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ULTRAVIOLET SENSITIVITY AND SPECTRAL OPPONENCY IN THE LOCUST

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SUMMARY

Intracellular recordings in the medulla of the locust optic lobe reveal units showing u.v. sensitivity and spectral opponency. Previously only a single population of photoreceptors had been recorded in the locust retina, with peak sensitivity from 450–480 nm. Behavioural measurements show that the dorsal light response is elicited only by u.v. light, unlike the optomotor response whose spectral sensitivity is probably attributable to inputs from the green-sensitive cells. The possibility that the cells described may be involved in maintenance of level flight is discussed.

INTRODUCTION

Insects use a variety of different visual behaviour patterns to maintain level flight (reviewed by Wehner, 1981). For convenience these may be divided into two functional groups: those that act as inertial systems correcting transient deviations, such as the optomotor response (Buchner, 1984) and the ocellar response (Taylor, 1981); and a number of sustained responses that provide a general course control, perhaps by orienting to the horizon or dorsal illumination (Goodman, 1965).

The retinula cell inputs and higher order neurones controlling the optomotor response have been studied in the fly (Hausen, 1981; Buchner, 1984), and it has been shown that the short visual fibres drive directionally-sensitive cells in the lobula plate. Similarly, Wilson (1978) has described the ocellar neural system of the locust, showing how it is suited to the rapid control of flight. In contrast, only two isolated studies have thrown light on the neural basis of horizon detection by the compound eye. Hertel (1980) suggested that a phasic neurone in the bee optic lobe possessed a combination of spectral and spatial opponencies which suited it to the task. Werhahn (1976) showed that the long visual fibres are used for height orientation by the fly *Musca*, whereas the short visual fibres subserve orientation to similar vertical stripes by *Drosophila* (Morton & Cosens, 1978).

This paper describes neurones recorded in a survey of the medulla of the locust optic lobe. These cells are distinctive in possessing u.v. sensitivity, spectral opponency and tonic responses. It is argued that these properties suit the units to horizon detection, a suggestion corroborated by the finding that the dorsal light

Key words: locust vision, optic lobe, chromatic opponency.

response driven by the compound eye is u.v.-sensitive, although spectral opponency was not detected in the response.

METHODS

Animals

Adult female *Locusta migratoria* from a crowded laboratory culture, kept under mixed incandescent and fluorescent (Osram White) illumination on a 12:12 L:D regime, were used. Experiments were performed during the afternoon on animals which had undergone their final moult about a week earlier.

Electrophysiology

Intracellular recordings were made from the medulla of the right optic lobe, with animals maintained in a light-adapted state. The animal was first immobilized and attached with wax to a collar set between the head and thorax. Portions of the cranium were removed to expose the optic lobe, and much of the muscle at the back of the head, and the ocelli, were then excised. A metal spoon was placed under the proximal part of the optic lobe and secured to a pillar, against which the front of the head was wedged and waxed. The preparation was perfused with Ringer's solution (Usherwood & Grundfest, 1965) to prevent desiccation, and with a gentle stream of oxygen blown from directly behind the head it remained viable for many hours.

Microelectrodes were pulled on a horizontal puller (Brown-Flaming P-77) from 1-mm diameter borosilicate capillary glass (Hilgenberg). These had an initial tip resistance of 200–250 MΩ when filled with 3 mol l^{-1} potassium acetate. The resistance often dropped to about 150 MΩ after entering the tissue, even though the outer sheath was usually torn beforehand. After penetrating a cell a negative current of about 0·2 nA, for a short period, often helped to improve the quality of the recording. Using this preparation many cells with large graded depolarizations and/or action potentials could be held for over an hour. Recordings were amplified and displayed using standard equipment. Data were recorded on a chart recorder, either directly, in which case as is evident in most figures frequencies of over 40 Hz were attenuated, or by slow replay from an FM tape recorder, to give more faithful reproduction.

Cell marking

Three marked cells are described here, one of which (2) was filled iontophoretically with Lucifer Yellow CH, and the others using pressure injection (Picospritzer II). The specimens were fixed with 4% paraformaldehyde in Millonig buffer (pH 7·4), dehydrated in alcohol, cleared with methyl salicylate and viewed in a wholemount using standard fluorescence microscopy.

Stimulation

The equipment described here was designed for the study of the wide variety of cells found in the medulla, and, although not designed for the study of wide-field units and their spectral properties, it is useful for qualitative description.

The ipsilateral eye faced a u.v.-transparent, diffusing tangent screen, which was illuminated from behind with a xenon arc (XBO 75W) or a 150-W quartz iodide filament filtered to 5500 K (80A colour correcting filter). The illuminated region subtended 60° at the locust's eye, and had a luminance of 200 cd m^{-2} under xenon illumination and 1000 cd m^{-2} with the filament. Some stimuli were provided by a focused dissecting lamp; the absolute intensity of this source was not measured, and relative intensities only are given. Whole-field stimuli were provided by placing filters directly in front of the eye. Filters attached to a chart plotter (HP 7004B) with narrow Perspex rods provided moving negative contrast stimuli, and flashes were produced by projecting the image of a plastic light guide tip upon the same screen. The contrast of a stimulus is defined as (I1–I2)/I2, where I1 and I2 are the intensities of the stimulus and screen respectively. The stimuli were calibrated with a radiometer using a vacuum photodiode (IL700) and camera exposure meter (Pentax spotmeter). All calibration is expressed as luminance or radiance. Filters used were: two broad band filters which had 70% transmission at their peaks (365 nm and 500 nm), and half-widths of 50 nm, narrow band (10 nm) interference (Schott & Balzers), and gelatin neutral density filters (Kodak Wratten series). The latter were unsuitable as they are not spectrally flat below 450 nm; individual calibration showed that the transmittance at 370 nm is approximately half that at 500 nm. The positions of stimuli are described relative to the animal in a level orientation, so the line viewed by the equator of the eye is called the horizon.

