

VISUAL PERCEPTION OF MOVEMENT IN THE LOCUST

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The locust, in common with many other insects, possesses two types of eye; the large compound eyes situated one on each side of the head, and three simple eyes or ocelli, two placed laterally and one frontally (Fig. 1). Previous studies, mainly concerned with the compound eyes, fall into the following groups: (a) optical studies of the refracting systems, either of the whole eye or its single units, the ommatidia (Exner, 1891); (b) responses of the intact insect to different visual stimuli, such as moving striped patterns (Hecht & Wolf, 1929; Kalmus, 1937; Gavel, 1939); (c) the electroretinogram, which, from many insect eyes, shows prominent on and off deflexions (Jahn & Crescitelli, 1938, 1939; Crescitelli & Jahn, 1939; Bernhard, 1942; Autrum, 1950).

The present paper introduces a new method of investigating the response of the eyes to visual stimulation, making use of large-fibre action potentials in the ventral nerve cord of the locust, which are initiated by visual activity. These potentials were first described by Parry (1947), who recorded them from the circumoesophageal connectives.

METHODS

The Preparation. Adult female specimens of the migratory locust (*Locusta migratoria migratorioides*, phase *gregaria*), bred in captivity, were used. The legs and wings were removed, and the insect was dissected from the dorsal side, the viscera being displaced so as to expose the full length of the ventral nerve cord. Action potentials were led off by silver wire loop electrodes, bipolar leads being used in the earlier experiments, monopolar leads in later ones, in which an indifferent electrode was placed in a pool of Ringer's solution in the abdomen, and a second electrode on the nerve-cord. The Ringer's solution used had the following composition: NaCl, 9 g; KCl, 0.42 g; NaHCO₃, 0.15 g; CaCl₂, 0.24 g; glass-distilled water to make 1 l. The same solution was used to irrigate the preparation from time to time. The cord electrode was placed between the 2nd and 3rd thoracic ganglia, leading off from the connecting nerves (Fig. 2). In the earlier experiments no anaesthetic was used; later it was found that small doses of urethane (0.1-0.2 ml. 12.5% solution), injected into the body cavity, reduced spontaneous movements without affecting the visual responses, and this anaesthetic was used in subsequent work. As a rule, preparations remained responsive for 2-3 hr with little loss of sensitivity to stimulation.

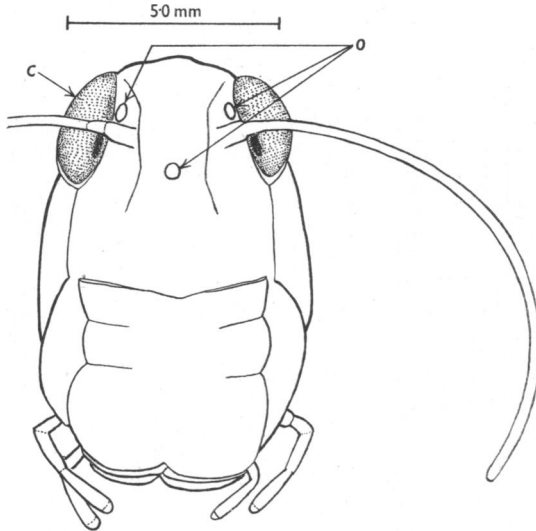


Fig. 1. Head of locust in front view. *c*, compound eye; *o*, ocelli.

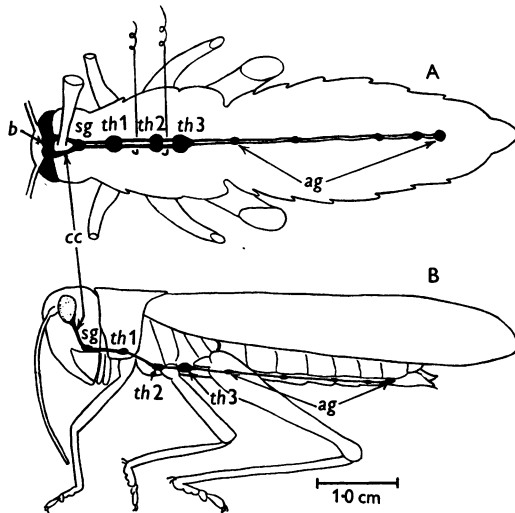


Fig. 2. Diagram of the central nervous system of the locust. A, in dorsal, B, in lateral view. *b*, brain or supraoesophageal ganglia; *cc*, circumoesophageal connectives; *sg*, suboesophageal ganglia; *th 1*, *th 2*, *th 3*, 1st, 2nd and 3rd thoracic ganglia; *ag*, abdominal ganglia.

