leaving only the metathoracic legs free to push the insect around on its sternum. The animal still made clear and reliable turning responses using the metathoracic legs (Table 4A). Therefore the optomotor transmission to a ganglion is independent of sensory inflow from the thorax.

As some degree of restraint does not affect transmission other factors must be responsible for the difference between the preparation for electrophysiology and the behavioural preparations. One difference is the illumination level. Whereas in behavioural tests the animals are usually left in bright light, electrophysiological experiments are usually made in a darkened room and stimuli are presented to one eye only while data is collected. As altering the illumination level was found to affect the head movement optomotor response, its effect on the walking optomotor response was also tested. The locust with its head free was first tested in normal light (see Table 4B) in which the luminance of the white stripes was 68.4 cd/m^2. The light was switched off and the animal was left quite undisturbed in the petri dish for a ½ hour in darkness. Then the room was lit dimly (luminance of white stripe was 0.36 cd/m^2) and the animal tested

TABLE 4 A. Optomotor head movements and walking responses with varying degrees of restraint. Each row represents data from 1 animal.

	Trials with following movements of head only	Trials with following movements of body & head	Trials with failures	Trials with errors
Head & prothorax free	8 12	37 33	5 5	0 0
Head & prothorax waxed to thorax	- -	46 45	3 3	1 2
Head & prothorax fixed to thorax pro- & meso-legs fixed to thorax	-	37	12	1

TABLE 4 B. Optomotor head movement and walking responses after changes in light intensity. Each row represents 1 animal. Here the head was free. Numbers in brackets are total no. of trials where the head followed.

	Trials with following movements of head only	Trials with following movements of body & head	Trials with failures	Trials with errors
Normal room light (pattern luminance 68.4 cd/m^2)	24 (45)	21	4	1
Dim light (pattern luminance 0.36 cd/m^2) after ½ hr in the dark	9 (20)	11	26	4
Normal room light 5-15 min after a ½ hr in the dark	23 (38)	15	12	0
Normal room light 40 min after ½ hr in the dark	20 (43)	23	7	0

5 minutes later. The testing took 5 - 10 minutes. In the dim light the number of head and body movements was reduced by 50% (Table 4B) but there were few errors. The animal was left in the dark again for a ½ hour. 5 minutes after full room light was turned on head movement responses had returned to their original level in the light but there were still only a small number of body movements. After an undisturbed ½ hour in the light, the body responses had returned to the pre-dark level (Table 4B).

The data in Table 4B shows that the alteration of illumination has a marked effect on body movement responses. Again, peripheral adaptation cannot be a cause as each test was made only when the animal was adapted to that light level. The poor responses in the dim light could be due to the luminance of the pattern falling in the lower part of the intensity-response function (see Thorson, 1966a). However body movements did not increase when the animal was tested in bright light after a ½ hour dark period. Therefore stimulus intensity was not the factor determining these responses. The same light related arousal mechanism which modifies the head movement responses appears to control body movement responses and the slower recovery of these body responses suggests that they are even more dependent on arousal than the head movement responses (Table 4B).

The dissected and restrained animal is at a much lower arousal level than the freely moving animal (Rowell, 1971b; Wiersma & Fiore, 1971). As the body movement response is extremely dependent on arousal level, the neural system mediating the response may be switched off in the standard electrophysiological preparation. Therefore a less restrained electrophysiological preparation was used in an attempt to maintain arousal. The animal was pinned ventral side up by 4 dissecting pins each in a corner of the thorax. The head and prothorax were left free to move and head movements were monitored. The legs were secured with plasticene over the coxae only and all other portions of the legs and the abdomen were free to

move. The meso- and metathoracic ganglia were lifted and pinned to a waxed spoon. Extracellular recordings were made with KCl-filled glass microelectrodes (5-30MΩ) and signals were amplified and photographed from the oscilloscope or stored on tape. Oscillating stripes were projected onto the white diffuser as in the previous electrophysiological experiments (Chap. 2).

Animals prepared in this way made reliable optomotor responses for only 2 hours after the start of dissection. Then the following responses disappeared and did not recover even after rests of up to 5 minutes. Blowing on the head did evoke short bursts of head movements but these were irregular and subsided quickly. Recordings could be made for a short time during head movements but most recordings had to be made after regular head movements ceased. The connective was penetrated at its anterior entrance to the metathoracic ganglion. Thorough searches were made but again no directionally sensitive neurons were found although many other neuron types could reliably be recorded from this preparation.

Abbreviated Schistocerca preparations can maintain continuous responses for up to 6 hours (Thorson, 1966a). So the failure of the inverted Chortoicetes to maintain an optomotor head response for more than 2 hours is surprising. It is possible that the inversion of the animal for simplest dissection placed an extra strain on the muscles supporting the head and that they fatigued quickly, preventing a response. But this is unlikely as any light touch or puff of air caused large fast head movements. The difference is more probably a species difference as various other abbreviated optomotor preparations which work in Schistocerca (Shepheard, 1969) also fail to show any normal optic lobe activity or optomotor responses when Chortoicetes is used.

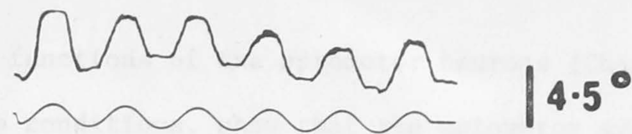
In Chortoicetes it appears that even in this minimally restrained animal arousal level is too low to maintain a regular head response. As

optomotor neurons B1 and B2 respond well under these conditions (Chap. 2), there is a failure of transmission from the circumoesophageal connectives to the neck muscle motoneurons. A similar failure of transmission at low arousal levels occur between circumoesophageal and cervical connectives and may explain the failure to find the appropriate units in the ventral cord. This would also explain the apparent absence of these units in the completely restrained preparations in other studies (Horridge et al., 1965; Catton & Chakraborty, 1969, and mine). These two failures of transmission may be linked so that when there is no transmission to neck muscle motoneurons there is no transmission to thoracic ganglia. This is obviously an economical method of preventing unwanted information from reaching the thoracic ganglia.

Small optomotor stimuli can elicit nonspecific responses

The locust makes many errors when movements of a striped pattern stimulate only a few ommatidia. Some of these error movements are larger and longer lasting than the following responses and these error movements will be called nonspecific responses. Similar responses can be produced even when the whole or most of the eye is stimulated by oscillations of a striped pattern, if the amplitude of the oscillation is small (Fig. 61). The occurrence of the response is variable. The same stimulus may have failed to evoke any responses when given previously. These head movements are often accompanied by movements of the limbs and body and both head and body movement take several minutes to die down, whereupon they can be evoked by the next stimulus.

When the background movement is so slight that it cannot evoke stabilising responses, then the background is effectively stationary for the animal. Therefore these large movements cannot be attempts to stabilise a head which has failed to follow a stimulus movement. Even if a tracking or fixating movement of any type is evoked by the tiny movement, the head should still stabilise itself with respect to what appears to be a stationary background.



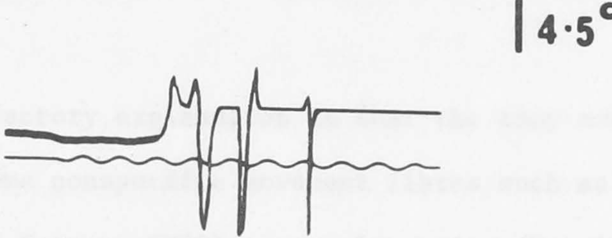


Fig. 61 Effect of small oscillations on head movement responses. As the stimulus movement decreases the head movements become smaller. Some stimuli evoke large nonspecific responses. Upper trace shows head movement, lower trace shows stimulus movement. In both cases an upward deflection indicates movement to the left (anticlockwise). Calibration bar shows degrees of head turning. The whole left eye was stimulated by movements of a striped pattern, repeat period 15.8°. (a) oscillation amplitude 15.4°, frequency 0.25Hz. Note the good following by the head. (b) oscillation amplitude 5.3°, frequency 1.0Hz. (c) oscillation amplitude 4.2°, frequency 1.0Hz. Although the movement is smaller, large head movements unrelated to the stimulus are evoked.

The amplitude-response functions of the optomotor neurons (Chap. 2) measured under open loop conditions, show that the optomotor system does not mediate these nonspecific responses as the p - n values decrease with movement amplitude and the discharges for movements in the preferred and null directions show very little change from spontaneous activity. Therefore the small stripe movements must stimulate other neurons which cause the large response.

The most satisfactory explanation is that the tiny movements of the pattern stimulate some nonspecific movement fibres such as the ON-OFF movement fibres (Burtt & Catton, 1960) or novelty units (Horridge et al., 1965; Northrop & Guignon, 1970) and nondirectional motion sensitive fibres found in the ventral cord (see below). All of these fibres signal only that a movement has occurred. Such neurons are maximally responsive to stimuli which are close to or below optomotor threshold but are insensitive to movements which trigger optomotor responses. For example, many of the neurons in the medulla (Chap. 4) respond as well to movements of a small spot as to stripes and the preference of novelty units and the DMD neurons for movements of a small object is well known (Palka, 1967, 1969; Northrop & Guignon, 1970). There is no conflict between two groups of neurons which can evoke different head movement responses as each neuron group has different optimum stimuli. As the random head movements are accompanied by a general increase in body activity we are justified in regarding these nonspecific responses as arousal responses and the neurons that mediate these responses can be considered to belong to an arousal system.

Flash evoked responses

Further evidence for the existence of a diffuse arousal system is provided by results from experiments where flashes from point lights were

applied singly or in pairs to create a virtual movement.

The point lights were produced in the following way. Light from two 50 watt, 12V quartz iodine lamps were focussed on the ends of two long flexible glass fibre optics (Townson & Mercer, length 30cm, internal dia. 3mm.). The light was passed from here directly to black coated Pyrex rods (dia. 3mm.) which had been pulled to a fine tip on an electrode puller. The tip diameter of the glass rod was controlled by breaking the tip against a glass slide under the microscope and diameters ranged from 10μm to 400μm. Photographs of the light issuing from the tip showed a uniform emission. As corneal facet diameter in Chortoicetes is 28μm and light in one ommatidium does not spread to others in locusts (Shaw, 1969), the precise number of ommatidia stimulated with a given tip diameter could be calculated. Electronically controlled shutters were used to control flash durations. Light intensity was varied by means of neutral density filters between shutters and flexible light guides. The lamp housing containing lamps, lenses, shutters, filters and the fixed ends of the flexible fibre optics was light proof so that the only light reaching the preparation was that emitted from the fine tip of the pyrex rod. The two tips could be independently positioned directly on the cornea and normal to it above any particular facet. When the behavioural effects of light guide stimulation were tested with the head free to move the tips were withdrawn just out of the range of head movement. Only the left eye was stimulated. Locusts required 1 hour in the dark before they responded at all to flashes of the finer light guides. The response habituated rapidly so flashes or pairs of flashes were given 1/minute. Myograms and head movements were recorded as described previously.