The receptive field is defined as the region in which a stimulus elicits a response. Only for cell 4 was the field mapped more precisely, by counting the number of spikes produced in response to isoquantal stimuli, modified either in area or position.

Behavioural studies

The spectral responses of the optomotor and dorsal light responses were tested using the equipment described by Horridge, Marčelja & Jahnke (1984). The stimulator oscillated through 20° at 0·1 Hz, and head roll was recorded using a capacitative detector (Sandeman, 1968), whilst the thorax was fixed to a support. The spectral efficiency of the dorsal light response (or horizon displacement response) was tested at contrast 0·5 with the visual field divided in two, usually with a bright dorsal region, an arrangement similar to that used by Taylor (1981). The spectral sensitivity of the optomotor response was measured at high contrast and threshold radiance with 20° stripes. All experiments were performed after ocellar cautery, and stimuli were calibrated with the equipment described above.

RESULTS

To demonstrate the presence of u.v. sensitivity and spectral opponency, six of the many cell types recorded in the medulla are mentioned here. The results are presented by describing the properties of individual cells, and no attempt has been made to draw quantitative comparisons between similar units. Apart from their chromatic properties all of these cells are distinctive in having substantial tonic

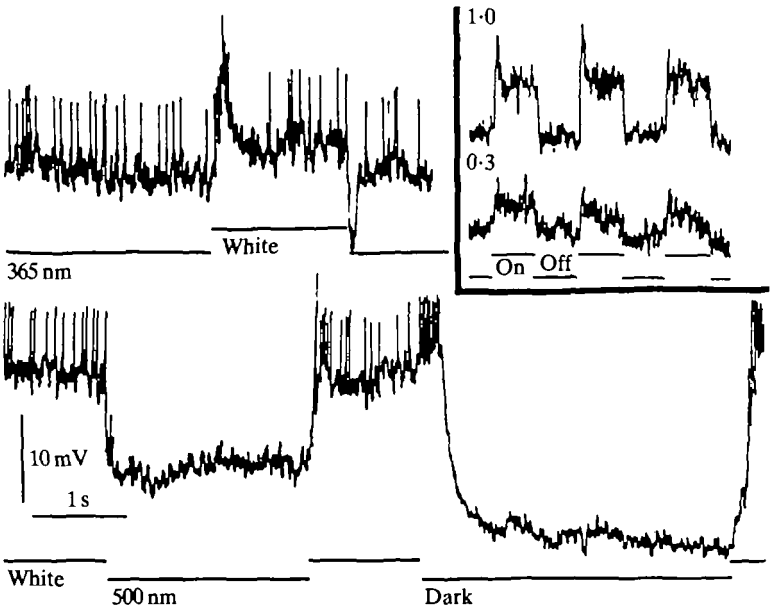

Fig. 1. Responses of cell 1 to isoquantal (5×10^{17} photons $m^{-2}sr^{-1}s^{-1}$) wide-field illumination at 365 nm and 500 nm, and a dark control produced by placing wide-band chromatic and an opaque filter in front of the eye viewing a white screen. Inset: responses to 3° spots of contrast 1·0 (upper) and 0·3 (lower) presented at 0·5 Hz.

components in their responses, compared with the more phasic units which constitute the majority of cells encountered in the medulla.

The first two cells described showed a much higher sensitivity to u.v. than to green light, indicating that a previously unreported receptor type exists in the locust retina. The other four cells showed spectral opponency; since the ocelli were absent this also indicates that more than one receptor class occurs in the compound eye. Cell 3 had a fairly small circular receptive field, and was the simplest of the opponent units; like all the opponent cells described here it was inhibited by u.v. and excited by green light (units with the reverse opponency have also been penetrated). Cells 4 and 5 were inhibited by u.v. and stimulated by green light, with narrow receptive fields extending along the horizon. These properties might suit them to the signalling of roll or pitch, by measuring changes in the relative intensities of long and short wavelength illumination, the ratios of which differ markedly about the horizon. The possibility that such units could discriminate roll from pitch is exemplified by the observation that cell 4 had an ipsilateral, and cell 5 a contralateral, receptive field. Finally, cell 6 had a receptive field covering the entire ipsilateral eye. The properties of these cells are now described in more detail.

Cell 1

This small-field (3°) u.v.-sensitive unit had the simplest properties of the cells mentioned. Such a cell may have provided inputs to any of the others described, as it was recorded distally, in the first chiasm. The latency, at 20 ms, was the shortest

measured, which is consistent with light-adapted photoreceptor latencies (Howard, 1981). The response to u.v. and green light in comparison to the unfiltered white screen is shown in Fig. 1, together with the responses to white flashes (inset). The waveform is similar to that of a photoreceptor, which, with the distal recording site, suggests that the cell was a long visual fibre. (More recently, u.v. receptors, with a single peak sensitivity at 370 nm, have been recorded in the proximal part of the retina, S. McFadden, personal communication.) This retinula cell class is present in the locust, projecting directly from the retina to the medulla (Nowel & Shelton, 1981). The small spikes noted here have been recorded in locust retina (Shaw, 1968) and in presumed long visual fibres in dragonfly (Laughlin, 1974). The absence of spikes during some of the recording (Fig. 1, inset) indicates that they were due to injury.