In order to limit the stimulation to one eye, or to exclude alternatively the compound eyes or ocelli, these structures were coated with a thick layer of bituminous compound, or covered by tinfoil moulded to shape and glued in place. Slits, pinholes or small circular apertures were made in this covering when it was desired to provide a restricted exposure, and holes the size of a few ommatidia could be made in this way.

Recording. A 2-channel a.c. amplifier was used in conjunction with a conventional cathode-ray tube recording system. A loudspeaker gave audible indication of the responses during movement-perception experiments.

Stimulation. On and off responses were obtained by switching on and off, or obscuring, the lamp illuminating the preparation. For testing movement perception, a simple apparatus was used, consisting of a pivoted arm on the end of which a 6 V tungsten-filament lamp was attached (Fig. 3). The apparatus was placed so that the lamp was $\frac{1}{2}$ –1 m from the preparation, and was moved rapidly over predetermined small arcs of varying extent. It was necessary to conceal the movements of the operator's hand behind an opaque shield. The effective angular movement (θ) referred to the centre of the eye was obtained from the value for $\tan \theta$, being the linear displacement of the lamp divided by the distance between lamp and eye. Alternatively, illuminated striped patterns, consisting of alternate black and white stripes, were caused to move rapidly through a fixed distance. The threshold of perception was then related to the minimum width of

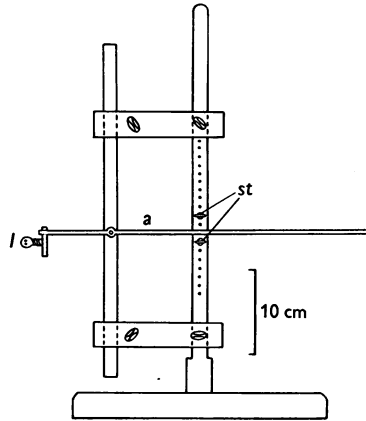


Fig. 3. Apparatus for moving a light (*l*) on the pivoted arm (*a*) over a predetermined distance controlled by the rubber covered stops (*st*).

stripe which just gave a response. In a few experiments, single ommatidia or small groups were illuminated by a microscope 'in reverse', using a $\frac{3}{8}$ in. objective to give a narrow pencil beam of light, a technique similar to that used by Hartridge (1946) on the human eye.

Histology. Paraffin sections of the optic and protocerebral ganglia, and of the ventral nerve cord connectives were prepared, and stained with iron haematoxylin.

Optical methods. Simple optical experiments were designed to give values for (*a*) the angular inclination of the optical axes of adjacent ommatidia, and (*b*) the angle of light acceptance by a single ommatidium, in the vertical and horizontal planes. For the measurement of (*a*), use was made of the 'pseudopupil' phenomenon. The pseudopupil is a small dark area seen apparently on the surface of the compound eye, when the eye is viewed through a low-power microscope under incident illumination (Pl. 1 A). It arises from that group of ommatidia, the optical axes of which are parallel to the line of sight, or nearly so. The dark effect is due to total absorption of the incident light by the pigment lying around the retinula cells at the base of the ommatidium (Fig. 4 B), so that there are no emergent rays parallel to the optical axis. In the case of the surrounding ommatidia, viewed obliquely, some of the incident light, falling on non-pigmented regions, is reflected. The centre of the pseudopupil thus represents a line of sight which is directed along the optical axis of the ommatidium which underlies it. When the eye is rotated so as to bring other ommatidia into this orientation, the pseudopupil remains stationary. The head bearing the eye was mounted on a rotating microscope stage, graduated in degrees, and fixed in a vertical

plane. Two marks were made on the eye surface, about thirty to forty ommatidia (1 mm) apart (Fig. 4A); the eye was rotated until each of these marks in turn lay in the centre of the pseudopupil, and the extent of angular rotation was read on the scale. This angle was the total angle subtended between the optical axes of the ommatidia underlying each mark. By counting the number of ommatidia between the marks, the mean angular inclination between the axes of adjacent ommatidia was obtained by simple division. This was measured for both the vertical and horizontal meridians of the eye.