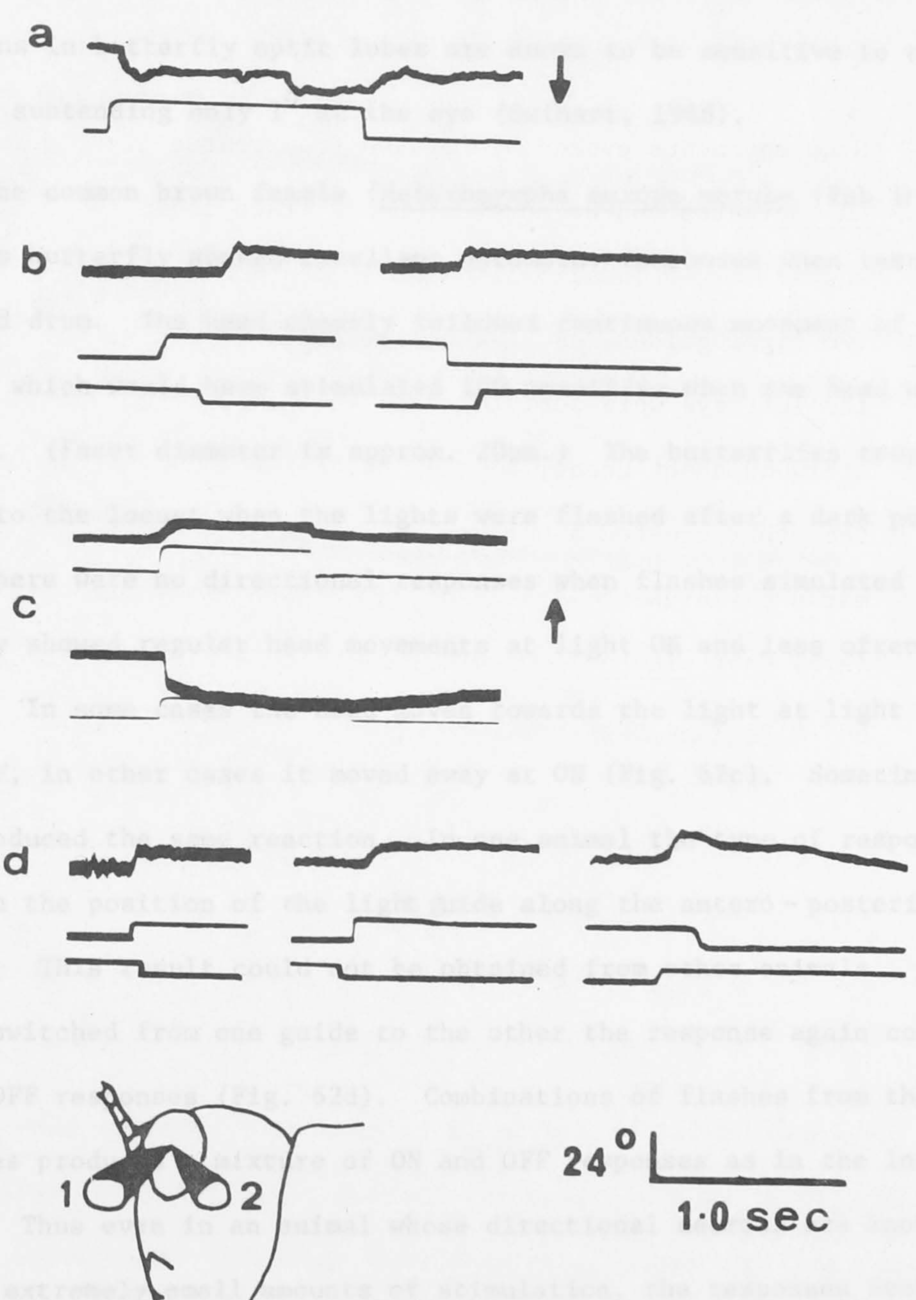
The locusts' head movements followed the continuous movement of light guides whose tip diameters were such that they stimulated 200 facets at any one time. No directional responses were found when flashes from

stationary light guides were used to simulate movement. Light ON in one light guide (illuminating from 1 to 200 facets) produced a small head movement to the side from which the light came, here the left side. Light OFF produced a small movement away from the light (Fig. 62a). This response occurred equally when stimulating anywhere within the whole flat central region of the eye. Most locusts responded more to light OFF than ON. When both light guide tips were positioned over the central region of the eye and light was switched from one to the other so as to produce a horizontal virtual movement, the response consisted of several movements which resulted only from OFF of one light (Fig. 62b) or ON of the other. That is, the locust responded only to the intensity changes. Reversing the switching sequence, i.e. reversing the direction of the virtual movement, did not change the response (Fig. 62b).

Similar tests using light spots projected onto a diffuser did not elicit any response from the M1 neuron whereas virtual movement of a stripe pattern did evoke a response (Chap. 3). This means that the failure to evoke a directional response with the light spots is due to inadequate stimulation of the optomotor system. As the lateral interactions in the direction detecting network do not spread further than approx. 9 facets; only the neighbouring borders of the two areas excited by the flashes receive stimulation which could be interpreted as movement. These border areas contain too few facets to stimulate the optomotor system even when each flash excites 200 ommatidia. As the optomotor neurons are not involved, the identity of the neurons mediating these visually evoked responses must be established. The requirement of a long dark period before the responses can be elicited suggests a link with the system mediating the random arousal responses evoked by lamp movements after a similar dark period.

The flash experiments were carried out on an insect with a low optomotor threshold to see which response type predominated when the light

Fig. 62 Head movements evoked by flashes from coarse light guides in *Chortoicetes* and *H. merope*. Upper trace indicates head movements, vertical calibration shows degrees of head turning. Two light guides, each stimulating 100 facets in the centre of the left eye were positioned so that they stimulated 2 immediately adjacent areas, so that switching the light from one to the other created a horizontal virtual movement. Stimulus markers represent light passing through the light guides. (a,b) *Chortoicetes* downward deflection of head marker indicates anticlockwise head movement (arrow). This is a movement towards the light. (a) single flash evokes a head movement towards the light at ON and away at OFF. (b) switching light from one guide to the other elicits a response only to light OFF. (c,d) *H. merope* upward deflection indicates anticlockwise head movement (arrow). (c) single flashes evoke movements in different directions. (d) switching the light from one guide to the other elicits a response at light ON. Variations in sequence or direction do not affect the response.


a
b
c
d
1
2
24°
1·0 sec

flashes could stimulate the optomotor neurons. Butterflies were chosen as they show a good optomotor head movement response which can be monitored by using the thickened end of the antenna as a flag. Also the direction detecting neurons in butterfly optic lobes are known to be sensitive to movements of stimuli subtending only 1° at the eye (Swihart, 1968).

The common brown female (Heteronympha merope merobe (Fab.)) was used. This butterfly showed excellent optomotor responses when tested with the striped drum. The head clearly followed continuous movement of a small light spot which would have stimulated 100 ommatidia when the head was stationary. (Facet diameter is approx. 20μm.) The butterflies responded similarly to the locust when the lights were flashed after a dark period. That is, there were no directional responses when flashes simulated movement. They showed regular head movements at light ON and less often at light OFF. In some cases the head moved towards the light at light ON and away at OFF, in other cases it moved away at ON (Fig. 62c). Sometimes ON and OFF produced the same reaction. In one animal the type of response depended on the position of the light guide along the antero - posterior axis of the eye. This result could not be obtained from other animals. When light was switched from one guide to the other the response again consisted of ON and OFF responses (Fig. 62d). Combinations of flashes from the two light guides produced a mixture of ON and OFF responses as in the locust (Fig. 63). Thus even in an animal whose directional neurons are known to respond to extremely small amounts of stimulation, the responses evoked by the paired lights are not optomotor responses. This result shows that the experimental conditions do not favour the expression of an optomotor response.

The head movements that are evoked by the light flashes are similar to the nonspecific responses as they can be elicited only after the animal has been left in the dark for at least 1 hour. However the flash evoked

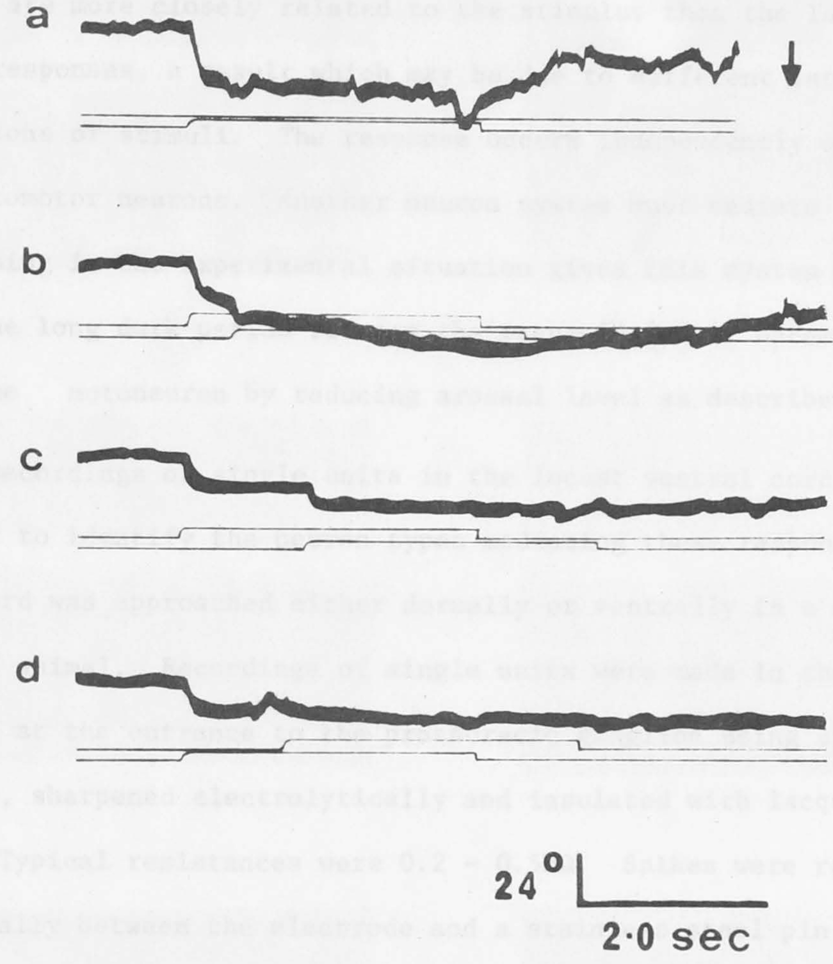


Fig. 63 Head movement responses of *H. merope* to paired flashes. The two 100 facet light guides were positioned as in Fig. 62. Upper trace indicates head movement, downward deflection representing anticlockwise (to the left) movement (arrow). Vertical calibration indicates degrees of head turning. (a) single flash. Paired flashes with different intervals between onset (b,c) or in the opposite sequence (c,d) all evoke a similar movement which is made up to responses to onset of each flash.