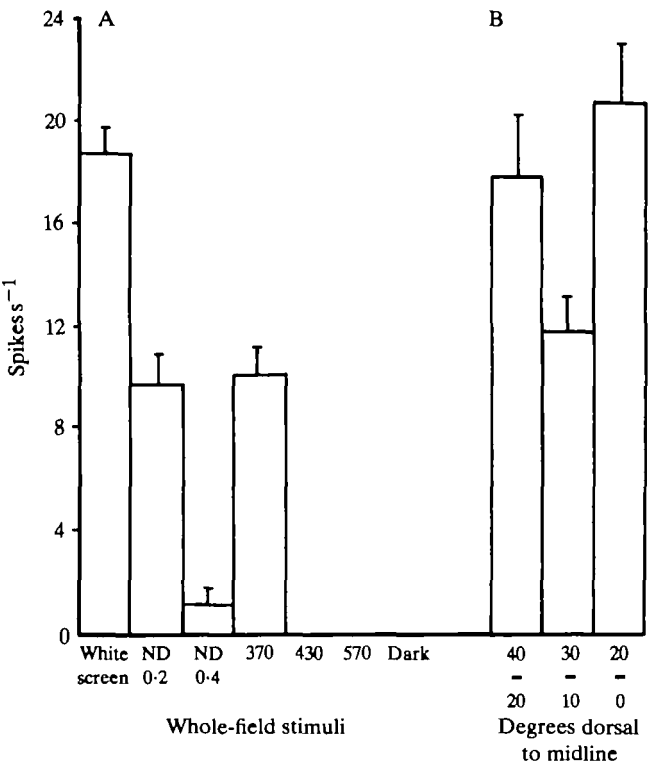

Fig. 2. (A) Mean spike rate of cell 2 after 20 s adaptation to whole-field stimuli. The three chromatic sources were approximately isoquantal (4×10^{16} photons $m^{-2}sr^{-1}s^{-1}$). The Wratten neutral density filters have densities 0·3 units greater than their nominal value to 370 nm light. All samples are based on a 10-s sample of the response, with standard deviations shown calculated with the assumption that the occurrence of spikes follows Poisson statistics. (B) Spike rate of cell 2 in response to dimming 20° square regions of a white screen with Wratten filter (density 0·2). The stimulus was placed in three overlapping positions on a vertical axis between 0° and 20° caudal of the midline, with the response to each position tested three times for 5 s immediately after dimming. The cell was insensitive to dimming outside this region, and, in contrast to cell 1, a 5° black spot had no effect on the firing rate.

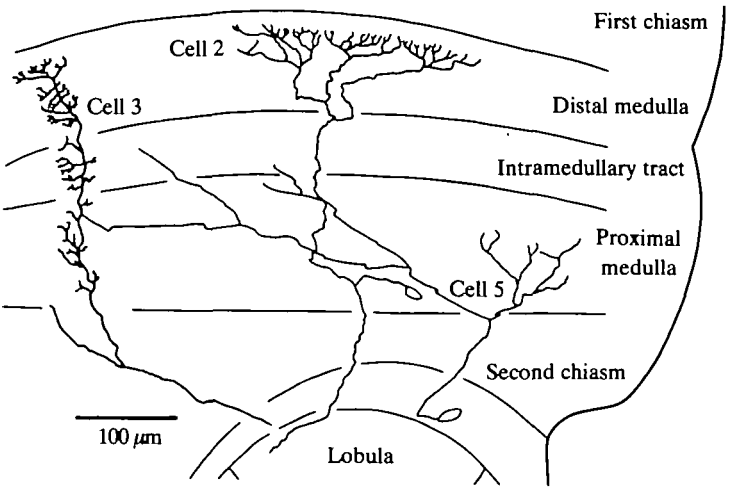

Fig. 3. Drawing of cells 2, 3 and 5 filled with Lucifer Yellow CH, reconstructed from anterior and posterior views. The boundaries of the structures shown are approximate, and the neurite diameters are not drawn to scale. The distal parts of cells 2 and 3 were well filled, whereas it is probable that parts of cell 5 were overlooked. The body of cell 3 was probably at the end of the secondary neurite in the medulla, and was removed during the preparation for microscopy.

Cell 2

Like cell 1, this unit was depolarized by u.v. and insensitive to green light, but the receptor field was about 20° in diameter (Fig. 2). The cell was marked with Lucifer Yellow (Fig. 3).

Cell 3

This cell showed chromatic opponency with a receptive field of less than 20° in diameter in the dorsal anterior part of the visual field. The unit was insensitive to changes in wide-field, achromatic illumination, with a tonic firing rate of about 10 spikes s^{-1}. Green light produced a sustained discharge at double the rate elicited by an unfiltered white screen, whereas u.v. light inhibited firing completely for at least 20 s. The cell was filled with Lucifer Yellow (Fig. 3) and was located close to the dorsal margin of the medulla.

Cell 4

The best characterized of all the units described, cell 4, was excited by green and inhibited by u.v. light (Fig. 4) with a narrow receptive field disposed along the horizon; these are properties that may be useful for horizon detection. Other features of interest are the presence of an inhibitory surround, and adaptation of the response.