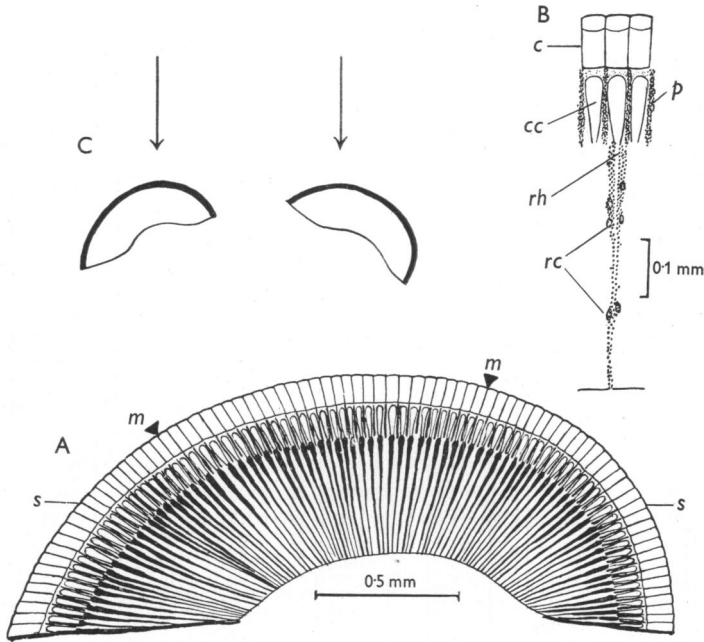


Fig. 4. A, horizontal section of locust's eye drawn to scale, somewhat schematic. The anterior surface is to the right. B, single ommatidium in more detail. C, positions assumed by the section A in determining the angle of inclination of the ommatidia. The arrows represent the line of sight. *c*, cornea; *cc*, crystalline cone; *m*, marks made on surface of eye which are aligned with the arrows in C; *p*, pigment separating the ommatidia; *rc*, retinula cells; *rh*, rhabdome; *s*—*s*, the plane of the eye slice examined in Fig. 5.

For measurement of (b), an apparatus (Fig. 5) was used, by means of which a tangentially-cut slice (*s*) from the compound eye was examined by transmitted light under a low-power microscope (*m*). The slice was mounted on a cover-slip (*c*), to which the cut surface was adherent by a thin film of Ringer's solution. The cover-slip was fixed on a cardboard rectangle (*cr*) with central hole, and this assembly was placed on the microscope stage, with the corneal surface of the eye facing the light source. With the light source (a 6 V tungsten-filament bulb) placed on the optical axis of the microscope, the inner surface of the eye slice was examined under low power, the field of view consisting of the inner cut ends of the ommatidia. In those regions where the level of section was such as to cut through the rhabdomes, small points of light were visible against the dark background of the ommatidial pigment layer (Pl. 1 B). The rhabdome (Fig. 4B, *rh*) is a long thin translucent rod-like structure which passes from the crystalline cone (*cc*) down the centre of the ommatidium, and is surrounded by the retinula cells (*rc*). The pin points of light represented light which had entered by the corneal facets and passed along the rhabdomes of those ommatidia

whose axes were aligned approximately parallel with the microscope axis, on which the light source was also situated. The substage condenser was not used.

If now the lamp was traversed along its graduated scale (Fig. 5, *gs*) whilst one particular pin point of light was observed, it was found that the light intensity diminished at first slowly, then more rapidly and finally became extinguished fairly sharply. When the lamp was traversed to the opposite side, a corresponding extinction point was found again. The total angular movement of the lamp with respect to the centre of the eye slice was calculated for each experiment, and was taken to represent the width of the cone of light acceptance of the ommatidium for the meridian in which the lamp was moved.

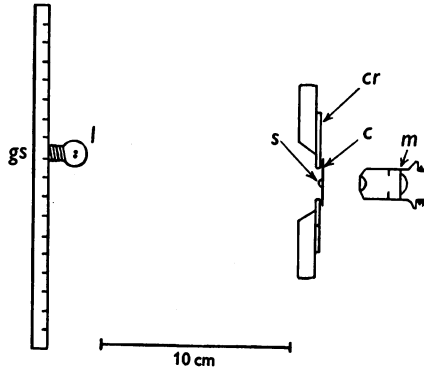


Fig. 5. Method of determining the angle of light acceptance by an ommatidium. The cover-slip (*c*) supported by the cardboard slip (*cr*) carries the eye slice (*s*) which is illuminated by the light (*l*) moved on the graduated scale (*gs*) and viewed by the microscope (*m*).

