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THE NEURONAL BASIS OF A SENSORY ANALYSER, THE ACRIDID MOVEMENT DETECTOR SYSTEM

I. EFFECTS OF SIMPLE INCREMENTAL AND DECREMENTAL STIMULI IN LIGHT AND DARK ADAPTED ANIMALS

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SUMMARY

1. The response of the movement detector (MD) system to proportionally constant incremental and decremental stimuli has been studied at various degrees of light and dark adaptation. Action potentials in the descending contralateral movement detector neurone were taken as the indicator of response.

2. Over a range of at least six $\log_{10}$ units of adapting luminance, the MD system behaves as an ON/OFF unit, giving responses to both incremental and decremental changes in the illumination of a 5° target.

3. With increasing amplitudes of stimuli, both the ON and OFF responses saturate rapidly. Saturation is reached sooner at higher levels of light adaptation. At all levels of light adaptation, the OFF response is greater than the ON. The ratio for saturating stimuli is approximately constant at around 3:2.

4. At the brightest adapting luminances used (20000 cd/m^2) the ON response is reduced but not lost. At the lowest (0·004 cd/m^2) the OFF response to a 5° disc fails, but can be regained by increasing the test area to 10°.

5. From what is known of the retina of locusts and other insects, it is thought that light and dark adaptation in the MD system can be adequately explained by events at the retinula cell.

General Introduction to the series of papers

The Movement Detector (MD) system of Orthoptera, best known in the acridid grasshoppers, is a system of interneurones which originates in the optic lobes and extends to the thoracic ganglia. When excited by appropriate visual stimuli, the final interneurones in the pathway (Descending Movement Detector (DMD) neurones; Rowell, 1971) excite or inhibit specific motoneurones in the thoracic ganglia involved in the escape jump and other defensive behaviour (Burrows & Rowell, 1973). The optimum stimulus to excite this system is a novel movement of a small contrasting object anywhere in the visual field of the eye (see Rowell, 1971, for review). The aim of this series of papers is to present the synaptic and

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neuroanatomical basis of the sensory filtration process which leads to this specificity. The majority of the retinal receptors must be excited throughout the life of the animal, whereas the MD system, like other high-order sensory interneurones in insects, is usually silent. Only when appropriate visual stimuli are presented, which result in neuronal activity passing the neural 'filters' interposed between the retinula cells and the MD system, is it excited.

As one traces outwards from the brain into the optic lobes towards the retina, the distinction between the MD system and the rest of the visual system becomes progressively less, until at the retina the distinction logically ceases to exist. It follows that no description of the MD system could be total without a virtually complete understanding of the visual system, and this we self-evidently do not have. The description we offer in this series of papers is based on two years of intracellular recording from the Lobular Giant Movement Detector neurone (terminology and morphological description in O'Shea & Williams, 1974) and associated experiments on other parts of the MD system. The inputs to the LGMD are numerous and complex, and we do not know the origin of some of them, but we believe the main elements of our understanding of the system to be sound.

The complexity of the circuit we are trying to elucidate and its stimulus-filtering functions are similar to those of the vertebrate visual pathway from retinal receptors to the lower levels of the visual cortex. Major differences in our understanding of the two systems are as follows. (1) The synaptic layers of the retina are the best understood part of the vertebrate pathway, whereas in the insect the more peripheral elements, with the exception of the retinula cells, are just now becoming accessible to investigation. Most of the cells for which there is some functional attribution and almost all of those which have also been characterized anatomically by dye injection come from the higher levels of the insect optic system, in the lobula or brain. (2) The vertebrate studies are backed by an impressive corpus of psychophysical research on man, for which there is no invertebrate counterpart. (3) In the vertebrate the higher reaches of the visual pathway vanish into the unknown of the CNS well before the level of the motor output, whereas in the insect system the connexions between identified visual interneurones and motoneurones are proven and accessible. The latter system therefore offers the promise of a total sensory/motor circuit in synaptic terms. It should be made clear that although the behaviour of insects shows that their visual system in some cases performs feats of stimulus filtration equal to those of the vertebrates (e.g. in recognizing specific complex visual situations) the MD system is not one of these highly tuned circuits; the optimal stimulus characteristics listed above allow some response to a broad category of stimuli. We stress, too, that the retinal input is processed in a great variety of ways within the optic lobe. The MD system is only one of many outputs of that processing, and our results apply to it alone, and not to insect 'vision' as a whole.

We believe that the shape of the receptive field and the gradient of sensitivities within that field (see Palka, 1967; Rowell, 1971) is determined by the anatomy of dendritic field A of the Lobular Giant Movement Detector (O'Shea & Williams, 1974). The response to novelty appears to be the result of response decrement at the afferent synapses from the retinotopic projection of excitatory units on to this dendritic field. The bias in favour of small, rather than large, objects is obtained

by a combination of a lateral inhibitory network acting prior to the LGMD (see also O'Shea & Rowell, 1975*a*), and a feed-forward inhibitory loop producing post-synaptic inhibition in the LGMD. The response to movement is derived by summation, from the relatively small response produced by change in intensity of illumination over a unit area of the retina (see also Palka, 1967); a moving object produces a succession of such local changes. The basis of the response to 'contrasty' objects lies in the sensitivity of the system to small changes of illumination relative to the level to which the receptors are currently adapted.