The response to a variety of wavelengths and white light is shown in Figs 4 and 5, relative to spontaneous activity in the dark. Opponency, combined with the localized receptive field, is compelling evidence for more than one receptor type in small regions of the retina. This is in contrast to Lillywhite's (1978) observation that all

retinula cells have a spectral sensitivity which can be attributed to a mixture of rhodopsins with peaks at 450 nm and 500 nm, whose ratio changes gradually in a dorsoventral gradient with no local variation.

The receptive field was mapped with 5° white flashes (contrast 9) (Fig. 7). The cell responded best to stimuli directly ahead of the animal, and the number of spikes elicited dropped by 50% 50° caudally and in less than 10° on the dorsoventral axis. The receptive field to u.v. in the dorsoventral axis is shown in Fig. 6 and is similar to

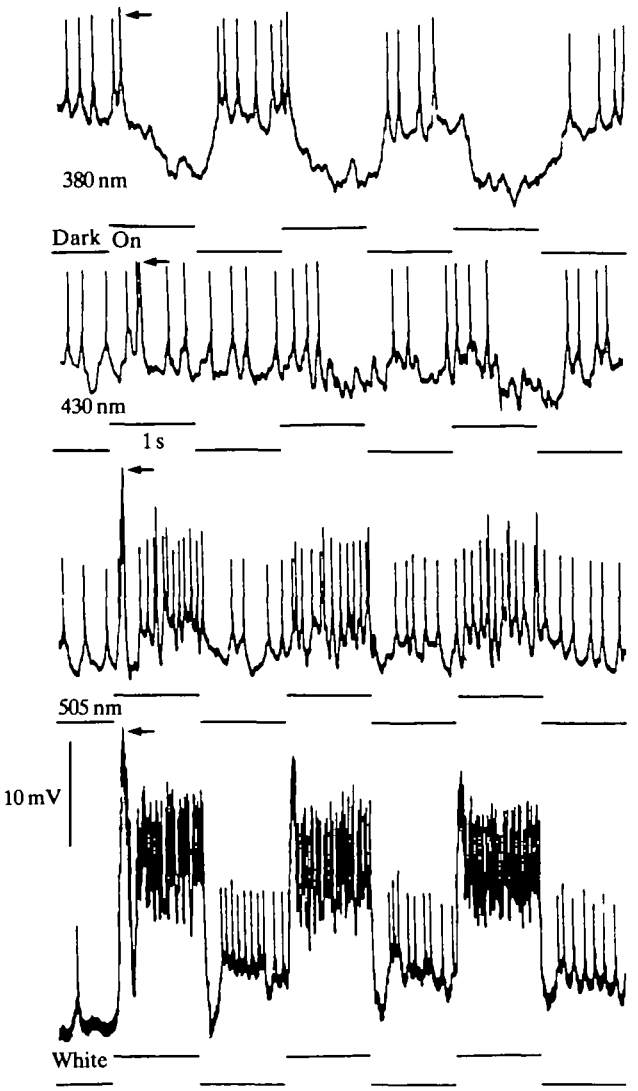

Fig. 4. Response of cell 4 to chromatic and white light presented as a 10° spot over a dark background directly in front of the animal. Each trace shows the response to the first three flashes after 30 s dark adaptation. Note the transient depolarization to the first flash in each case (arrowed), which is attenuated or absent in subsequent presentations. Effective intensities of the spots are given in the legend to Fig. 5.

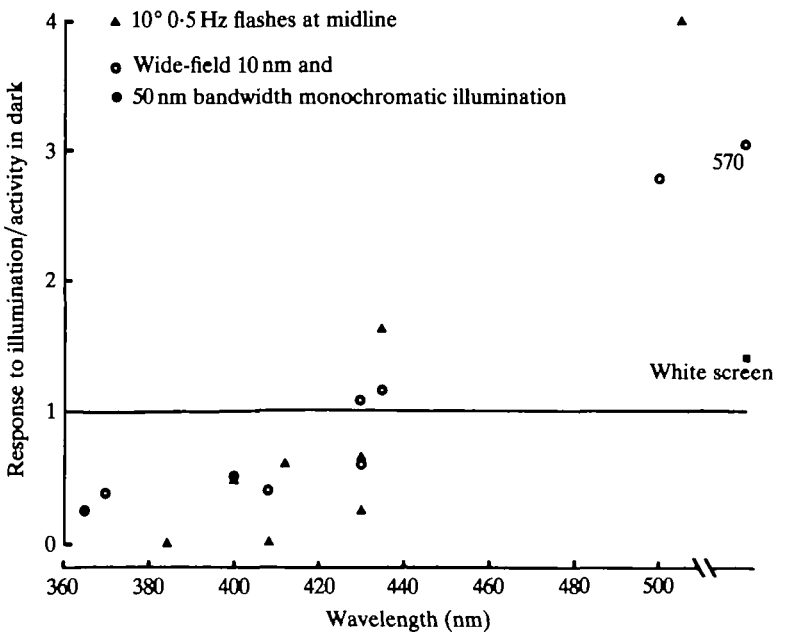

Fig. 5. Firing rate of cell 4 compared with spontaneous activity during the period immediately before and after the presentation of test stimuli. The response to flashes was measured by counting the number of spikes elicited by the 2nd to 5th presentations in a series like that illustrated in Fig. 4. The effective intensities of the flashes were: 370 nm 8; 383 nm 45; 401 nm 52; 408 nm 100; 412 nm 40; 430 nm 130; 435 nm 180; 505 nm 340×10^{13} photons $m^{-2} sr^{-1} s^{-1}$. The wide-field stimuli were provided by placing filters in front of the eye illuminated with a focused microscope lamp. This gave relative intensities as follows: wide band filters; 365 nm 8, 500 nm 260: narrow band filters; 370 nm 1, 400 nm 2, 408 nm 4, 430 nm 6, 435 nm 10, 505 nm 40, 570 nm 110. The white screen had a luminance of 1000 cd m^{-2}. The responses to green and to white light were luminance-dependent.

that to white light. It was plotted by moving a u.v.-transmitting filter subtending 20° at the eye behind the white screen.