RESULTS

On and off responses

When the light falling on the eye from the 40 W lamp providing general illumination was suddenly switched off or on, or if it was obstructed by an opaque shield, trains of spikes were recorded from the ventral nerve cord. By occluding alternately the compound eyes and ocelli, it was found that the former gave on and off responses, the latter off responses only. In neither case were there any responses to constant illumination.

Movement responses

Brief trains of spikes were recorded in the ventral nerve cord when illuminated objects were moved sharply in the visual fields of the compound eyes (Fig. 7). These responses were only elicited when the movements were rapid and exceeded a small value of angular displacement, of the order of 0.33° , with respect to the eye. If the same movement was repeated several times in rapid succession, the responses ceased. This effect of 'fatigue' of the response could be avoided by presenting movement stimuli at intervals of not less than 10 sec, a procedure adopted as routine for later experiments. The ocelli gave no movement responses.

Ocellar responses

The ocellar off responses did not fatigue on constant repetition (Fig. 6A). They showed about the same latency (50 msec) to photic stimulation by short duration flashes (2.5 msec) as the compound eye responses (Fig. 6C, D).

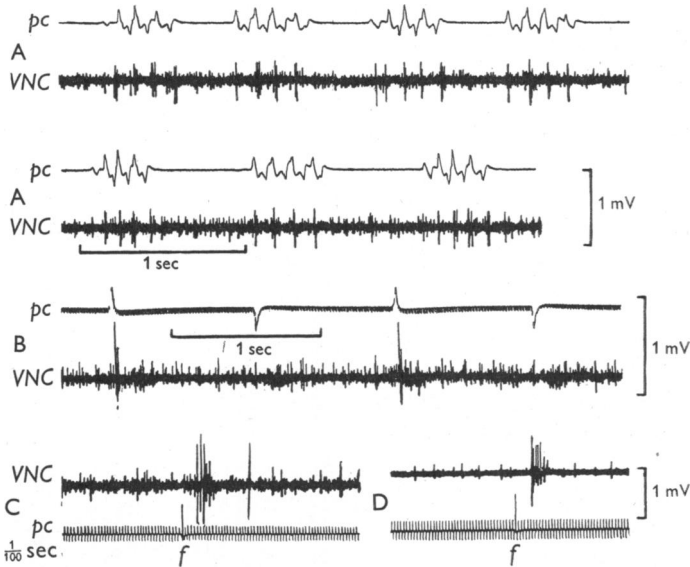


Fig. 6. Ocellar and compound eye responses. *pc*, photocell output; *VNC*, action potentials in ventral nerve cord. A, ocellar responses to passing four fingers of hand through light beam (compound eyes occluded). Response does not fatigue with rapidly repeated stimulation. B, ocellar off responses. C, compound eye response to very brief light flash (*f*). Time (lower trace) $\frac{1}{100}$ sec. D, ocellar response to similar light flash. Time (lower trace) $\frac{1}{100}$ sec. B-D retouched.

Characteristics and mediation of the responses

The compound eye responses, both for on, off, and movements, consisted of trains of one to about five spikes, whose amplitudes fell in the range 0.65–0.85 mV. The maximum duration of the trains was 60–80 msec. The ocellar responses were trains of a few spikes, whose amplitudes were from 0.30 to 0.50 mV, and duration of train not exceeding 10–15 msec.

Examination of sections of the ventral nerve cord connectives (Pl. 1C) showed the presence of numerous large amyelinate axons, ranging in diameter from 5 to 15μ , along with many small fibres. Since the action potentials composing the visual responses were the largest observed in every preparation, and in view of the established proportionality between spike height and axon diameter, it seems reasonable to conclude that the visual responses are mediated via these large fibres. In all preparations a more or less regular back-

ground activity of smaller potentials was observed, which could be ascribed to the numerous small fibres present; these small potentials were much reduced by the application of 1% nicotine to the cord ganglia, a procedure which did not affect the transmission of the large visual-response spikes.

By leading off from one connective only, it was found that there was almost complete crossing of the compound eye responses, these being elicited only by stimulation of the contralateral eye.

Impulse discharges in response to visual stimulation were also detected in the large motor nerves to the hindlimbs. These discharges were irregular, rarely gave a one-to-one correspondence with the ventral nerve cord potentials observed simultaneously, and often showed a long latency or failed completely. Nicotine (1% solution) applied to the 3rd thoracic ganglia, from which these hindlimb nerves originate, rapidly blocked transmission.