These different aspects of responsiveness are dealt with in detail in the various papers of this species. This first paper examines the basic sensitivity of the MD system to changes in illumination of small areas of the retina, and explores the extent of light adaptation and its effect on responsiveness.

INTRODUCTION TO PAPER I

Until recently, most published work on the MD system has used the extracellularly recorded action potentials of the Descending Contralateral Movement Detector (DCMD) as the indicator of function. This is a cerebral interneurone running to the thorax (a morphological description is given by O'Shea, Rowell & Williams, 1974). It receives its input via a spike-transmitting electrical synapse (O'Shea & Rowell, 1975*b*) from the Lobular Giant Movement Detector (O'Shea & Williams, 1974), and normally follows that unit 1 to 1. In most of the earlier work, these units were excited by targets moving in the visual field. While very effective, these stimuli allow little analysis of the fundamental response characteristics. A target moving against a contrasting background produces equal numbers of ON and OFF stimuli (these terms are here used to refer to incremental and decremental changes in illuminance of the retinula cells) and no information about the relative sensitivity to these two classes of stimuli can be obtained in this way. Palka (1967), however, worked primarily with static stimuli; in most of his experiments a small area of the visual field (usually the end of a lightpipe) underwent a rapid change in luminance. Most of his experiments were made with more or less dark-adapted animals and the MD system was excited by turning off the light behind the lightpipe, producing an OFF stimulus. He also tried some ON stimuli, and reported that the DCMD responded to both, but possibly more weakly to ON. Horn & Rowell (1968) confirmed this finding using light-adapted (background luminance 10–100 cd/m^2) animals.

There has, however, been no systematic study of the response of any element of the MD system to quantitative changes in light intensity, and furthermore the effect of dark or light adaptation, if any, is totally unknown. This is an important omission, for the relative importance of ON and OFF responses could well be greatly modified by the conditions of light adaptation. For example, if adaptation is inadequate to preserve at all times the dynamic range of response, it is possible that either the ON or OFF response will be lost at extreme adapting intensities, or at least that they will change their relative values. There is an extensive literature on light and dark adaptation in the arthropod compound eye, but little of it presents data which show how retinal responses to standard stimuli change as a result of adaptation, and only one work (Glantz, 1971) relates these changes to those seen in high-order visual

interneurones. The majority is concerned directly or indirectly with the mechanism of adaptation, either at the morphological or membrane physiological level. The morphological work stems from Exner, and is concerned with the physical regulation of light entering the diopteric apparatus; recently much attention has been paid to movement of pigment granules, movement of mitochondria towards and away from the rhabdom, the possibility of 'intracellular pupils', changes in ommatidial acceptance angle as a result of the alteration of light paths, and similar aspects. The membrane work has centred on changes in permeability, mostly in the eccentric cell of the retina of *Limulus*. A third group of papers relates adaptation to indirect indexes of visual function, such as the ERG, or to visually dependent behaviour.

A few papers do present quantitative data on the receptor potentials of the retinula cells as a function of adaptation. Naka & Kishida (1966) plotted membrane potential against light intensity (V/I curves) for the retinula cells of male *Apis* at a variety of levels of adaptation, and showed that they followed the Rushton (1965) modification of the Fechner equation, $V = k \times \log(1 + I + I_b/I_a)$; in other words, the V/I curves did not change their slope, they were merely displaced along the I axis with increasing adaptation. The adapting intensities, unfortunately, were not stated. Glantz (1968) was able to show a similar effect in the crayfish, using known adapting luminances, and derived equations relating the intensity of the adapting light to the displacement of the V/I curve, and (1972) to change of gain in the receptor cell. No experiments comparable to these have been made on the acridid retina. Morphological changes have been seen as a result of adaptation, but these changes are confined to mitochondria (Horridge & Barnard, 1965), and do not involve pigment migration, a point confirmed by Burtt (1967). The visual acceptance angle of the retinula cell almost doubles with dark adaptation (Tunstall & Horridge, 1967; Wilson, 1975), indicating a change in the optical properties of the system which is probably caused by the mitochondrial movement. Changes are also seen in DC field potentials recorded at various depths in the optic lobe (Burtt & Catton, 1964) and ERG (Giulio & Lucaroni, 1967) as the eye adapts. Cosens (1966) recorded the response of units in the VNC to whole field flashes at the eye, and his records must have included the DCMD. He was able to show that threshold was 5–10 × lower after 15 min dark adaptation than it was under room lighting.

This paper presents data which partly fill these gaps in our knowledge of acridid adaptation processes, at least as far as the MD system is involved. It is shown that over a wide range of adapting light intensities the LGMD and DCMD behave as ON/OFF units; that is, they respond with depolarization and spikes to both positive and negative changes in illumination (ΔI) of a test target previously kept at the adapting intensity. The dynamic range is small, the response saturates quickly, especially when adapted to bright light, so that usually the magnitude of the MD response is almost independent of the degree of contrast between target and background. The response to a constant proportional change in illumination of the target relative to the adapting intensity ($\Delta I/I$) is approximately constant. For small-amplitude stimuli, however, the response increases with increasing light adaptation, resulting in steeper and steeper response curves up to saturation level. The absolute gain falls dramatically with increasing light adaptation, as can be seen by calculating the response to constant absolute increments in test intensity at different levels of

adaptation. The absolute size of the saturated response to either ON or OFF stimuli is fairly constant except at extreme values of the adapting intensity, but over virtually all the range the OFF response (i.e. the response to an OFF stimulus) exceeds the ON response. At very low light intensities (0·004 cd/m^2) the OFF response to a 5° target fails, but can be regained if the test area is increased. By contrast, at the highest adapting luminance we could obtain experimentally (20000 cd/m^2) the ON response was never completely eliminated, even though its response saturated at a very low level.