The unit may have had an antagonistic surround, as isoquantal white flashes subtending 10°, 30° and 60° elicited responses of 7, 2 and 0·5 times the spontaneous rate, respectively. The flashes were centred on the horizon 20° caudally, and projected over an illuminated screen. The possibility that u.v. inputs had a lower sensitivity threshold than the green ones, which would also explain this observation, was precluded because dim 10° flashes were always excitatory.

Finally we turn to the waveform of the response (Fig. 4). The main features are an adapting phasic depolarization to all wavelengths (arrowed), followed by the more tonic chromatic opponent response. The phasic response had a shorter latency (40–45 ms) than the tonic (65–70 ms for both depolarization and hyperpolarization), which was measured after the phasic component had adapted. The tonic depolarization to long wavelengths also showed some signs of adaptation. This is most evident in the response to 430 nm flashes, which in the course of the three presentations illustrated in Fig. 4 changed from excitation to inhibition. This effect

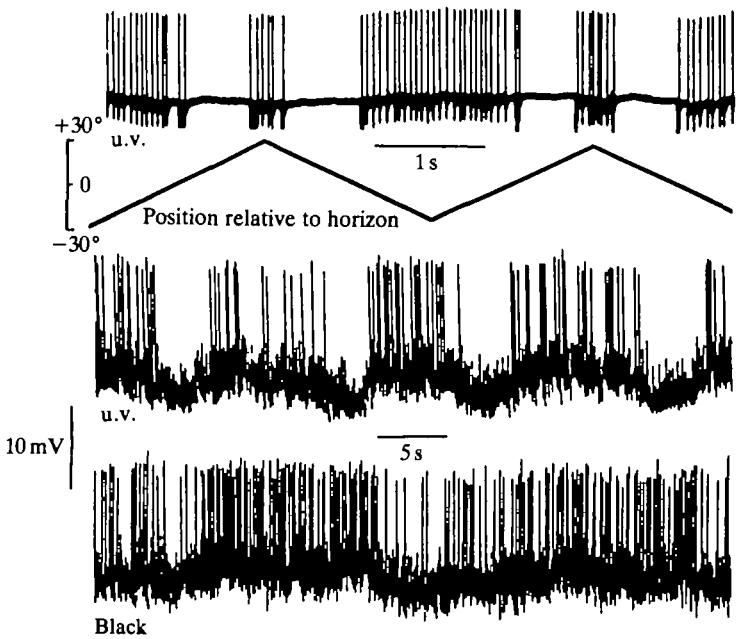

Fig. 6. The responses of cell 4 (middle) and cell 5 (above) to vertical movement of a 20° diameter u.v. filter on an illuminated screen. In both cases inhibition occurred in receptive fields close to the midline, but appeared to be in different places because the head was tilted, and the receptive field of cell 5 was in the contralateral eye. The lower trace is a control for cell 4, showing that there was no response to a black target (the irregular firing is uncorrelated with the target position) and indicating that the unit was more sensitive to chromatic than to luminance signals. No control is shown for cell 5, but the regular firing pattern was completely unaffected by similar green and black filters.

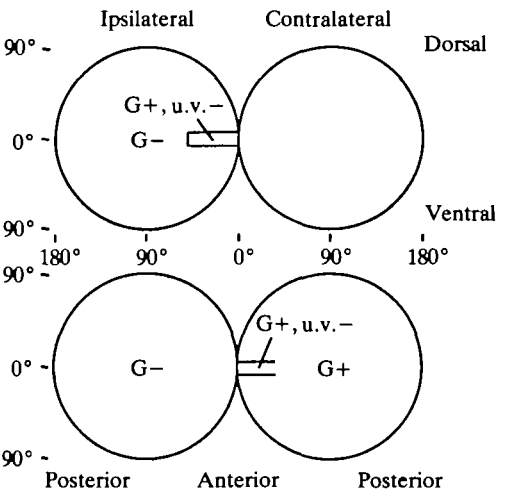

Fig. 7. Diagram of the receptive fields of cell 4 (above) and cell 5 (below). No data are available for the extent of the inhibitor surround of cell 4, or the lateral extent of the spectral opponent receptive field of cell 5. In addition, the contribution of u.v.-sensitive inputs outside the regions designated G+, u.v.− is unknown, and u.v., as well as green, receptors may contribute to the inhibitory surround.