The acuity of movement perception

With test movements of gradually decreasing angular extent, and using the ventral nerve cord impulse discharge as indicator of a response, the angular threshold for movement perception was determined in a large number of experiments. These experiments were performed under bright general illumination, provide by a 40 W tungsten filament lamp at $\frac{1}{2}$ m from the eye, and the results thus all relate to the light-adapted eye. Little difference in movement perception threshold was found however as between dark-adapted and light-adapted preparations.

As the extent of the movement of the test object was progressively reduced, the duration of the ventral nerve cord impulse train decreased, until near threshold only one impulse occurred. Fig. 7 shows the results of a typical experiment in which the threshold value was 0.33° . Precise determination of the threshold of response was made difficult by the fact that for movements near threshold the response became irregular. In earlier experiments an arbitrary criterion demanding ten responses out of ten trials was adopted. This led to threshold values of about 1° for movements in the vertical plane, which agreed well with the angular inclination of the axes of adjacent ommatidia in this plane (Burt & Catton, 1952*a*), and agreed also with the results from behavioural responses to striped patterns obtained by earlier workers (Hecht & Wolf, 1929; Kalmus, 1937; Gavel, 1939). The threshold for the horizontal plane was found to be close to 1° also, when the 10/10 criterion was used, although the mean angular inclination of the axes of adjacent ommatidia was found from the pseudopupil measurements to be 2.4° in the horizontal as against 1.09° in the vertical plane.

It was later found that, in favourable preparations, 10/10 responses could be obtained down to angles of 0.33° , and results exceeding 1/10 for angles of 0.16° (Burt & Catton, 1952*b*). Table 1 shows the results of a number of

Action potentials in ventral nerve cord of locust

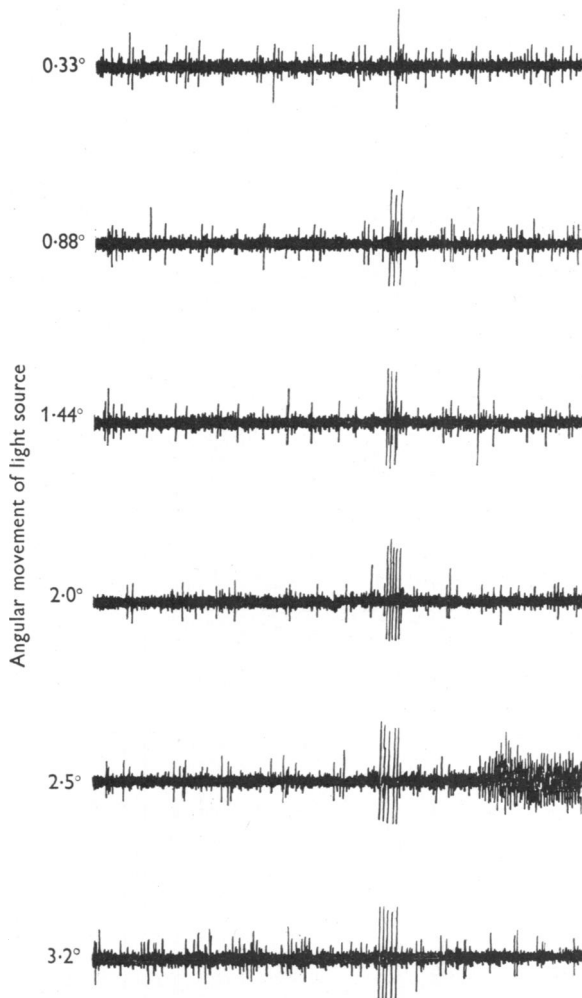


Fig. 7. Responses of compound eye to movement stimuli. Threshold value 0.33°. (Retouched.)

TABLE 1. Acuity of movement perception and inclination of ommatidial axes

	Movement threshold (°)	Inclination of ommatidial axes (°)
Vertical movements	0.22	1.15
	0.16	1.15
	0.33	1.033
	0.38	1.033
Mean	0.27	1.09
Horizontal movements	0.32	2.5
	0.45	2.5
	0.32	1.97
	0.25	2.47
	0.16	2.47
Mean	0.30	2.4

experiments in which the threshold for movement perception, based on responses exceeding 1 out of 10 trials, and the angular inclination of ommatidial axes (pseudopupil method), were determined on the same eye. It is clear that there is no correlation between the movement threshold and the inclination of the ommatidial axes.

With different test objects (white disk, striped patterns) movement perception acuities were found to be of the same order as that for the bulb, but the striped patterns were the least effective form of stimulus.