MATERIALS AND METHODS

Experiments were performed on adult males and females of *Schistocerca vaga* (Scudder) from laboratory culture. The animals were held down with 'Plasticine', and the activity of the DCMD monitored by extracellular hook electrodes placed on the ventral nerve cord following a minimal dissection. We purposely avoided dissection techniques which produce large-scale deafferentation, as this reduces the responsiveness of the MD system via a decrease in arousal (Rowell, 1974, and subsequent papers in this present series). The nervous activity was amplified conventionally, discriminated by a variable window pulse-height discriminator, and DCMD impulses counted with a gated digital counter.

The eye which was not to be tested was covered by an opaque wax. The other eye saw a white screen formed by the front of the apparatus shown in Fig. 1, which was illuminated at the adapting intensity by light from a tungsten filament projector bulb, controlled by a variable-voltage transformer and equipped with filters to compensate for changes in colour temperature. A solenoid-operated shutter opened a circular hole in the screen, through which the animal could see, via a neutral density filter, a hemispherical white diffuser (half of a table tennis ball) illuminated from behind by a small tungsten filament bulb, which was also driven by a variable voltage source. The filter and diffuser were considerably recessed from the hole, and were not illuminated by the adapting light, which was arranged to shine obliquely on the screen (Fig. 1). A perimeter allowed movement of the apparatus relative to the animal at distances at which the hole in the screen subtended 5° or 10° at the eye, and the screen filled almost all the rest of the visual field. Any peripheral parts of the field not filled by the screen were always much darker than the rest of the field.

In use, the intensity of the adapting luminance was chosen, and measured with a Tektronix Type J16 digital photometer equipped with a Type J6503 luminance probe. A 1·0 or 2·0 $\log_{10}$ unit neutral density filter was placed in front of the diffuser, and the intensity of the test light source varied until the luminance of the test area as seen through the open aperture was exactly that of the surrounding screen. Fine matching of spectral composition was then carried out by eye and final matching adjustments made. When these were complete, we had difficulty in perceiving visually whether the shutter was open or closed. By altering the value of the interposed ND filter in the 'test' light path, a known value increment or decrement of luminance in the test area could be obtained by opening the shutter. The small size of the aperture and the high speed of the solenoid resulted in an opening time of less than 10 ms. As the intensity of both sources was primarily controlled by varying the current

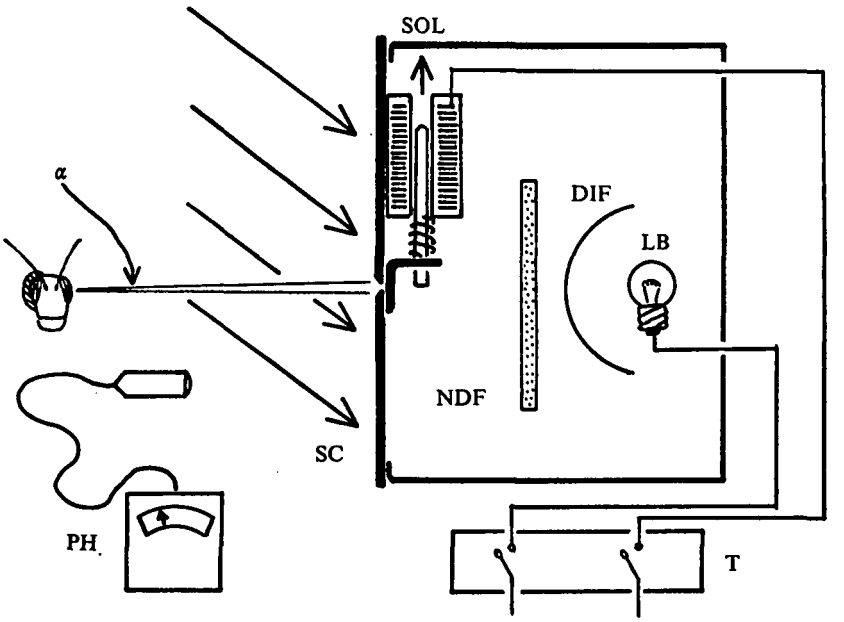

Fig. 1. Schematic diagram of the apparatus used to present proportionally constant incremental and decremental stimuli at various levels of adapting luminance. The animal, whose other eye is occluded, sees a large screen, SC. In the centre of the screen is a hole with chamfered edges, and a metal plate shutter (SH) behind it. Screen and shutter are painted with a matt white paint, and illuminated obliquely by collimated, colour-corrected light of variable intensity (I). A digital photometer (PH) probe records the luminance of the screen. Some distance back from the hole in the screen is a variable neutral density filter (NDF), a hemispherical white diffuser (DF) and a light bulb. The whole is enclosed in a light-tight box. Semiconductor switches actuated by a timing device (T) control both the solenoid (SOL) carrying the shutter and (to prevent overheating) the lamp bulb, the latter a little while before the former. A perimeter allows the whole apparatus to be moved relative to the eye, maintaining the hole in the screen at a distance subtending 5° or 10° at the eye.

through a filament bulb, their spectral composition was different at each level. We minimized these effects by using yellow filters in both light paths – thus reducing the amount of short-wave radiation, and by the use of colour-temperature correcting filters. Small differences were still present, however, and their effects on both the photometer readings and the eye should be borne in mind.