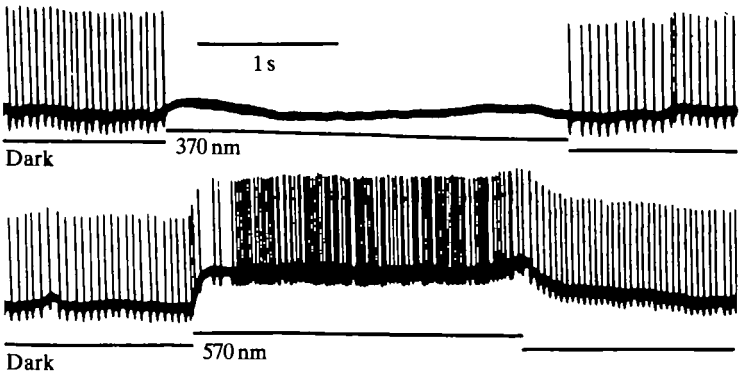

Fig. 8. The response of cell 5 to whole-field, contralateral illumination. Intensities are given in the legend to Fig. 5.

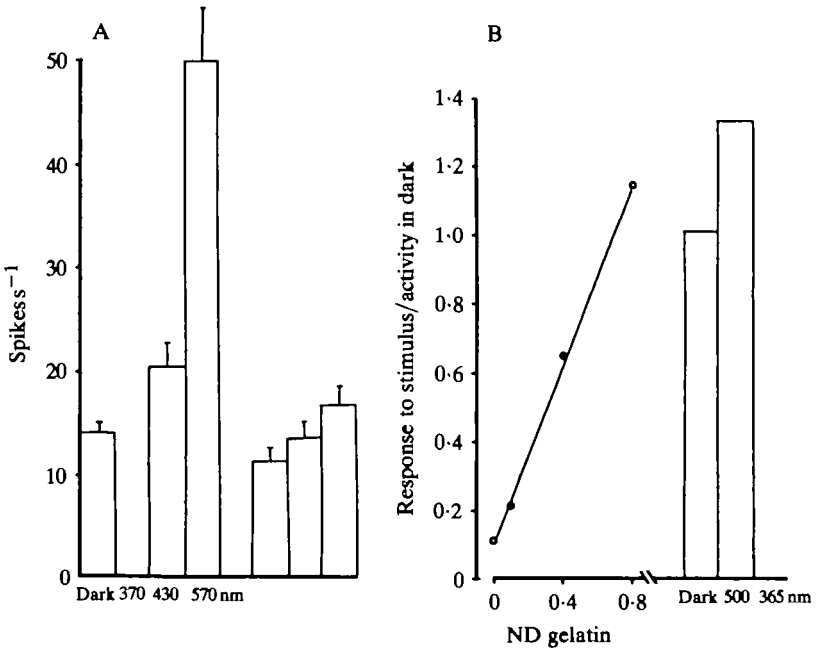

Fig. 9. (A) Response of cell 5 to wide-field, contralateral stimuli. Total inhibition by 370 nm light was sustained for over 30 s. Other data were obtained by measuring spike rate over a 5- to 10-s period. Stimulus intensities are given in the legend to Fig. 5 (wide-field). (B) Response of cell 6 to wide-field stimuli, relative to activity during dark periods before and after each stimulus presentation. The screen luminance was 1000 cd m^{-2}; the 365 nm and 500 nm chromatic filters gave radiances of 1 and 4×10^{15} photons m^{-2} sr^{-1} s^{-1}, respectively. The Wratten neutral density filters of nominal densities 0·1, 0·4 and 0·8 had values of 0·36, 0·72 and 1·1 units at 365 nm, and were close to their normal densities at 500 nm. The differences between the response to 500 nm and the 0·8 density unit Wratten gelatin (ND gelatin) and the dark controls are highly significant ($P < 0{\cdot}001$ and 0·004, respectively, assuming Poisson statistics). The cell had a tonic response with no adaptation to a 0·1-log unit filter in 30 s, and a maximum activity of 55 spikes s^{-1}.

was repeatable after 30 s dark adaptation, and makes accurate measurement of the spectral sensitivity difficult.

Cell 5

This unit showed chromatic opponency at the horizon, like cell 4, but the spectral opponent part of the receptive field was in the contralateral eye (Figs 6, 7, 8, 9A). The sensitivity to a small change in the ratio of u.v. to green light, in a restricted part of the contralateral receptive field, is well illustrated in Fig. 6, which shows the response to vertical movement of a u.v. filter against a white background. Activity drops sharply from the normal spontaneous rate to nothing, despite the fact that the absolute amount of u.v. was reduced and the receptive field was not filled by the filter.

An important difference between this unit and cell 4 is that excitatory inputs were received from the entire contralateral eye; the spectral opponent region of the receptive field being due to an area of u.v inhibition embedded in the wide excitatory field. Stimulation of any part of the ipsilateral eye inhibited activity, irrespective of wavelength (Fig. 7). This spatial opponency emphasizes the possible role in allowing the locust to compare inputs received by the two eyes with one another. The presence of contralateral inputs to the medulla is consistent with Honegger & Schurmann's (1975) observation that the axons project directly between medullas of the cricket, *Gryllus campestris*.

As in cell 4, the response to repeated ipsilateral flashes adapted. When moved by a few degrees the spot elicited an unadapted response. By comparison, this localization of adaptation was not seen in cell 4. A powerful long-term adaptation effect was indicated by the observation that 370 nm light did not inhibit firing if the eye was illuminated after a minute in darkness; instead a weak excitation was recorded. If the eye was stimulated with 570 nm or 430 nm light up to 30 s before u.v. illumination, there was a total inhibition, lasting over 30 s.

Two similar units were penetrated, in one of which prior illumination was not necessary for u.v. light to elicit inhibition. Another was incompletely filled with Lucifer Yellow by pressure injection (Fig. 3). There was no evidence of any arborization or axon outside the proximal region of the medulla, and it is unlikely that this unit projected directly to the contralateral eye.