responses are more closely related to the stimulus than the large nonspecific responses, a result which may be due to different intensities and distributions of stimuli. The response occurs independently of excitation of the optomotor neurons. Another neuron system must mediate the response and something in the experimental situation gives this system predominance. Perhaps the long dark period reduces the transmission of optomotor information to the motoneuron by reducing arousal level as described previously.

Recordings of single units in the locust ventral cord were made in an attempt to identify the neuron types mediating these responses. The ventral cord was approached either dorsally or ventrally in a completely restrained animal. Recordings of single units were made in the cervical connective at the entrance to the prothoracic ganglion using stainless steel electrodes, sharpened electrolytically and insulated with lacquer except for the tip. Typical resistances were 0.2 - 0.5MΩ. Spikes were recorded differentially between the electrode and a stainless steel pin pushed through the mouth parts with AC coupled low impedance amplifiers (Devices 3160).

A variety of nondirectional motion sensitive neurons with large contralateral or, more rarely, binocular receptive fields were found. They are similar to those found elsewhere in the ventral cord by Catton & Chakraborty (1969). The neurons responded to flashes stimulating a single facet (ON, OFF or ON-OFF responses, latency 50 - 100msec.). The response was definitely light dependent as it diminished when light intensity was reduced (Fig. 64). The units usually showed little or no spontaneous activity in the dark or the light. Stimuli had to be given at a maximum rate of once per minute to avoid habituation. The responses of many neurons were extremely labile and some changed their response from ON to OFF and back again. They responded only to the first of two flashes even when the flashes were 2 seconds apart (Fig. 65). This suppression occurred regardless of the separation of the two light guides, whether they stimulated

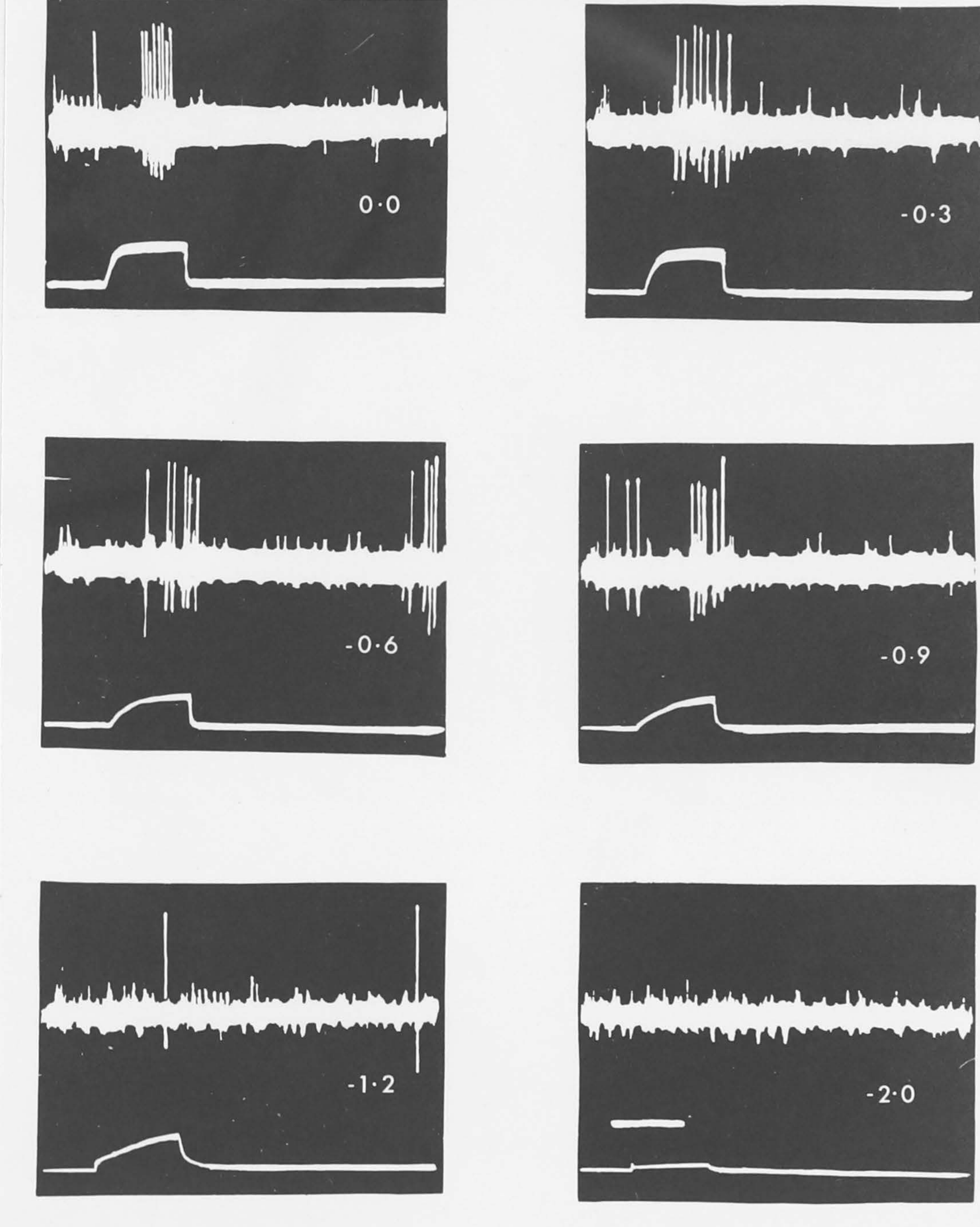


Fig. 64 Responses of a ventral cord unit to stimulation of only one facet. Brief flashes (lower trace) of different intensities were delivered through a light guide covering only one facet. Intensity of each flash is shown in relative log units. Calibration bar marks 100msec. The response is completely light dependent as it is abolished by a 2 log unit decrease in light intensity.

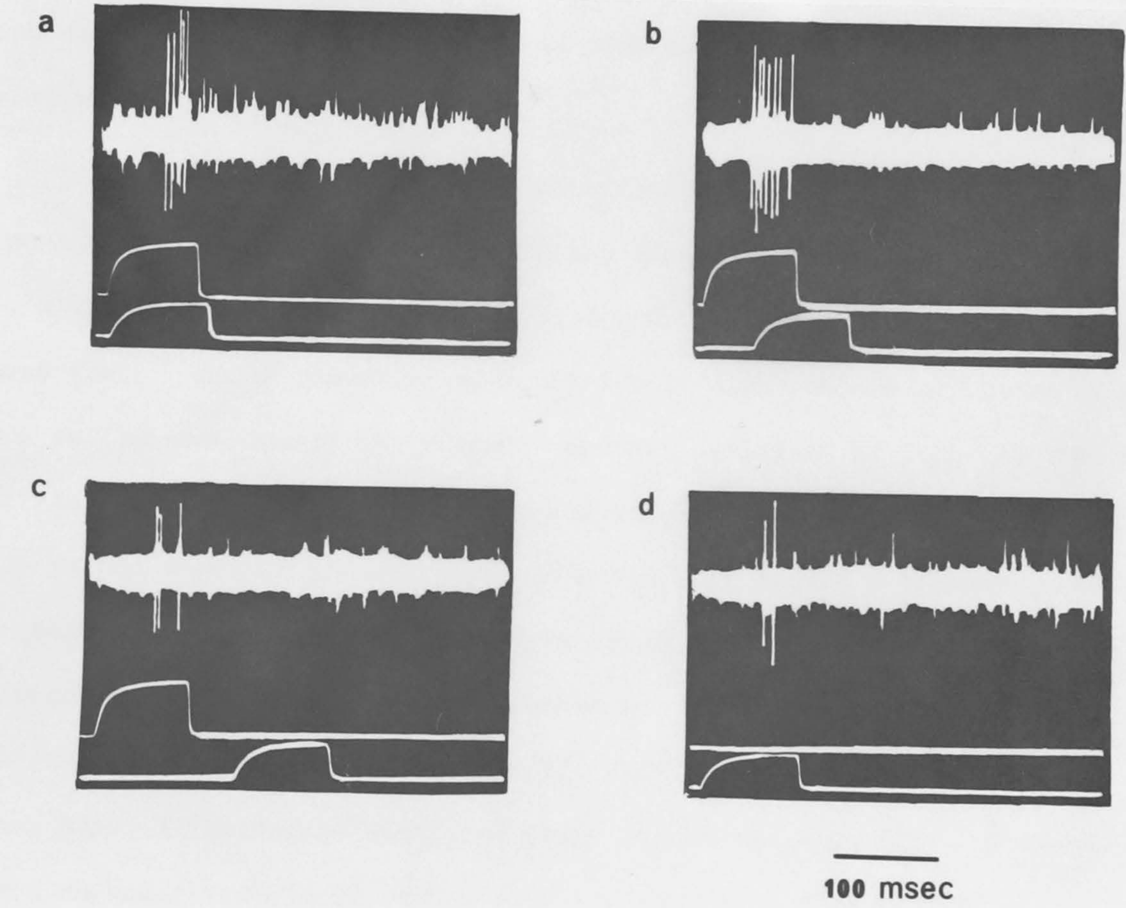


Fig. 65 Response of a ventral cord unit to paired flashes. Each flash (lower traces) is delivered through a light guide covering only one facet. Here the two stimulated facets were one facet apart. Although the unit responds to each single flash (d), no response is seen to the second of 2 flashes (b,c). Simultaneous presentation of the flashes does not necessarily enhance the response.

adjacent facets or those up to 13 facets apart. Two bimodal neurons were found which responded to auditory and visual stimuli in a way which varied from one stimulus to the next.