We found it difficult to obtain matched luminances of more than a few hundred cd/m^2 when using normal tungsten filament bulbs in this apparatus, and for higher intensities we transferred the apparatus outside. Direct sunlight on Californian afternoons in April produced an adapting luminance of 18–20 000 cd/m^2, and the test luminance was boosted the necessary 1 log unit above this value by the use of a concave mirror, a focusing lens and heat filters.

The MD system fires phasically, and hence the duration of the stimulus is relatively unimportant; we used a 1 s stimulus. We counted the spikes only in the response to the onset of the stimulus, and ignored the response to the offset when the shutter was closed and the test area reverted to the adapting luminance. This second response is much less, the system being habituated by the immediately preceding onset response (see Horn & Rowell, 1968, and the subsequent paper in this series).

At the start of an experiment, the animal was adapted to the adapting luminance for at least 15 min and usually for more than 30 min; the longer adaptation time was always used for low-intensity adapting lights. Bernhard & Ottoson (1960*a*, *b*) found that dark adaptation was complete in less than 30 min for diurnal lepidoptera, which, like locusts, do not employ pigment migration in adaptation. The adapting light was the only light source in the otherwise totally darkened laboratory, ensuring that only it influenced the eye. Stimuli were then presented, usually covering the range ± 1 log unit in $0{\cdot}1 \log_{10}$ unit steps, plus isolated large values either side. Between stimuli the test apparatus was moved sufficiently to transfer the test area to a new patch of ommatidia. Several different runs over the whole range were made with each animal, and several different animals were tested at each different level of adapting luminance.

The response of the MD system to changes in the luminance of a 5 or 10° target is relatively weak, especially when the increment or decrement is small. It is not possible to increase this response appreciably by increasing the target area, for the system discriminates against large-area stimuli, as first described by Palka (1967). Furthermore, habituation is rapid and recovery from habituation is slow (Horn & Rowell, 1968), especially under the conditions of restraint and monotonous sensory environment implicit in these experiments (Rowell, 1974). To minimize habituation effects, it is essential to move the test stimulus to a new area of the retina for each trial, as described in the Methods. The receptive field of the LGMD is, however, not of uniform sensitivity, and responses differing up to a power of ten in size can be obtained (Palka, 1967; Rowell, 1971). In the experiments reported here we tried to avoid the least sensitive area, and only variations of about 2–3 times are to be expected here on the basis of this effect alone. Within the more sensitive area, we tried to randomize the position of the test stimuli.

None the less, the accumulated variability of response – attributable to residual habituation, small variations in arousal, and spatial variation of sensitivity of the visual field – is very considerable, and taken together with weak responses means that large numbers of trials and individuals are necessary to obtain even a generalized picture. Most of the variance comes from occasional deviant responses, and this, together with the relatively small numbers of data points for any given value, led us to adopt medians rather than means as the best estimate of the response, and to indicate the observed variation in response by showing the actual range rather than by standard deviations. In Figs. 2 and 3 are drawn trend lines, curves drawn by eye through the median responses. The closeness of fit of these curves to the data cannot be tested, but they represent our best estimate of the underlying truth. The general fit of these results to those obtained from other visual systems is encouraging, as we were ignorant of most of these earlier results until after we had drawn our curves. We take the correspondence to mean that the trend lines are reasonably accurate!