Cell 6

This cell was excited by green and inhibited by u.v. light, throughout the ipsilateral eye's receptive field. Two sets of records were made after ocellar removal, and unlike ocellar units (Wilson, 1978) there was a large tonic component in the response. For example, the firing rate showed no adaptation after 30 s in response to a 0·1-log unit dimming (0·4 at 370 nm).

Whilst previous units were excited by a white screen, the firing rate of cell 6 was depressed by white light compared with the dark activity. This implies that the u.v.-sensitive inputs dominate the green in 'white' light. The chromaticity of Wratten

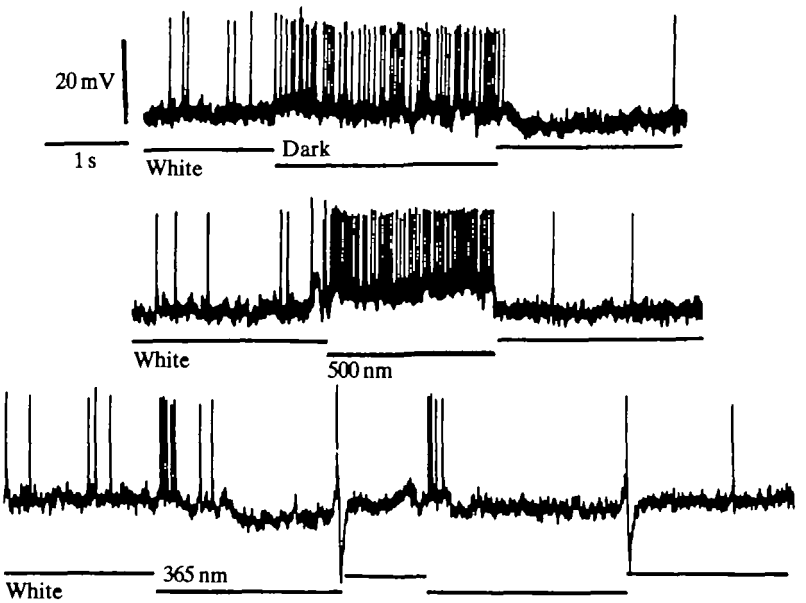

Fig. 10. Response of cell 6 to wide-field stimuli, produced by placing filters in front of a white screen. Note the transient excitation to dimming with a u.v. filter (hyperpolarization recorded on the removal of the 365 nm filter may be a stimulus artefact). Data on illumination are given in the legend to Fig. 8A.

filters to a u.v.-sensitive system is shown by the observation that a filter of density 0·8 excited the cell more than darkness. All the gelatin filters used had twice the transmittance at 500 nm as at 370 nm. The steep slope of the curve produced by a series of neutral density filters, which have a constant chromaticity, indicates that the unit would confound intensity with the spectral composition of light (Fig. 9B). Finally, there is a transient excitation produced by placing a u.v. filter in front of the eye (Fig. 10), which may be analogous to the phasic response of cell 4 to u.v. light.

Like the previous three cells, this unit would signal changes in the position of the horizon, increasing its firing rate as the eye viewed more of the dim green ground. The wide visual field means that the unit is less well adapted to accurate localization of the horizon than cells 4 and 5. Nevertheless, there are related functions to which it is suited. For example, the small effect of spectral, compared with luminance, changes on activity means that the cell might have a role in setting the adaptation state of the visual system by altering the relative sensitivity to green and u.v. light, or mediating a conversion from opponency to pooling of inputs on adaptation to dim conditions.

Behaviour

The properties of the cells described above suggest that u.v. sensitivity and chromatic opponency have a role in behaviour. Therefore, the spectral responses of the animal were tested using experiments found to elicit the optomotor (Thorson,

1966), and dorsal light responses (Taylor, 1981). The spectral sensitivities of the optomotor response in the compound eyes of other insects (Kaiser & Liske, 1974; Kaiser, 1975) and locust ocelli (Wilson, 1978) are known, allowing useful comparisons to be drawn.

The optomotor response was measured by finding the threshold intensity required to elicit a response after an hour's dark adaptation. Three determinations were made at each wavelength on each of two animals, with a minute in darkness between tests. In both cases, the sensitivity to 370 nm was anomalously high compared with other u.v. wavelengths. The spectral sensitivity of the optomotor response, tested in this way (Fig. 11), is similar to the curve obtained for fly optomotor (Kaiser, 1975) and landing responses (Tinbergen & Abeln, 1983). Ultraviolet sensitivity is rather high and variable, a point which needs clarification, but may in part be due to similar variability observed in locust short visual fibres (Lillywhite, 1978; L. Marčelja, personal communication).

The dorsal light response had quite different spectral properties (measured as spectral efficiency), with little or no response to wavelengths above 410 nm. The wavelength dependence of the response amplitude is shown in Fig. 11, measured after ocellar ablation, at high radiance and contrast 0·5, with a bright dorsal hemisphere. Green light (500 nm) of 20 times the maximum u.v. intensity was used without eliciting a response. (In two of the five animals tested a small response occurred; however the amplitude was less than 20 % of that to u.v. light, irrespective of intensity.) Green light in reverse contrast (i.e. with the ventral field brighter than the dorsal) neither elicited a response nor affected the response to u.v. light over a wide range of intensities.