The angular limits of the field of view of a single ommatidium

Early estimates of the field of view of a single ommatidium (e.g. Exner, 1891), based on theoretical predictions, led to the conclusion that the angle within which light could enter the ommatidium was much greater than the angle of inclination between adjacent ommatidial axes. Thus extensive overlapping of the fields of neighbouring ommatidia would be expected.

Attempts to determine the limits of the ommatidial field of view were made by the following experimental procedures: (a) study of the movement responses from a single exposed ommatidium, (b) direct measurement of the angular limits of light acceptance by the method of transillumination, and (c) study of the movement responses for vertical movements presented to an eye in which only a narrow vertical strip of ommatidia was exposed.

For method (a) both eyes were covered with the bituminous compound or by tin foil, and small pinholes were made by means of a sharp needle so as to expose if possible only one, or at the most a group of two or three ommatidia. It was found that as a rule no movement responses could be obtained from preparations with these minute exposures, or if responses were obtained they were so irregular as to preclude the use of the method for delineating the limits of response. Weak on and off responses were however detected in some of these preparations.

In method (b), reproducible results were obtained from many slice preparations, and an average angle of 20.3° , standard deviation $\pm 2.9^\circ$, was obtained, to the limits of extinction of transmitted light as viewed by the human eye. This value is the mean of readings in the vertical meridian (19.4° , standard deviation $\pm 2.6^\circ$) and in the horizontal (21.3° , $\pm 3.0^\circ$ standard deviation).

For method (c), slits ranging from 2 to 17 ommatidia wide, and of length much exceeding their width, were made. Trial movements in the vertical plane were performed over a wide range, at different zones in the horizontal plane; it was found, as expected, that the field of view was markedly restricted in the horizontal direction, in accordance with the width of the particular slit employed. It was relatively easy to measure the angular width of this restricted field, by finding the limits at which the movement responses vanished.

After measuring this angle (the 'response' angle, β), we measured the mean width of the slit in terms of the number (n) of ommatidia, using a low-power microscope. The angle (α) subtended between the axes of the most peripherally placed ommatidia was calculated from the product of the number of ommatidia (n) and the mean axial inclination in the horizontal plane as determined by the pseudopupil method. By simple optical geometry an estimate could now be made of the extent of the visual field of a single ommatidium. Fig. 8 shows a row of n ommatidia forming the width of a slit, with the limit of axes (α) and

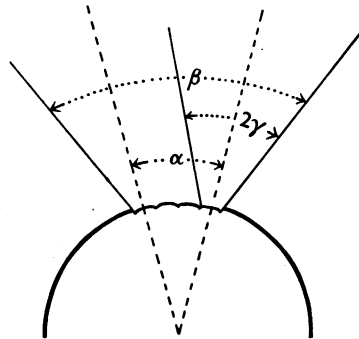


Fig. 8. Method of estimating the visual field angle of an ommatidium. Not drawn to scale. α , the angle subtended by the axes of the outermost ommatidia of the group. β , the maximum angle over which responses to movement are obtained. 2γ , the visual field angle of one ommatidium.

TABLE 2. Estimation of the ommatidial visual field angle

Inclination of ommatidial axes (horizontal) ($^{\circ}$)	Maximum slit width in ommatidia, n	Limit of optical axes, α ($^{\circ}$)	Response angle, β ($^{\circ}$)	Ommatidial field angle by method (c), $\beta - \alpha (= 2\gamma)$ ($^{\circ}$)	Ommatidial field angle by method (b) ($^{\circ}$)	
2.4	2	4.8	30	25.2	} Mean value (horizontal) 21.3 ± 3.0 s.d.	
2.4	2-3	4.8-7.2	16	11.2-8.8*		
2.4	4-5	9.6-12	21	11.4-9*		
2.4	6	14.4	42	27.6		
2.4	9	21.6	39	17.4		
2.4	7	16.8	37	20.2		
2.4	12	28.8	58	29.2		
2.4	16-17	38.4-40.8	61	20.1-22.7		
Mean value (2γ)				20.15 \pm 7 s.d.		21.3 \pm 3.0 s.d.

* Values which fall close to half the mean. Low values are due to low results for response angle, which may be due to use of excessive thickness of coating material, restricting the field of view of the ommatidia in the slit.

the response angle (β). If optical symmetry be assumed, the difference between these angles ($\beta - \alpha$) represents the angular width of the visual field of a single ommatidium (2γ). Table 2 gives values for individual experiments. It is seen that the mean value for visual field angle obtained by method (c) agrees with that from method (b), although there is considerable scatter, and two results by method (c) are markedly low, being about half the mean value.