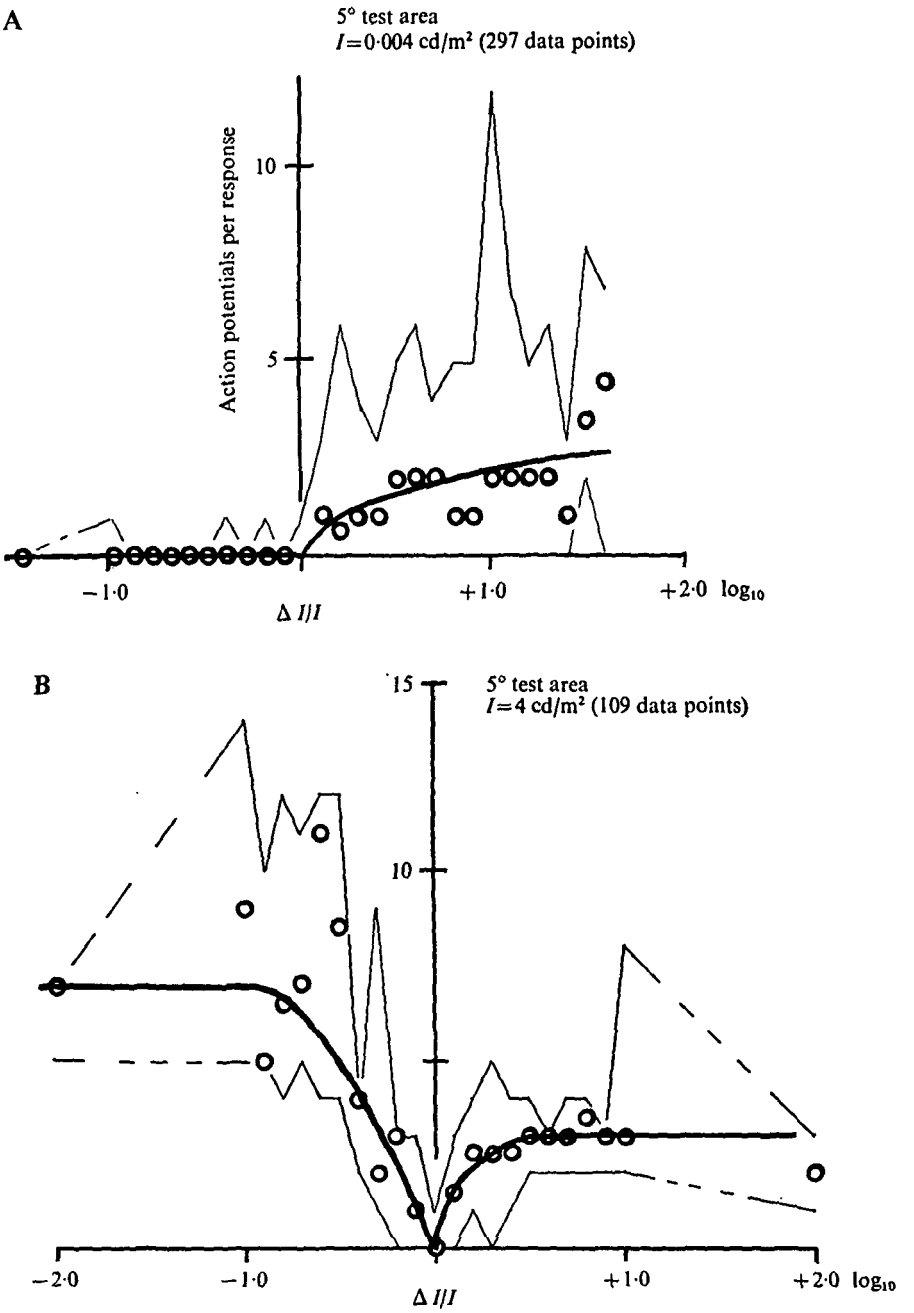

Fig. 2. Responses of the MD system (action potentials in the DCMD neurone) to proportionally constant incremental and decremental stimuli. Test area subtends 5° at the eye. Heavy circles represent median values of response, and the thin line encloses all individual data points. The heavy line is drawn by eye through the medians. (A–D) plots derived with an adapting luminance of 0·004, 4, 40 and 20000 cd/m² respectively. The 'control' point given on Fig. 2D shows mean and standard deviation (N = 30) of numbers of spikes recorded in the absence of any experimental stimulus during several 'dummy runs', and is a measure of background activity in the neurone. It does not change appreciably with intensity of adapting luminance.

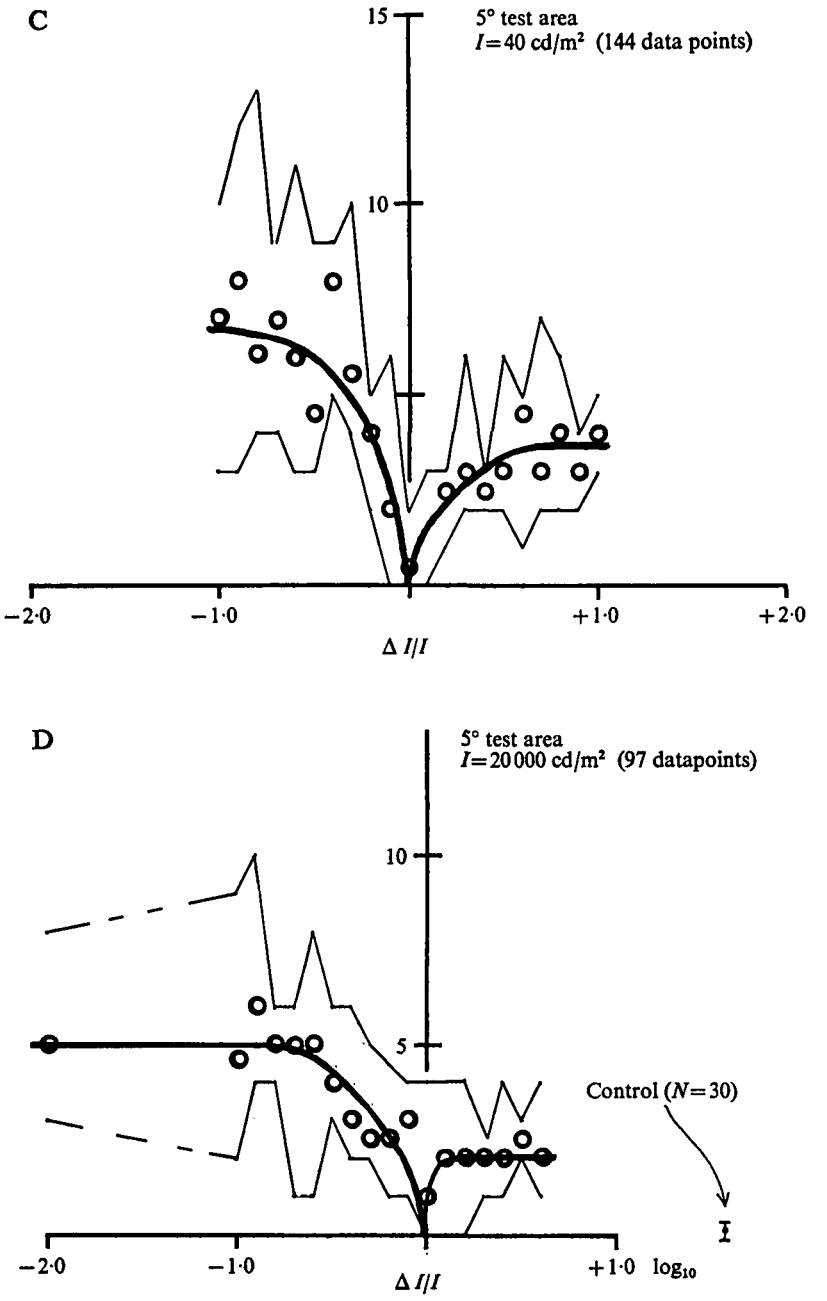
C
15
10
5° test area
I=40 cd/m² (144 data points)
−2·0
−1·0
+1·0
+2·0
Δ I/I
D
5° test area
I=20000 cd/m² (97 datapoints)
10
5
Control (N=30)
−2·0
−1·0
+1·0
log₁₀
Δ I/I