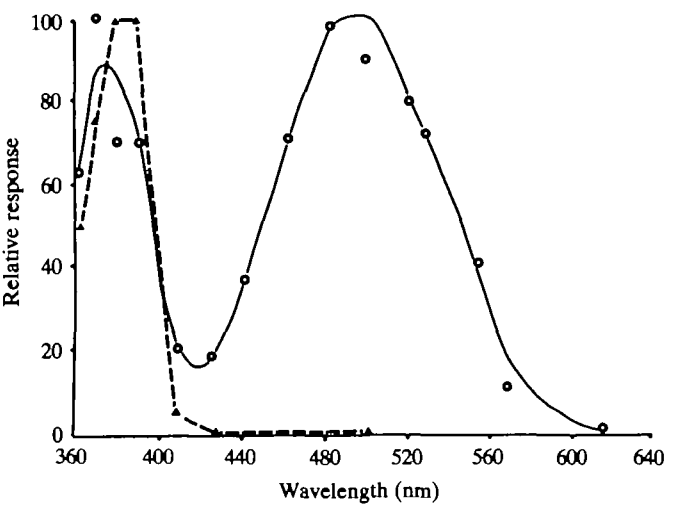

Fig. 11. Spectral sensitivity of the optomotor response (○——○) and spectral efficiency of the dorsal light response (▲---▲). The optomotor threshold after 60 min dark adaptation was approximately 5×10^{14} photons $m^{-2}sr^{-1}s^{-1}$ at 499 nm. The dorsal light response was tested at u.v. intensities of 1 to 5×10^{17} photons $m^{-2}sr^{-1}s^{-1}$ and with green light up to 10^{19} photons $m^{-2}sr^{-1}s^{-1}$.

DISCUSSION

The results show that spectral opponency occurs amongst the outputs of the locust compound eye. This suggests that at least one spectral class of receptor exists in addition to the population of green cells described by Lillywhite (1978), and it is conjectured that these are u.v.-sensitive, long visual fibres. The tonic responses and spatial properties of some of the neurones described suggested that they have a role in controlling a sustained orientation to the horizon. Moreover, the response to a bright dorsal hemisphere and the optomotor response can be distinguished from one another by their spectral properties. There is no evidence that colour vision is used in the dorsal light response, although this response probably involves an input from the u.v. receptors. The optomotor response probably uses inputs from green-sensitive cells, as in the fly, the bee and the butterfly (Kaiser & Liske, 1974; Kaiser, 1975; Horridge *et al.* 1984), although high sensitivity to 370 nm light may reflect a contribution from u.v. receptors.

Flight control by the locust appears to use at least three separate visual mechanisms; the optomotor response and the two responses to dorsal illumination and/or horizontal contrast. Of the latter, one response is driven by the ocelli and the other by the compound eyes. It is interesting to see how these three responses compliment one another in their spatial, spectral and temporal properties. The optomotor response has high spatial and temporal acuity (Buchner, 1984), with a spectral sensitivity resembling that of the short visual fibres in the fly (Hardie, 1979) and, perhaps, in the locust. This high spatial resolution is in marked contrast to that of the unfocused ocelli, which are u.v. sensitive and, like the optomotor response, give a short latency phasic response (Wilson, 1978; Taylor, 1981). The ocellar and optomotor responses act as inertial systems allowing the animal to correct transient deviations from the flight path, using fine structures and changes in overall illumination of the ocelli, respectively. The u.v. sensitivity of the ocelli means that they will be particularly sensitive to changes in the amount of light received from beneath and above the horizon (Wilson, 1978). The dorsal light and horizon responses, both mediated by the compound eyes, are relatively sluggish and sustained, allowing tonic orientation to the horizon, from which transient deviation could be corrected by the other responses (Goodman, 1965; Taylor, 1981).

Let us turn to the properties required by a neural system which is to give tonic orientation to the horizon. The animal must be able to obtain a large amplitude signal, free from local distortions, and readily discriminated from other objects in the environment. The most straightforward requirement is to have high acuity in the vertical but not the horizontal axis. Cells with horizontally elongated receptive fields, like cells 4 and 5, would be sensitive to changes in illumination as the animal tilted about its horizontal axes, but less responsive to vertical structures.

The effect of poor horizontal acuity may be enhanced by temporal blurring, ensuring that the animal is able to locate the true horizon, without being distracted by local variations caused by vegetation and landscape. Such temporal blurring may be implemented by a neural system with a long integration time, explaining the long latency of the compound-eye-mediated dorsal light response (Taylor, 1981). The

cells described here have more tonic responses than the majority of units recorded in the medulla (personal observation).

We now consider the spectral properties required for detection of the horizon, which is distinguished by having a high u.v. and a low green contrast (Wilson, 1978). However, since the sky is normally brighter than the ground at all wavelengths, spectral opponency, as observed here, will attenuate the signal provided by the horizon. This indicates that opponent units would be unsuited to horizon detection, but perhaps adapted to another role – for example, the navigational task described in the bee by Rossel & Wehner (1984). Alternatively, there may be a more subtle explanation for the use of chromatic opponency in horizon detection; for example, colour contrast may distinguish the horizon from other structures (such as silhouetted vegetation) with high contrast at all wavelengths. Finally, the green input may serve as an adaptation mechanism, effectively backing-off the u.v. signal to maintain the units in a state of high sensitivity to changes in u.v. illumination. At present, the function of spectral opponency in the locust and its role in the dorsal light response, awaits more stringent behavioural and electrophysiological studies, as well as measurements of the spectral properties of natural scenes.

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