Even though these results may be taken as approximate values, it is clear that the visual field angle of an ommatidium is much greater than the angular inclination of adjacent ommatidia.

Illumination of single ommatidia

By the use of a microscope 'in reverse', with a $\frac{2}{3}$ in. objective, it was possible to illuminate single ommatidial facets, as confirmed by direct observation under the low-power binocular microscope. Under these conditions of relatively intense illumination, on and off responses were readily obtained from single illuminated facets. Small movements of the microscope lamp enabled the point of illumination to be transferred from one facet to another, and this was accompanied by discharge of impulses in the ventral nerve cord. On closer examination with the binocular microscope, however, it was observed that in addition to the bright point of light reflected from the facet, there was a general 'glow' from deeper-lying structures. It was uncertain to what extent this internally scattered light might stimulate ommatidia other than the one whose facet was illuminated. By reducing the light intensity the 'glow' could be eliminated, but it was then difficult to identify the illuminated facet. Thus the method could not be used with the certainty of illuminating a single ommatidium. In addition, this form of stimulation bears little relation optically to the normal stimulus from a distant source of light, forming an image in the ommatidium by means of its own refracting system. The validity of the reversed-microscope stimulation of the vertebrate eye (Hartridge, 1946) of quite different structure is of course not questioned.

The effect on acuity of movement perception of limiting the area of eye exposed

If the acuity of movement perception were a function of the activity of many ommatidia, the ventral nerve cord impulses could be regarded as integrated responses, and their intensity would be expected to diminish progressively, for a given movement, as the number of ommatidia taking part was reduced. Alternatively, a reduction in the number of exposed ommatidia would be expected to cause a rise in the threshold of movement perception. This supposition was tested as follows. The acuity of movement perception was determined for the whole eye, and for the same eye partially covered, clear circular areas of various sizes being left. It was found that the acuity of movement perception was markedly lowered as the number of functional ommatidia was reduced (Table 3).

DISCUSSION

The discussion can be considered under three headings: (1) the overlapping of the ommatidial visual fields, (2) the mechanism of movement perception, (3) the origin of the impulses in the ventral nerve cord.

(1) The overlapping of the fields of adjacent ommatidia is very extensive. On the basis of our results it is seen that light enters the ommatidium, and is an effective stimulus, if it comes from any point within a cone, the apex of which subtends an angle of about 20° at the ommatidium. In other words, light enters the ommatidium at points lying 10° in any direction from the optical axis. Remembering that the inclination of the axes of adjacent ommatidia is about 1° in the vertical and 2.5° in the horizontal meridians of the eye we see

TABLE 3. Effect of reduction of exposed area of eye on movement perception acuity

Expt. no.	Size of exposed area	Movement response threshold ($^\circ$)
1	Whole eye	0.55
	24 ommatidia	1.43
	8 ommatidia	3.57
2	Whole eye	0.5
	21 ommatidia	1.27
	7 ommatidia	4.83
3	Whole eye	0.27
	24 ommatidia	2.0
	10 ommatidia	4.4

at once that overlapping of about twenty ommatidial fields would be expected to occur in the vertical and about eight in the horizontal. This point seems worth emphasis, for the general theory of the action of the ommatidium assumes that the reception of light is restricted to a limited region. Thus Wigglesworth (1953) expresses clearly the view which is implicit in most work on the subject when he says 'each ommatidium receives the impression of a luminous area corresponding to its projection on the visual field'. It follows from this that a point source of light would on this view illuminate only a single ommatidium, or at most two adjacent ones. Indeed Barlow (1952), in the course of a discussion of the theoretical resolving power in compound eyes, sees this as a possible limiting factor in the perception of light of low intensity, in, for example, the hive bee. If, however, a point source illuminates many ommatidia then Barlow's difficulty largely disappears. In *Locusta*, we see that a group of ommatidia twenty high and eight broad must be illuminated by a single-point source, and the effective aperture of the eye is far greater than is usually supposed. Exner (1891) expressed the view that light must enter the ommatidium from points inclined to the optical axis and hence overlapping of fields would occur, but he gives no measurements of this.

It might be suggested at this point that the locust eye is exceptional. Nothing in its structure points to this, and a preliminary examination of a slice of the eye of the hive bee makes it clear that overlapping of ommatidial fields occurs here also, and is, one suspects, quite general.