Fig. 2 (*cont.*)

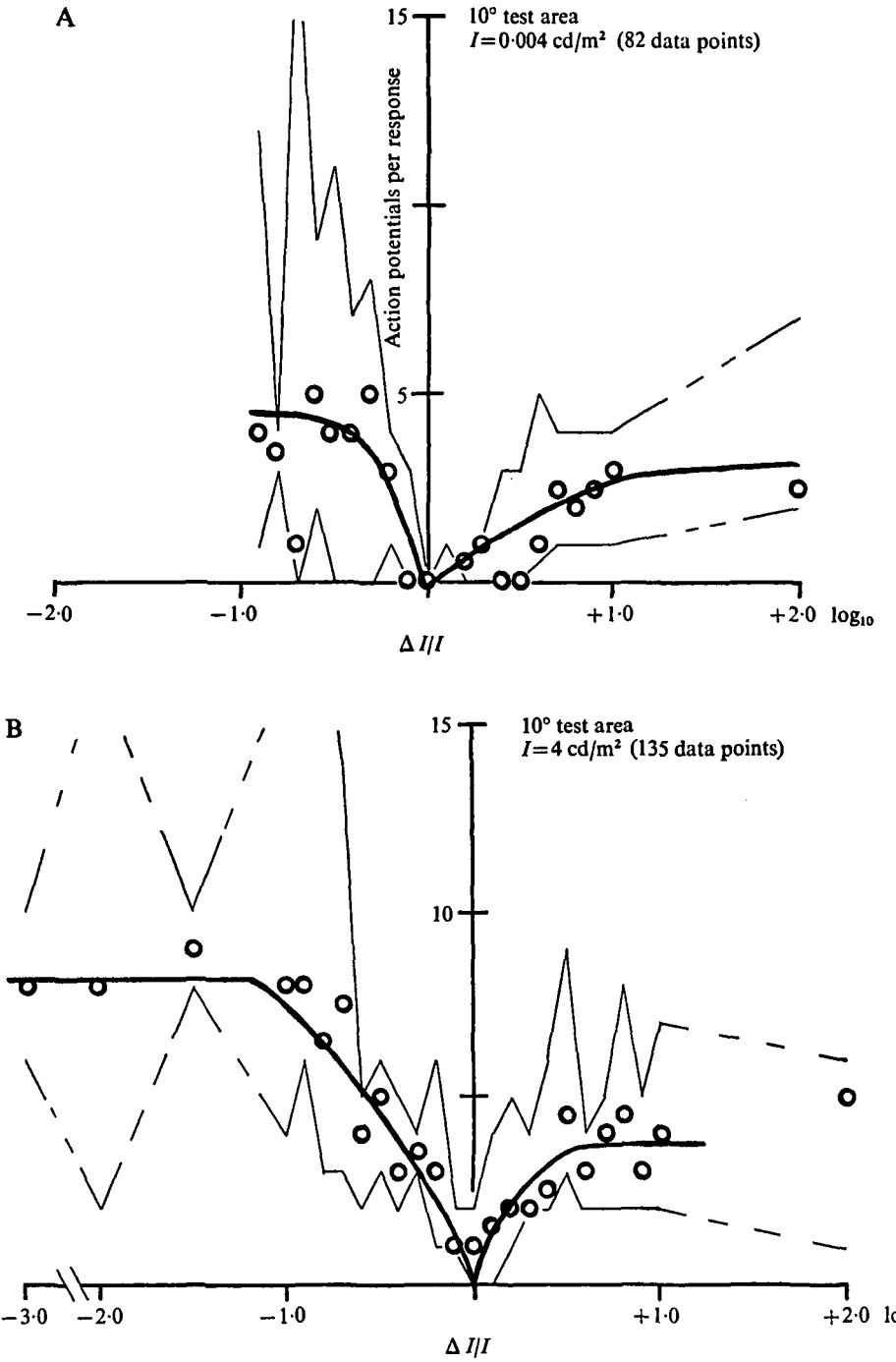

Fig. 3. As Fig. 2, but the test area is enlarged to subtend 10° at the eye, a fourfold increase in area on the retina. A and B, plots derived with adapting luminances of 0·004 and 4 cd/m² respectively.