The same flash stimuli evoked activity in the neck muscles. Responses were recorded in muscles 50 and 51 during a flash stimulating only a single facet while the head was fixed. Decrease in light intensity showed that these responses were completely light dependent but at other times in the same muscle the response was not abolished by large reduction in flash intensity (Fig. 66). The residual response may have been a response to the sound of the shutters. The visually evoked responses could be elicited by light guides stimulating up to 16 facets only after the animal had been in complete darkness for some time; the largest responses were obtained when the animal had been in the dark for 15 hours. The presence of any other illumination abolished these responses completely. Sensitivity increases and threshold decreases with the length of dark period.

Paired flashes from the two light guides evoked a variety of large responses in the muscles either to the first or second flash or both (Fig. 67). Note that there usually is a small response at ON and OFF of the first flash. These responses were not dependent on the direction of the virtual movement produced by the two flashes. No real change was seen when the flash sequence was reversed. Again, the separation of the light guides did not show any clear effect on the response (Fig. 68).

The same stimuli were applied with the head free to move and both myogram and head movement were recorded. ON and OFF responses in the muscles could be seen even where there was no movement. Where there was a movement these potentials were followed by increased activity coinciding with the movement (Fig. 69). The first ON or OFF potentials evoked in the muscle are very similar to those in the ventral nerve cord units.

A

B

0·0
-0·3
-0·6
-0·9
-1·2
-2·0

1 sec

1 sec

Fig. 66 Response of left muscle 51 to stimulation of 4 ommatidia in a locust with its head fixed. Flashes of different intensities (given in relative log units) were delivered through a light guide covering 4 facets in the centre of the eye. A. Light dependent response. B. A response not clearly light dependent, observed some time later in the same animal.

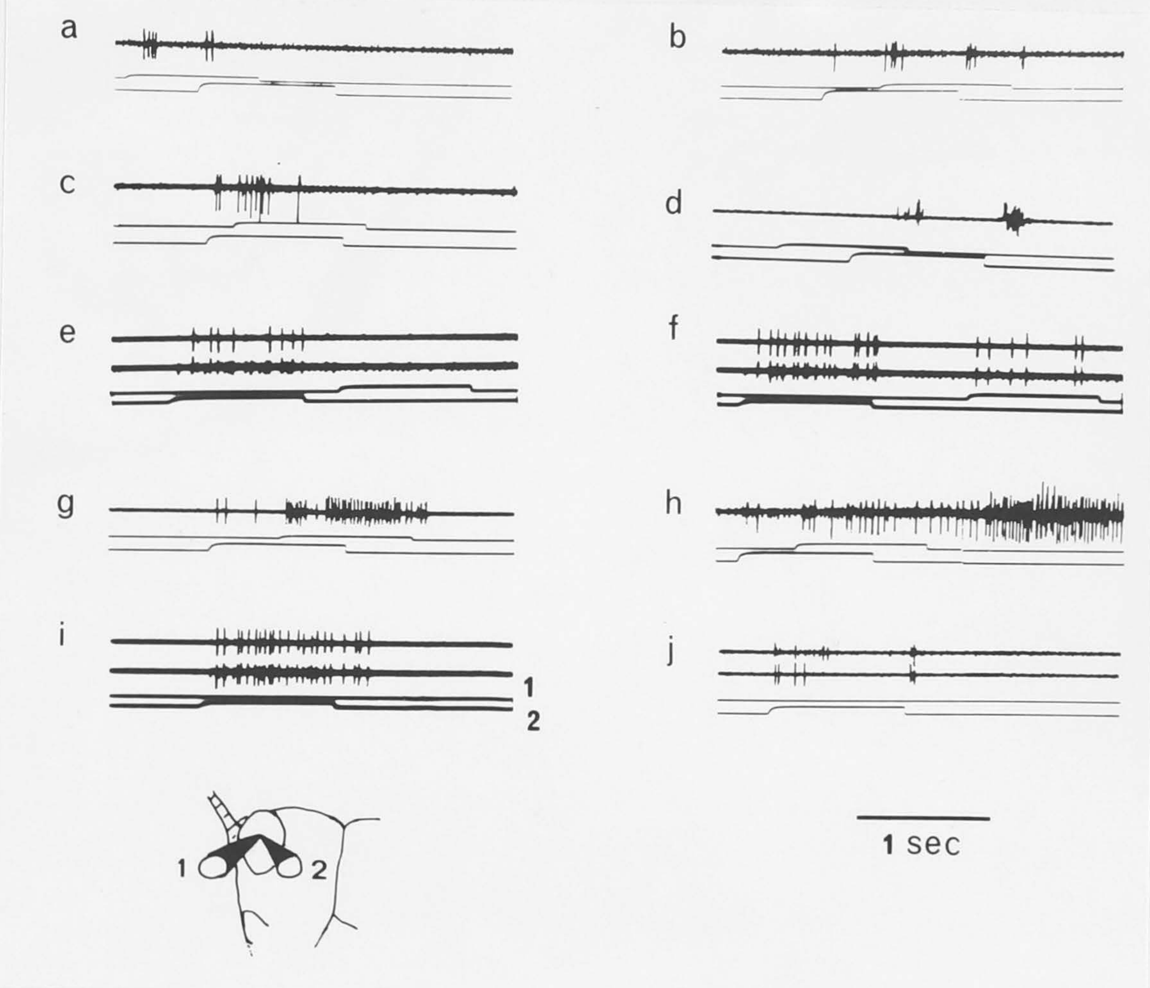


Fig. 67 The variety of responses in different animals elicited by paired flashes. The head was fixed in all cases. Light guides covered 4 facets and were positioned in the centre of the eye either adjacent or separated by one facet. (a-d, g,h) right muscle 51 in different animals. (e,f,i,j) top trace shows left muscle 51, lower trace right muscle 51. (i,j) response to a single flash in different animals.

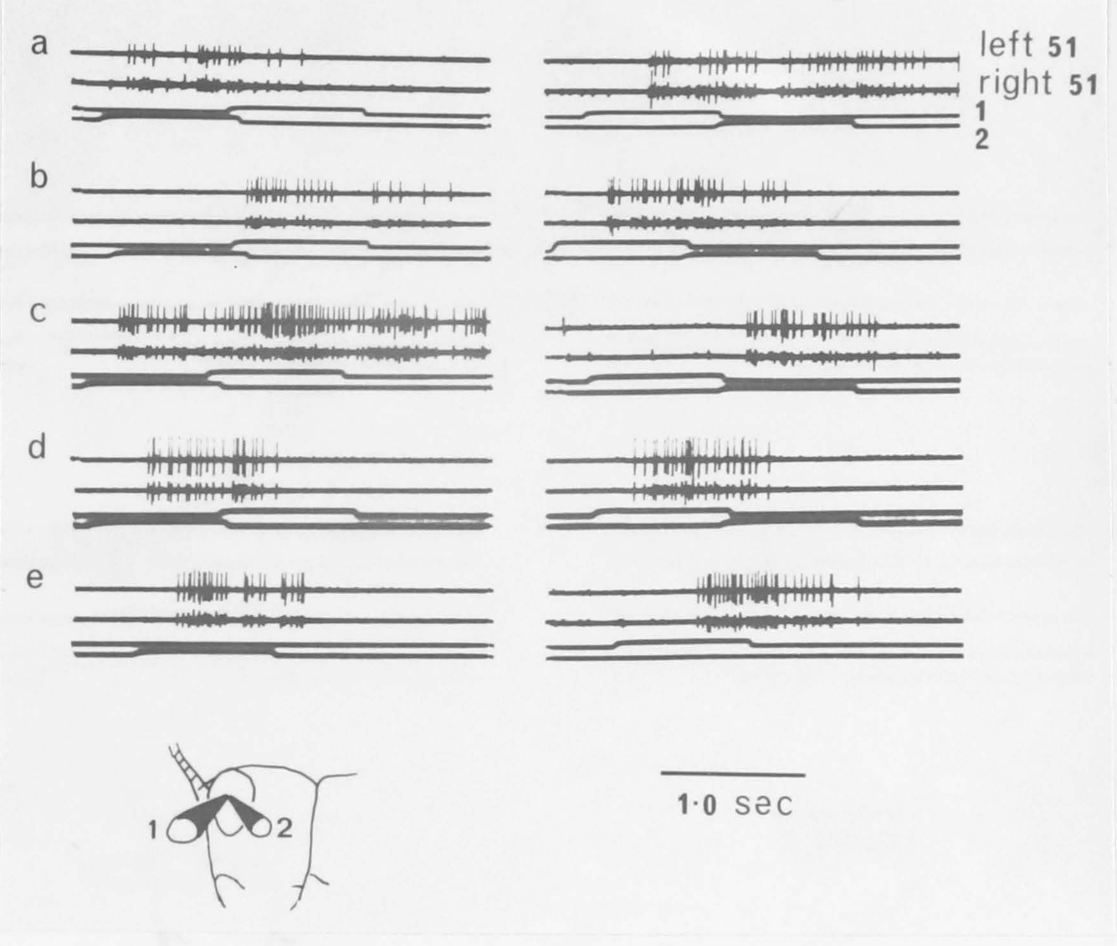


Fig. 68 Effect on muscle response of increasing the separation between two flashing light guides each stimulating 4 facets. The head was fixed. Upper trace shows left muscle 51, lower shows right 51. Upper stimulus mark shows light guide 1, lower shows light guide 2 (see inset). (a) light guides 1 and 2 are positioned adjacent to each other. (b) guide 2 was moved posteriorly so that there were 3 facets between the light guide tips. (c) light guide 2 further posterior, separation 9 facets. (d) further movement of guide 2, tips separated by 30 facets. (e) responses to each guide in position (a). Reversing the stimulus sequence has no clear effect at any position nor does increasing the separation of the light guides have any clear effect.