(2) The overlapping of fields of adjacent ommatidia gives a possible mechanism for the perception of those movements which are of much smaller

angular extent than the inclination of the optical axes. Suppose that a single ommatidium is capable of giving only simple on and off responses. (Exposures of very small groups of ommatidia, which gave only on and off responses, suggest that this is so, in respect of movement stimulation.) Imagine a point source of light illuminating the eye; there will be a central group of ommatidia receiving maximal illumination, surrounded by a group with somewhat lower illumination, until the region is reached which is occupied by those ommatidia into whose fields of view the light does not enter. Movements of the point source of angular extent comparable to the angular inclination of the ommatidia will illuminate a completely new peripheral zone of ommatidia in one direction, while it will cut off a corresponding zone in the other. On the earlier theory, such a movement would merely cause the light to pass from one ommatidial field to that of its neighbour. The difference comes when movements of the source of much smaller extent than the angular divergence of ommatidial axes are considered. On the usual theory these would be only likely to cause an on or off response if they occurred across the boundary of adjacent ommatidia, but on the present view a whole zone of ommatidia are concerned, and it is reasonable to suppose that at least one will come 'on' or 'off' even for slight movements. The above suggestion is possibly far too simple. In its defence it can be pointed out that restriction of the area of eye exposed leads, as we have shown, to a marked reduction of sensitivity to movements. Against this it should be said that reduction of the exposed area of the eye reduces sensitivity to movement even when the exposed area is still longer than the twenty vertical and eight horizontal ommatidia suggested above. Evidently it is a more complex situation than this; all that can be certainly claimed is that a large number of ommatidia are illuminated at once by a point source, and restriction in the exposed area of the eye reduces sensitivity to movement.

(3) Definite conclusions about the origin of the impulses in the ventral nerve cord await a better knowledge of the changes going on within the optic ganglia and the nervous pathways from these to the ventral nerve cord. We know nothing of the nature of the impulses coming from the retinula cells themselves. Their fibres enter the optic ganglia, the complexity of which is clearly seen from morphological studies (Snodgrass, 1935). The large fibres in the ventral nerve cord have been traced in our sections as far as the posterior part of the 'brain', where they appear to originate in large cell bodies. We are confident that detection of impulses in the ventral nerve cord gives a sure indication of effective stimulation of the eye, by whatever means this is brought about. It does not follow that an absence of such impulses would justify the opposite conclusion in any experiment. The nervous pathways are so complex that we cannot yet exclude the possibility that the retinula cells are generating impulses which enter the optic ganglion, but do not reach the ventral nerve cord. The sensitivity of the locust eye to movement, recorded in this paper, is thus to be

taken as a minimal one. We hope that further studies on central nervous activity accompanying visual stimulation may extend our knowledge of these visual responses.

SUMMARY

1. Action potential discharges were recorded from the ventral nerve cord of the locust, in response to two types of visual stimulation; (a) light on or off, (b) movement of objects in the visual fields.

2. The compound eyes gave rise to such responses for light turned on and off and for movements; the ocelli gave off responses only.

3. The discharges in the ventral nerve cord consisted of short trains of large spikes, whose amplitudes ranged from 0.65 to 0.85 mV for the compound eye responses, 0.30 to 0.50 mV for the ocellar responses.

4. Numerous fibres of large diameter (range 5–15 μ) were identified in sections of the ventral nerve cord connectives; it is likely, but no direct proof is offered, that these are the fibres which mediate the responses.

5. There was almost complete crossing of the compound eye responses, from each eye to the contralateral ventral nerve cord connective.

6. The compound eye movement responses were used to give a value for the threshold of movement perception; responses were obtained down to angular displacements of small objects of 0.16° of arc with respect to the centre of the eye. The threshold was not affected by light or dark adaptation.

7. The average angular inclination of adjacent ommatidia determined by an optical method was about 2.4° in the horizontal and 1° in the vertical meridian of the eye.

8. Optical and movement-response testing methods for determining the visual field angle of single ommatidia are described. This angle was found to be about 20° by either method.

9. The acuity of movement perception was progressively reduced by restricting the exposed surface of the eye.

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EXPLANATION OF PLATE 1

- A. Photograph of locust's eye to show the pseudopupil (*ps*). Anterior margin of eye to the left.
- B. Photograph of inner surface of an illuminated eye slice showing the structures cut across at different levels. (Retouched.) *c*, cornea; *cc*, crystalline cone; *rh*, rhabdome.
- C. Transverse section of one connective in nerve cord between second and third thoracic ganglia, showing large fibres (*lf*).