RESULTS

We obtained results for the following values of adapting luminance:

Target size	Adapting luminance (cd/m^2)	Relative intensity of adapting luminance (log_{10})
5°	0·004	1·0
	4	4·0
	40	5·0
	240	5·8
	20000	7·7
10°	0·004	1·0
	4	4·0

Fig. 2 shows the data for the four most widely separated conditions (0·004, 4, 40 and 20000 cd/m^2) using the 5° test area, and Fig. 3 shows the data for the experiments using the 10° test area. In Fig. 4 the curves drawn by eye through the 5° data are superimposed upon a common axis. The following conclusions can be derived from these figures.

1. Both ON and OFF responses rise to plateau values, and after this value is reached increasing values of ΔI do not increase the size of the response, which can be said to be saturated.

2. The saturated response to OFF stimuli is consistently greater than for ON stimuli. The response to OFF stimuli also shows a considerably higher variability.

3. Except at extreme values of adapting luminance, and apart from small differences in the slope of the curves (see 4 below), the various sets of data do not differ significantly from each other. Within these limits, the response to constant proportional increments or decrements is itself constant at all levels of adapting luminance.

4. The response curve rises quicker with stimulus amplitude at higher levels of adapting luminance. This is most clearly seen in Fig. 4, where the curves for ON responses are superimposed. Thus the ON response saturates sooner when adapted to strong light. This is probably true of the OFF response too, but there is too much variance in the data to allow a useful comparison.

5. At very low levels of adapting luminance, approaching total darkness, the OFF responses fail (Fig. 2A). They can however be regained if the area of the stimulus is quadrupled (Fig. 3A), allowing more spatial summation at the interneurone. The increase in area does not significantly alter the slope nor the saturation level of the ON curve. At higher levels of adapting luminance there is no significant difference related to the increase in area (Figs. 2B, 3B).

6. At the brightest adapting luminance the ON response saturates at a significantly lower response level (Figs. 2D, 4), probably indicating the approaching limit of the dynamic range. Under these circumstances the DCMD begins to approximate to an OFF unit, rather than an ON/OFF one.

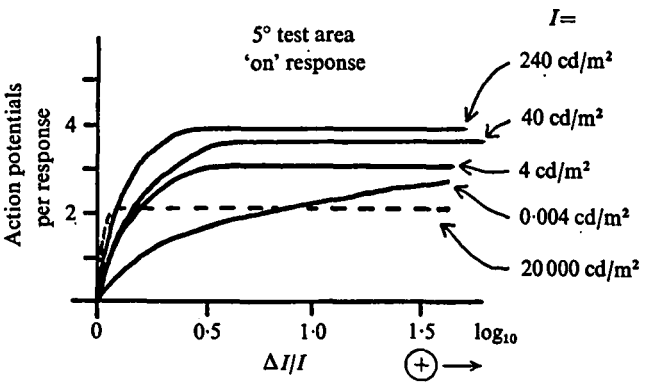

Fig. 4. The curves for ON responses drawn on each of Figs. 2A and 2B, plus a curve for an adapting luminance of 240 cd/m², are here replotted, superimposed on a single set of axes. Note increasing initial slope of the curve with increase in adapting luminance. The difference in slope is especially marked and highly significant between the lowest adapting luminance (0·004 cd/m²) and the rest. There is no significant difference between the final plateau levels for the lower three luminances, but that for an adapting luminance of 20000 cd/m² (dotted line) is significantly lower than the others.

7. Light adaptation greatly decreases the absolute gain of the system. The absolute amount of light corresponding to one $\log_{10}$ unit increment relative to an adapting luminance of, say, 4 cd/m² corresponds to an increment of only 0·06 log units relative to 240 cd/m², or of 0·001 log units relative to 20000 cd/m². These increments produce negligible responses when the eye is adapted to these levels.

DISCUSSION

The visual receptors in the acridid, as in other insects, are all ON units which are depolarized by light (e.g. Scholes, 1964; Shaw, 1967; Tunstall & Horridge, 1967; Winter, 1967; Wilson, 1975) and all indubitably second-order visual interneurones so far recorded in insects are OFF units which are hyperpolarized by light (e.g. Järvilehto & Zettler, 1973; Laughlin, 1973; Menzel, 1974). Spiking cells with more complicated characteristics have been recorded in the first optic chiasma (Arnett, 1972; Mimura, 1974; DeVoe & Ockleford, 1976; J. Kien, personal communication) but without the anatomical characterization necessary to establish what order of cell they are. It is clear that an ON/OFF unit such as the LGMD or DCMD must be derived by convergence of two separate pathways each originally derived from the primary receptors, and in this case this implies the convergence of two separate projections each covering the whole retina. The site of this convergence is treated in the next paper of this series (O'Shea & Rowell, in preparation) but it should be said here that the curves presented in Fig. 3 suggest that the two channels share a common origin responsible for the adaptation (as indeed they must since both derive from a homogeneous population of receptor cells, or at least homogeneous in this particular respect) but that they differ from each other in other details. Thus it is possible for the two classes of responses to be affected differently by the experimental variables.