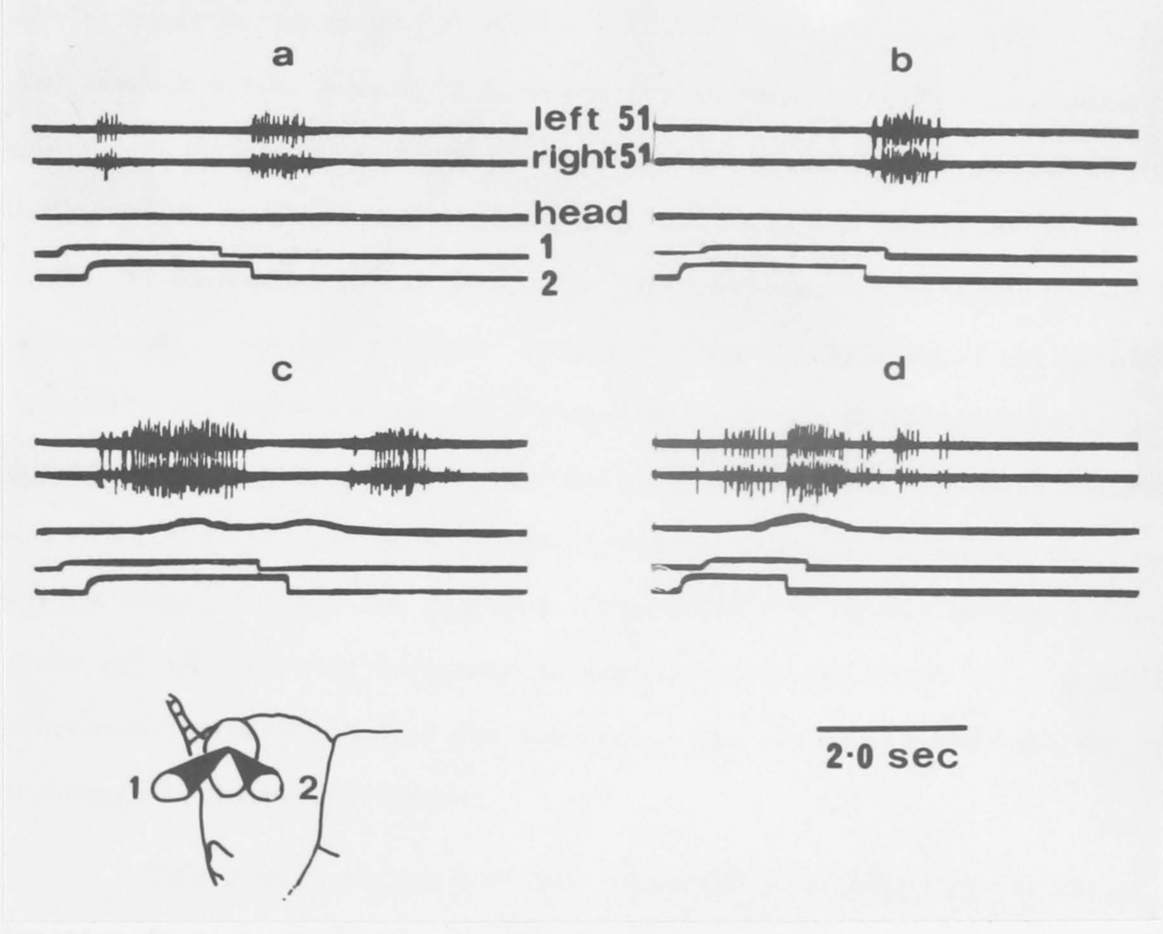


Fig. 69 Responses in neck muscles and head movements evoked by flashes of adjacent light guides stimulating single facets in the centre of the eye. Upper myogram is from left muscle 51, lower from right muscle 51. Middle trace shows head movement, upward deflection for movements to the left (anticlockwise). (a,b) flashes evoke activity in the muscles but the head does not move. (c,d) the flashes evoke greater muscle activity and the head makes a slight movement. Note the first potential at light ON before the head moves.

The system mediating the flash evoked potentials is obviously quite different from the optomotor system. It functions when the animal is in a low arousal state (animal in the dark for at least 1 hour). Its sensitivity increases and absolute threshold decreases as arousal level decreases with long periods in the dark. It is highly labile in its responses and its input requirements are not specific. For instance, activity was evoked by a nonvisual, probably auditory, stimulus. The nondirectional motion and intensity sensitive neurons in the ventral cord may mediate the early potentials evoked in the neck muscles by visual stimuli. Similar neurons are thought to be part of a diffuse thoracic network influencing the flight system (Page, 1970). The response of these neurons is not sufficient to evoke all the activity triggered in the muscle by the flash or to evoke the increased activity required for movement. The neurons responsible for the increased activity are unknown.

This neural system acts as a nonspecific arousing system whose function is to increase the arousal level of the animal and 'to maintain the nervous system in a state of excitation adequate for the continuance of motor activity' (Hoyle, 1970). Any sudden stimulus or change in the environment activates this system in a quiescent animal and increases the muscle tone enabling the insect to make further movements with greater efficiency and speed (e.g. Kammer, 1970). The arousing system becomes less effective as the animal becomes more active because continuous sensory inflow quickly habituates it. An active animal has no special requirement for a nonspecific system to maintain excitability as all the specific reflexes which are now taking place will effectively maintain excitability themselves (Hoyle, 1970).

Regeneration of retinula axons and the optomotor response

Experiments where retinula axons are cut and allowed to regenerate

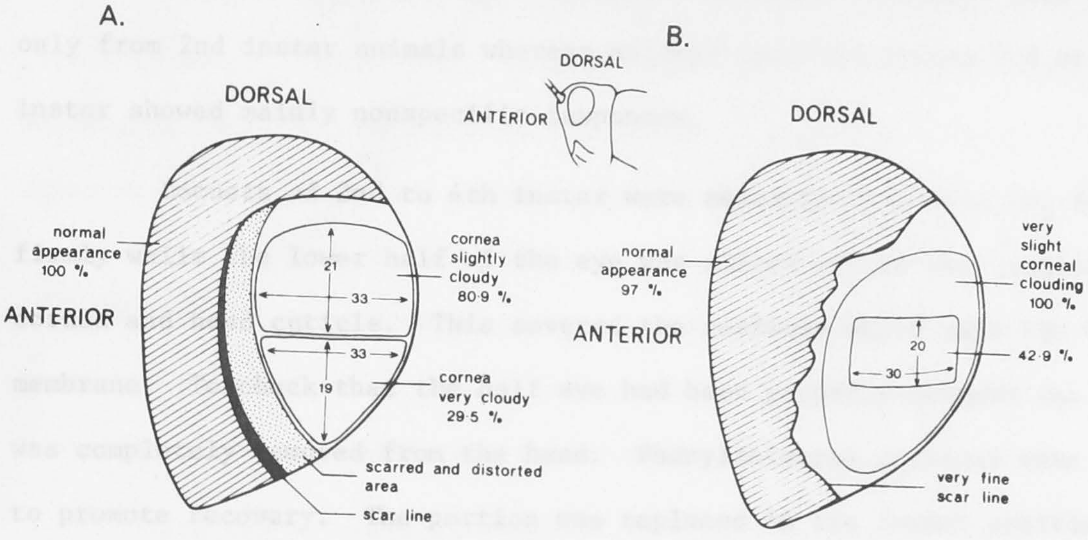


Fig. 70 Responsiveness of different parts of regrafted eyes which were sectioned during (A) 3rd instar and (B) 2nd instar. The scar line marks the cut, ommatidia which have developed post-operatively lie anterior. The 'old' (pre-operative) ommatidia lie posterior to the cut. Percentages are the percent following responses to optomotor stimuli, obtained when only that part of the eye was stimulated. The numbers on the regraft areas show the actual numbers of facets within that region.

can be used to demonstrate various differences between arousal and specific reflex responses. When eye pieces were removed and replaced at 2nd, 3rd or 4th instar Chortoicetes it was found that stimulation of the regraft evoked head movement responses. Reliable following responses were obtained only from 2nd instar animals whereas animals operated during 3rd or 4th instar showed mainly nonspecific responses.

Locusts of 2nd to 4th instar were anaesthetised with CO_2 and held firmly while the lower half of the eye was sliced off at the junction of the cornea and head cuticle. This severed the retinula axons near the basement membrane. To check that the half eye had been properly severed the portion was completely removed from the head. Phenylthiourea crystals were applied to promote recovery. The portion was replaced in its former position and was kept in place by the haemolymph.

Locusts were tested 3 - 4 days after final moult when the cuticle was hard. Optomotor responses were examined in the usual way, with oscillating stripes (period 15.8^{o}) stimulating the whole eye. The luminance was 596 cd/m^2 (tungsten lamp). The right eye and the ocelli were covered with opaque paint (Kodak Opaque Red) and only the left eye was tested.

In the adult a scar line of cloudy to yellow cornea running vertically from the lower part of the eye could be seen (Fig. 70). This scar line, marking the actual cut, separates the old facets from those which have differentiated since operation. New ommatidia differentiate during each instar, the older facets lying most posterior (Bernard, 1937; Shelton, 1973). During testing the new part of the eye (post-operative) was blinded with the paint and only the regrafted area was tested. Then different portions of the regraft were covered while the remainder was tested. Finally the whole regraft was covered and a blind control was made. After behavioural testing the paint

was removed and both eyes were fixed in glutaraldehyde buffered at pH 7.2 and embedded in Spurr's (1969) or Epon epoxy resin. Random 1μm sections were stained with toluidine blue.

Animals which were operated on during 4th instar showed very little recovery. Much of the regraft consisted of opaque scar tissue. Where individual facets could be recognised, the normal regular hexagonal array was quite disrupted. None of these animals showed optomotor function in the regraft. When clearer areas of the regraft were stimulated, however, pattern movements still evoked some responses. These responses consisted of a series of random head movements, which resembled in all ways the nonspecific responses described previously.

3rd instar operated animals showed a much better recovery. The scar line was still clearly visible as a white or yellow opaque line surrounded by an area where the hexagonal pattern was distorted. In the regraft area most of the hexagonal array was regular although there were distortions in places and the cornea appeared cloudy but not opaque. Fig. 70A shows a schematic drawing of an eye sectioned in 3rd instar.

The optomotor behaviour of 3rd instar operated locusts was also much better than that of 4th instar operated animals. Optomotor responses could be elicited when the whole regraft was stimulated, although the animals tended to be less responsive than their normal counterparts. Some areas, usually the distorted ones, were found to be quite blind. When other parts were stimulated some head movements could be evoked (Fig. 71). In 6 out of 12 animals (see Table 5) evoked head movements were related in size and direction to the stimulus movement i.e. were following optomotor responses. In the other animals they were nonspecific movements (Fig. 71). In 2 cases following responses increased as an area of the eye was covered (from 69.5% to 80.9% and from 23.7% to 34.3%), the areas causing the depression of performance being regions of distorted ommatidia. The

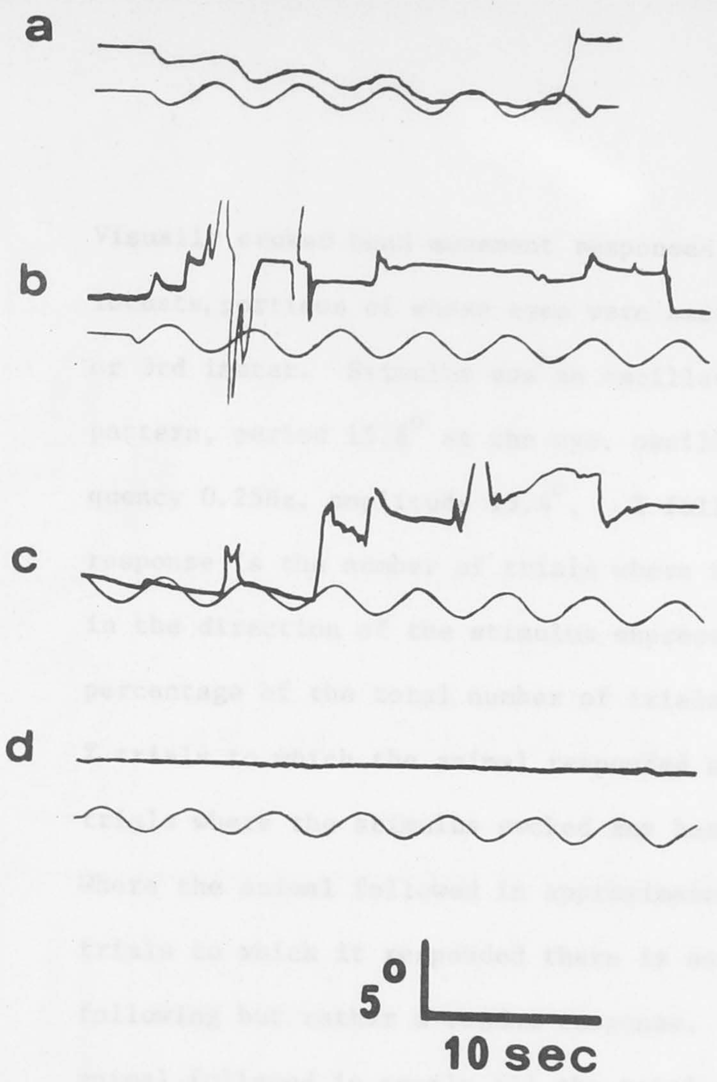


Fig. 71 Head movement responses of a locust whose eye was cut during 3rd instar. Stimulus was the moving stripe pattern, repeat period 15.8°, oscillation amplitude 15.4°, oscillation frequency 0.25Hz. Upper trace shows head movements, lower shows stimulus movement. In both an upward deflection indicates an anticlockwise (to the left) movement. Vertical calibration shows degrees of head turning. (a) stimulating the whole left eye. (b) stimulating the entire regraft, here c. 3,000 facets. (c) stimulating 2,000 facets within the regraft. (d) stimulating 1,000 facets in a different area of the regraft. Note that in (b) and (c) head movements are evoked by stripe movements but the head does not follow the oscillations. In (d) the area tested appears blind.

Table 5A & B (over)

Visually evoked head movement responses of adult locusts, portions of whose eyes were sectioned in 2nd or 3rd instar. Stimulus was an oscillating stripe pattern, period 15.8^{o} at the eye, oscillation frequency 0.25Hz, amplitude 15.4^{o}. % following response is the number of trials where the head moved in the direction of the stimulus expressed as a percentage of the total number of trials given. % trials to which the animal responded are those trials where the stimulus evoked any head movement. Where the animal followed in approximately ½ of the trials to which it responded there is no true following but rather a random response. Where the animal followed in nearly all the trials to which it responded there is a genuine return of a directional response. Each set of data refers to one animal. The first test of the regraft gives the total regraft size. This was then successively reduced. Asterisks mark testing of different regions of the regraft from that used in the test just previous.

A. Eyes sectioned in 3rd instar (pages 130 & 131).

B. Eyes sectioned in 2nd instar (page 132).

TABLE 5A Eyes sectioned in 3rd instar

STIMULATION OF WHOLE LEFT EYE		STIMULATION OF REGRAFT AREAS			BLIND CONTROLS	
% following responses	% trials to which animal responded	No. of facets stimulated	% following responses	% trials to which animal responded	% following responses	% trials to which animal responded
99.0	99.0	2500-3000 828 *600	78.7 32.2 57.7	82.0 36.5 60.3	11.8	17.6
51.5	85.9	5200 2500	35.7 28.0	48.6 47.5	9.0	15.8
100.0	100.0	4000 2500 650 *650	69.5 79.1 29.5 80.9	73.7 83.8 37.9 82.6	9.8	13.7
55.0	65.8	3000 2000	39.5 17.1	72.1 18.4	12.0	19.3
51.4	55.1	3000 2000	42.5 13.5	42.5 20.2	11.3	21.0
95.8	97.9	1500 225	57.7 58.7 50.7	61.6 63.0 57.7	19.7	31.4
62.0	66.2	4000 1000	11.3 2.4	20.0 7.1	2.1	4.0

TABLE 5A (Cont'd.) Eyes sectioned in 3rd instar

STIMULATION OF WHOLE LEFT EYE		STIMULATION OF REGRAFT AREAS			BLIND CONTROLS	
% following responses	% trials to which animal responded	No. of facets stimulated	% following responses	% trials to which animal responded	% following responses	% trials to which animal responded
ǂ17.2	28.7	4000 1000	45.8 13.1	56.3 18.2	10.3	18.7
54.6	58.6	4000 800	23.7 34.9	36.6 45.3	7.8	12.4
87.1	94.7	4000 3000	33.8 26.1	36.6 32.6	2.1	6.5
98.7	100.0	450 225	62.4 36.8	64.5 42.1	10.0	22.5
51.9	53.2	400	13.6	25.0	20.9	32.6

ǂ The improvement in the response of this animal after the post-operatively developed part of the eye was painted over, was artefactual. This animal gave very poor optomotor responses and had to be tested on 3 occasions before any responses were obtained. The increase in % responses when the regraft was tested was due to a sudden behavioural arousal which later subsided.

TABLE 5B Eyes sectioned in 2nd instar

STIMULATION OF WHOLE LEFT EYE		STIMULATION OF REGRAFT AREAS			BLIND CONTROLS	
% following responses	% trials to which animal responded	No. of facets stimulated	% following responses	% trials to which animal responded	% following responses	% trials to which animal responded
84.0	98.9	2500 750 *2000	87.1 25.6 52.3	93.5 26.9 52.3	13.5	18.9
54.3 79.8	59.8 79.8	2500 1050	88.6 57.1	88.6 57.1	5.8	22.4
88.5	92.3	2000	77.1	81.3	20.8	39.6
94.1	97.6	1000	74.2	78.8	12.4	21.7
90.5	91.9	2000 550	83.1 23.3	86.7 32.1	16.9	34.4
100.0	100.0	3000 600	64.1 47.5	66.0 55.6	9.4	15.3
80.0	82.4	2500 500	60.0 4.2	64.2 6.8	4.7	8.2
97.0	99.0	2500 300	100.0 42.9	100.0 57.2	26.7	37.8

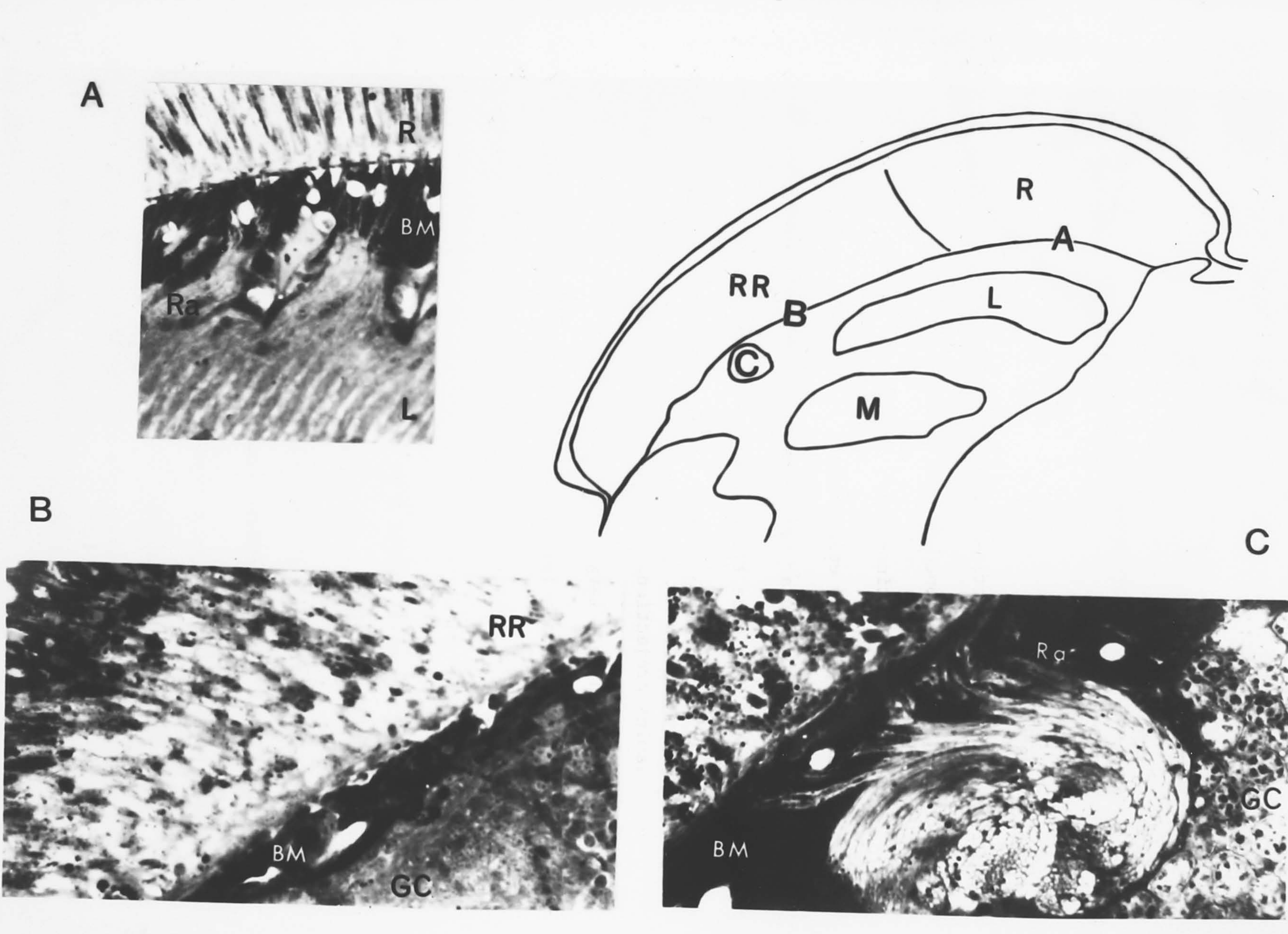
functioning areas of the regrafted eye could not be identified histologically. Random sections through all the eyes showed the same picture of disorganisation and complete disruption of the retina-lamina projection (Fig. 72). The visual information necessary for any response must have been transmitted by only few intact retinula axons.