The results show that the animal can light-adapt effectively over at least 6–7 $\log_{10}$

units of luminance. The receptors must respond over an even larger range, as increased test areas of retina (more receptors summating on to the recorded interneurone) extend the effective range. This is comparable to the best vertebrate performance. In other ways, too, the results fit very well with what is known from other visual systems, vertebrate or invertebrate. Thus for example Barlow & Levick (1969) examined the responses of cat retinal ganglion cells (which like the LGMD are also visual interneurones receiving summated and processed input from a number of primary receptors) during dark adaptation. They found that: (1) the response varied with the proportional stimulus ($\Delta I/I$) at all levels of adaptation; (2) a given level of response is obtained sooner at higher levels of light adaptation ('vision is contrastier at higher levels of illumination'); and (3) response speed increases with higher levels of adaptation. All these three features were found in the present experiments, allowing for the fact that the LGMD gives a saturated response to all but low-contrast stimuli (the speed of the response can be assessed by the latency of the first spike, and this fell with increasing levels of light adaptation). The actual curves obtained for ON and OFF stimuli to the MD system are closely similar to those obtained from respectively ON- and OFF-centre cat ganglion cells (Barlow, 1969). They are also what would be expected if the LGMD were synaptically connected to receptors with the $\Delta I/I$ properties found in the bee (Naka & Kishida, 1966) or the crayfish (Glanz, 1968). Although no investigation has specifically examined the V/I curve of the locust retinula cell or its dark and light adaptation, there are no data which suggest that it differs in any of these respects from that of other arthropods. The data presented incidentally in a figure in the paper of Wilson (1975) actually show that the second Barlow & Levick generalization (see above) is true of the locust *receptor* cell too; the cell has a steeper response to a standard incremental $\Delta I/I$ series when light adapted than when dark adapted, and this can be assumed to be directly responsible for the same effect observed in the DCMD. Glanz (1971) examined various aspects of the response of both the crayfish receptor and of a population of tonic ON units (the 'sustaining' fibres of Wiersma and co-workers) in the optic lobe. He concluded that the adaptation properties of the interneurones were fully explained by those of the receptors, and this seems likely to be the case also in the locust MD system.

The functioning of the MD system is based on its ability to detect movement in the visual field. This ability is maximized if the system responds to very small differences in contrast between the background and the moving object. The results presented above show that at all light intensities experienced by a diurnal insect (i.e. greater than about 1 cd/m^2) the MD response saturates within 0·5 $\log_{10}$ unit of contrast, and within even less at higher adapting luminances. Only at very low levels of background illumination is there a greater dynamic range, a more graded response to contrast. The corollary is that variations in background intensity make no difference to the response elicited by a moving object, as long as it differs from its background by more than a small amount in either direction. The adaptive significance is that this allows the system to respond uniformly to a moving object, regardless of an environment which is heterogeneous in its light intensity.

As mentioned in the Introduction, a moving object which differs in luminance from its background causes equal numbers of ON and OFF stimuli at the retina. The

fact that the MD system is biased in favour of OFF responses is therefore at first sight unimportant. The data show, however, that at high luminance levels the adaptation process is apparently inadequate to sustain the full ON response; for this reason the system would be at less of a disadvantage under these conditions if the OFF response were arranged to be the larger. Acridid grasshoppers are predominantly diurnal animals of tropical or sunny temperate climates, and in many of their habitats environmental light intensities comfortably exceed the maximum used here. Where acridids are known to be active at night, it is for the purpose of dispersal flights, and the MD system is not known to have any function in the flying animal. Until one has taken a portable light meter outside, it is hard to realize how great is the gulf between the level of illumination normally present in a visual physiology laboratory and that in which diurnal animals function in the wild. It is particularly unfortunate that so much work in visual physiology is done on completely dark-adapted animals, largely for reasons of tradition and technical convenience. This may be biologically justifiable in the case of a primarily nocturnal animal, but certainly is not for a diurnal insect.

The only previous work on the MD system which presented step changes in luminance over small areas of the visual field is that of Palka (1967), and we have confirmed almost all his results. Only one of his findings seems to need reinterpretation. He found that OFF stimuli tended to produce not only excitation but also inhibition of the system, inhibition which could curtail either an ongoing or a subsequent response. We failed to observe inhibitory effects with 5° and 10° targets, even with large-amplitude OFF stimuli. What is the reason for this difference? In a previous paper (O'Shea & Rowell, 1975*b*) we showed that the inhibition Palka described is due to postsynaptic inhibition in the LGMD, but that this is produced by large-field, but not small-field, stimuli. Because of what we now know about sensitivity and adaptation in this system, we believe that Palka's stimulus generated not only the desired large changes in illumination over small areas of the retina, but also caused a whole-field OFF stimulus. The experiments were performed on dark-adapted animals, and the sensitivity of the retina rises very greatly during dark adaptation (Horridge (1966) says by more than 10^3, and our results show even higher factors of around 10^5). The stimuli used were the quenching of either an illuminated lightpipe a little distance from the eye, or of back-illuminated diffuse light sources at greater distances. Our experiences with similar lightpipes and sources have convinced us that there is enough non-directional light emitted to affect the whole of the retina in the dark-adapted state, and we would therefore imagine that the stimulus would invoke a massive postsynaptic hyperpolarization of the LGMD, derived by a convergent pathway from the whole visual field (see Rowell, O'Shea & Williams (in preparation) in this series of papers). We have made records showing this to be true under conditions close to those described in the earlier work.

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