2nd instar operated animals showed excellent recovery. Apart from a faint and narrow scar line and slight corneal cloudiness, the eye appeared quite normal. Fig. 70B shows a schematic drawing of an eye sectioned in 2nd instar. All animals showed a definite recovery of optomotor function in the regraft (Table 5). When the new part of the eye was covered the percentage following response dropped but not more than would be expected when half the eye is covered in a normal animal (see Figs. 3 and 4). As parts of the regraft were covered the responses diminished in size but did not change qualitatively (6 / 8 animals). This is illustrated in Fig. 73. In 2 animals the responsiveness of small areas was as low as the blind control. The recovery of function is much greater and more uniformly distributed than in 3rd instar operated animals. Sections of 2nd instar operated eyes show no obvious differences from the normal eye.

No first instar nymphs were used. In Chortoicetes these are too fragile to survive the operation.

There has been very little work on regeneration of the insect compound eye, most of the work being centred on the development of neural projections rather than regeneration (see Meinertzhagen, 1973 for review). The previous work on locusts has demonstrated what appears to be regeneration of function but failed to distinguish between old and new parts of the eye (Horridge, 1968a). As can be seen in Figs 71 and 73 the response of the whole eye is dominated by the new part of the eye. This agrees with more recent finding in Schistocerca where old and new parts of the eye have been examined separately. The failure to see any regeneration in eyes

Fig. 72 Disruption of retino-lamina projection in the regrafted part of an eye sectioned in 3rd instar. The drawing shows the area of disturbed retino-lamina projection and the distorted lamina. Micrographs show enlargements of the various areas of the eye. A. Normal, regular retina in the post-operatively developed region with orderly projections to the lamina. B. Degeneration of retina in regraft areas. C. Interruption of retino-lamina projection. A bundle of regenerating retina axons entwined in large spherical whorls from which few if any axons enter the lamina. R, post-operatively developed retina; RR, regraft retina; Ra, retinula axons; L, lamina; GC, lamina monopolar ganglion cells; M, medulla; BM, basement membrane.



A
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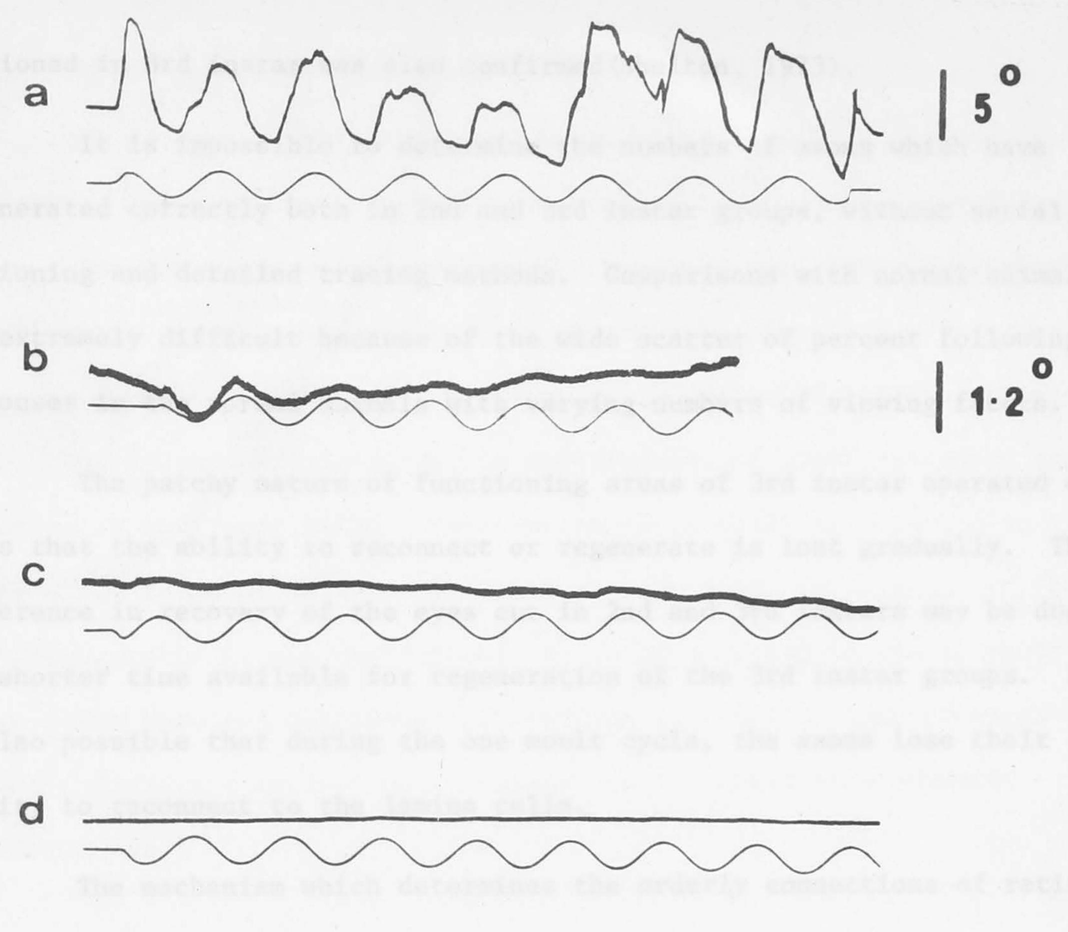

Fig. 73 Head movement responses of a locust whose eye was sectioned during 2nd instar. Stimuli and responses displayed exactly as in Fig. 71. (a) stimulating the whole left eye. (b) stimulating the regraft, here c. 3,000 facets. (c) stimulating 600 facets within the regraft. The response is very small but the head still follows the stripe movement. (d) a blind control, all ocelli and both eyes are completely painted over. Calibration mark in (c) applies to (b) and (d) also.

sectioned in 3rd instar was also confirmed (Shelton, 1973).

It is impossible to determine the numbers of axons which have regenerated correctly both in 2nd and 3rd instar groups, without serial sectioning and detailed tracing methods. Comparisons with normal animals are extremely difficult because of the wide scatter of percent following responses in the normal animals with varying numbers of viewing facets.

The patchy nature of functioning areas of 3rd instar operated eyes shows that the ability to reconnect or regenerate is lost gradually. The difference in recovery of the eyes cut in 2nd and 3rd instars may be due to the shorter time available for regeneration of the 3rd instar groups. It is also possible that during the one moult cycle, the axons lose their ability to reconnect to the lamina cells.

The mechanism which determines the orderly connections of retinula axons to lamina cells is not known. At present it is thought that there is a sequential growth of axon bundles along the path of previously developed bundles, probably by mechanical or contact guidance. In the fly at least, there seems to be no specific position recognition in the retino-lamina projection (Meinertzhagen, 1973). These ordered growth sequences are quite different from the patterns thought to exist in the retino-tectal projections of lower vertebrates (Gaze, 1970) and no real comparison can be made. The experiments reported here shed no light on the mechanisms involved in regeneration. The recovery of optomotor function of 2nd instar sectioned eyes does show a definite recovery of the previous spatial order but it cannot be determined if each axon reconnected to its former lamina cell. Possibly, the rotation experiments at present being performed on <u>Schistocerca</u> (Shelton, 1973) will find answers to some of these questions.

The nonspecific responses elicited in the regraft animals resemble those described earlier. They are elicited in animals with regrafted eye pieces by stimuli which would evoke an optomotor response in the normal

animal. These responses may arise, in the regraft, as a result of regeneration either of only a few axons or of incorrect retino-lamina connections which would not stimulate the optomotor neurons in a sequence resembling motion. The few cases where covering parts of the eye improved directional following provide evidence for the existence of incorrect connections. That the nonspecific responses can occur in spite of transmission through erroneous connections further demonstrates the independence of these responses from the stimulus characteristics. This independence would be expected in a system which responds to any small stimulus, in order to signal that there has been a change in the environment, in sharp contrast to the optomotor system which requires particular connections of large numbers of axons to extract precise information on the direction and speed of a movement across the eye.

Discussion: Arousal Systems in Insects

The locust shows a variety of behaviours which indicate different levels of general excitability or arousal. Reflex movements such as the optomotor head and body responses occur only in a sufficiently excited animal (Fig. 60), as does transmission of optomotor information to thoracic ganglia (Table 4). When excitability level is too low, stimuli which previously elicited optomotor responses elicit a nonspecific, nondirectional response (Fig. 60). The lack of any specificity of this response is emphasised by the fact that it can be evoked by stimulation of an eye where retinula axons are incorrectly connected to second order cells (Fig. 71). During the response muscles in all parts of the body are activated. The nonspecific responses, by increasing muscle activity, cause an increase in excitability. The neuronal system which triggers these responses may be described as a general arousing system.

The need for such an excitatory system in insects has long been

recognised. In 1964 Hoyle postulated the existence of a 'general driver neuron' or a general excitor system to explain results from chronic muscle recordings in freely behaving locusts. He found spontaneous variations of firing rate occurred simultaneously in many antagonists. Any massive stimulus such as turning on the light after a dark period elicited simultaneous increases of firing in antagonists. This has also been described in Oncopheltus (Chapple, 1966). Often, when one set of muscles was engaged in making a meaningful movement unrelated muscles showed parallel changes in activity. The precise patterns of activity for a specific response could be seen in the muscles of a stationary locust, but the firing rate was about ¼ that when the response was actually being made. A similar phenomenon has been observed in locust flight muscle motoneurons where EPSP's with the correct time relationships for flight were seen while no muscle activity was recorded (Burrows, 1973). The general driver neuron was postulated to increase the excitability of motoneurons on both sides of the animal, possibly via 2nd order driver neurons, each supplying a small group of muscles. Activation of a motoneuron by the general driver neuron was thought to raise the excitability of the motoneuron so that either simple actions could be initiated or 'programmes' for specific behaviours could be supplied to neurons excited sufficiently to cause actual muscular contractions. In other words, this general driver neuron performs the functions of, and is equivalent to, what we have termed the arousal system. Hoyle (1964, 1970) suggests that only a small number of neurons is required but these must have far ranging effects.

Since the general driver neuron concept was first suggested more and more evidence for an arousal system in invertebrates has been accumulating. Crayfish show behaviours described as sleep and wakefulness, these being behaviours mediated in the mammal by the reticular arousing system (Lindsley, 1951). As the crayfish wakes the firing rate of the visual

sustaining fibres, movement fibres and jittery movement fibres increase considerably. A further increase can be seen with increase in locomotor activity and during defense behaviour the firing rate may be four times that in the tethered awake animal (Arechiga & Wiersma, 1969a). These effects may be modulated by efferent 'activity' fibres in the optic nerve which respond to movements in the joints of various body parts. These fibres differ from primary mechanoreceptor fibres in that their activity reaches a maximum slowly as the animal becomes aroused and subsides slowly (Wiersma & Yamaguchi, 1966; Arechiga & Wiersma, 1969a). Water vibration sensitive neurons in crayfish, with inputs from statocysts, antennules and antennae also show a dependence on arousal state. Any novel stimulus or any body activity depresses the activity of these neurons for 5 - 10 minutes (Taylor, 1970). Taylor also noticed that the firing of many other unidentified and unrelated neurons showed similar decreases or increases, supporting the presence of a general arousing system.

The responses of insect interneurons also change with arousal level. The DMD neurons show spontaneous fluctuations in responsiveness and habituation rate. Dishabituation and increase of responsiveness were correlated with increase in arousal (Rowell, 1971a,b,c). Any sensory inputs to the animal, including proprioceptive inputs resulting from a movement, cause dishabituation of the neuron. Responsiveness of the DMD neurons is also, to some extent, light dependent, decreasing markedly if the animal is left in dark. The behavioural state of quiescence which coincides with this decrease in responsiveness was termed 'sleep' (Rowell & Horn, 1968). Reduced DMD responsiveness often coincides with periods of grooming, a behaviour generally seen at a low arousal level (Rowell, 1971b,c). These findings have led Rowell (1970, 1971b) to postulate that a single central arousal system, similar to the vertebrate midbrain reticular system, influences both DMD excitability and occurrence of other behaviours.

Optomotor neurons show noticeable changes in spontaneous activity and spike frequency during evoked responses. The changes have been described in locust optomotor neurons (Chap. 2) where they do not affect the p - n value. Increases in spontaneous activity and evoked firing rate in an optomotor neuron in the bee coincide with unrelated body movements (Kaiser, personal communication). The increased firing rate of crab and crayfish optomotor motor neurons in aroused animals (Wiersma & Oberjat, 1968; Wiersma & Fiore, 1971) may be partly due to increases in the firing rate of interneurons. It is possible that in the locust, the arousal mediated increase in the firing rate of optomotor interneurons may be necessary to evoke a response in the neck muscle motoneurons. When the firing rate of the interneurons drops due to decrease in arousal, the excitation reaching the motoneurons may be too small to depolarise them, or may be able to produce only a small potential change. Certainly the variability of incoming activity has been demonstrated in locust flight motoneurons where inputs necessary for coordinated flight appear and disappear in the dissected preparation. Burrows (1973) relates their occurrence to the 'flight mood' of the animal as he recorded common EPSP inputs to the motoneurons only in insects showing spontaneous or easily evoked flight activity. Some reflex muscular contractions, such as contraction of the metathoracic extensor tibiae evoked by stimulation of the tarsal spines are also arousal dependent (Runion & Usherwood, 1968).

The effects of arousal in insects are improvement of reflex responsiveness, increase in muscle activity, increase in excitability of motoneurons and command neurons, and increase in firing rate of some sensory interneurons. These effects are very similar to those of activation of the vertebrate arousal system. Electrical stimulation of the reticular formation accentuates the responses of single units e.g. increases firing in light activated units or decreases firing in light inactivated units (Fuster, 1961). Reticular stimulation also improves the speed of transmission and

amplitude of evoked potential in sensory systems (Dumont & Dell, 1958; Fuster & Doctor, 1962). During attentional behaviour the midbrain reticular arousal system exerts a selective or switching control. It improves transmission only in the system of the sensory modality attended to and depresses transmission in the sensory systems of other modalities (Jouvet, Schott, Courjon & Allegre, 1959). The effect of reticular activation on motoneurons in clear. The muscles are relaxed in a sleeping animal, while tone is maintained in the awake animal. Therefore, measurement of neck muscle tone can be used as a measure of arousal (Thomas, Groves & Verzeano, 1968). As reticular stimulation has been found to improve performance of a difficult learned task (Fuster & Uyeda, 1962), the behavioural effects of reticular stimulation must be the result of interactions at many levels of the nervous system.

Anatomical location of an 'arousal centre'

Lesion or stimulation studies in insects have located some central regions which control or modulate a variety of behaviour patterns. In both mantids (Roeder, 1937) and locusts (Hoyle, 1970) removal of the suboesophageal ganglion has been shown to cause complete immobility, suggesting an excitatory role in locomotion. However an inhibitory influence of the suboesophageal ganglion has been demonstrated on the DMD neuron (Rowell, 1971b), the α auditory neuron (Rowell, 1970) and on local reflexes such the prothoracic cleaning reflex in locusts (Rowell, 1964) or copulatory behaviour of male mantids (Roeder, 1937; Roeder, Tozian & Weiant, 1960). This ganglion must be important in selecting particular behaviour patterns by exciting some and inhibiting other behaviours. The known inputs to the ganglion are certainly compatible with this function as there is a direct connection with the β lobes of the mushroom bodies (Vowles, 1964). Briefly, the mushroom bodies are known to be involved in selecting motor patterns

and the formation of behavioural sequences (Vowles, 1964; Huber, 1967; Howse, 1973) and in the formation of visual and olfactory memory traces (Howse, 1973; Menzel, Erber & Masuhr, 1973). The suboesophageal ganglion may be able to modulate the activity of these lobes as it passes to lower motor centres.

Studies using localised ablations, lesions or electrical stimulation within the protocerebrum of bees and locusts (Howse, 1973), mantids (Roeder, 1937), crickets (Huber, 1970) and cockroaches (Drescher, 1960) have shown that removal or section of the central complex markedly affects the responsiveness to external stimuli, with results ranging from hyperactivity to inertness. The variation of results suggests that the central complex is involved in setting the level of responsiveness and that interference with this can leave the insect at a wide range of possible settings (Howse, 1973). The central complex is remarkably constant in proportion to head size in many insects despite their different behaviours. It has no direct connection with the mushroom bodies or optic and antennal lobes but it may connect with the suboesophageal ganglion (Howse, 1973). Thus, present data all point to the central complex and the suboesophageal ganglion as the main sites for central control of excitability or arousal.

A large amount of circumstantial evidence for an arousal system has accumulated. Although the functions of this system are clear, little is known of its mode of operation. We can, however, piece together a picture of what may occur when a visual arousing stimulus is given. The response to small flashes of light and subthreshold optomotor stimuli suggest that the novelty fibres found in locust medulla (Northrop & Guignon, 1970) and lobula and protocerebrum (Horridge et al., 1965) are the neurons detecting

the arousing stimulus. The novelty fibres may supply an input to the arousal system whose central representation lies in the central complex and sub-oesophageal ganglion. The fibres recorded in the ventral cord appear to be related to the novelty fibres as they respond to both intensity changes and movement and habituate quickly, and therefore it is possible that these ventral nerve cord fibres are the output fibres from the arousal system. They appear to mediate arousal changes as they increase the excitability of the motoneurons and prepare the muscle for faster contraction by initiating the first muscle potentials. The arousing system also increase the excitability of command fibres (e.g. Rowell, 1971a,b,c) and raises the firing rates of at least some sensory interneurons (e.g. sustaining fibres and optomotor neurons). The increase in arousal improves the animal's ability to respond quickly and precisely to any changes in the environment. The arousal system ensures that the animal can react efficiently when required to do so but when no response is required the arousal system 'switches off' those systems not being used, to guarantee maximum economy within the central nervous system.

CONCLUSION

The locust has a variety of motion detecting systems which range from novelty systems that alert the animal to the highly specific optomotor inputs which are responsible for head stabilisation after body movement. Functionally, all motion detecting systems may be related hierarchically. A nondirectional motion system with an extremely low threshold responds to any new movement. Also a large command fibre responding to small movements primes the neuropile to respond to cerebral input rather than local or intersegmental reflexes. The command and the arousal type fibres prime the animal nonspecifically for any subsequent response. A variety of more specific activities can now take place. A direction detecting network, responding to small movements, informs the animal of the direction of movements in the environment while other motion detecting neurons, with small receptive fields, may code the position of the movement within the visual field. A further direction and velocity detecting network, sensitive to large amounts of stimulation, responds to the animal's own movements. Thus the animal can determine the position and direction of a movement which aroused it and is also informed of the nature of the body movements which it has made in response to the stimulation.

At present, the neural substrate of head stabilisation only is known. The detailed description of the locust optomotor system given here shows it to be comparable in many ways to the vertebrate optomotor system. It seems probable that as more is discovered in insects and crustaceans of the neural basis of behaviours such as arousal, fixating and tracking, more similarities to vertebrates will be revealed and then the differences in

neuronal organisation in all these different animals may be regarded, not as reflections of basically different integration processes, but as variations on a single theme.

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