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Spectral properties of movement perception in the dronefly *Eristalis*

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Summary. 1. Spectral-sensitivity functions of large-field movement-detecting units in the lobula plate of the dronefly *Eristalis tenax* L., which is a Batesian mimic of the honeybee, were measured using visual stimuli consisting of light flashes, or moving gratings. Two classes of units were studied, one class responding to inward horizontal motion in the contralateral eye (presumably the homologue of the well-known 'H1' in other fly species), and the other class responding to vertically-downward motion in the contralateral eye.

2. In both classes of units, the spectral-sensitivity function of the response to 'flashes' is characterized by two peaks, one in the UV at ca. 350 nm and the other in the blue at ca. 475 nm (Figs. 3, 8). It resembles the spectral-sensitivity function of the R1–R6 class of receptors in other flies.

3. In both classes of units, the spectral-sensitivity function of the response to 'movement' is characterized by a single peak, occurring in the blue at ca. 450 nm (Figs. 7, 9).

4. Control experiments on homologous units in the Australian Sheep Blowfly *Lucilia cuprina*, using identical stimulating conditions reveal that the response to flashes as well as movement possesses a dual-peaked spectral sensitivity, with one peak in the UV and the other in the blue-green region of the spectrum (Figs. 10–12).

5. The results indicate that the pathways subserving the inputs to movement-detecting neurons in *Eristalis* are driven by more than one spectral class of photoreceptors. They also reveal that the spectral sensitivity of movement detection in *Eristalis* bears a closer resemblance to that of the honeybee, than to that of other flies. This similarity to the honeybee may arise from the fact that the dronefly and the honeybee occupy similar ecological niches, both foraging for nectar in flowers.

Key words: Fly – Colour vision – Movement perception – Electrophysiology

Introduction

The dronefly *Eristalis* forages for nectar in flowers and it is, in fact, a Batesian mimic of the honeybee. Like the bee (rev. Menzel 1979), the dronefly appears to be endowed with colour vision (Ilse 1949), and the retina has at least 3 distinct spectral classes of photoreceptors (Bishop 1974; Horridge et al. 1975). The retina of the dronefly, however, possesses an open-rhabdom structure that is typical of flies (Bishop 1974), and not the fused-rhabdom configuration that is typical of bees. Moreover, the spectral sensitivities of bee receptors (Menzel 1979) do not seem to match those of the dronefly receptors (Horridge et al. 1975). The most common class of receptor in the fly retina exhibits a spectral-sensitivity function that is dual-peaked – with one peak in the UV and the other in the blue-green region of the spectrum (rev. Hardie 1985) – whilst the most common class in the bee retina exhibits a spectral sensitivity that is characterized by a single peak in the green (rev. Menzel 1979). The intriguing question arises, therefore, as to whether the similarity between the dronefly and the honeybee is only skin deep, or whether it extends to the ways in which the visual information captured by the retina is processed by the nervous system.

Here we examine the spectral properties of movement-detecting interneurons at a relatively high stage of visual processing (in the lobula plate) to see if the analysis of visual signals in the dronefly bears a closer resemblance to that in the bee – with which it shares an ecological niche – or to its genetically closer relatives, the flies.

Methods

Visual stimuli. Two kinds of visual stimluli were employed: (i) Flashes of light from a point source and (ii) Moving gratings.

Light for either stimulus originated from a xenon arc lamp. The intensity and wavelength of the light were set by means of neutral-density and interference filters. The animal was positioned

at the centre of a cardan arm, and the stimulus was delivered to the eye via a light guide whose exit end was carried on the arm. With this arrangement it was possible to stimulate any region of the animal's visual field. The tip of the light guide was positioned 12.0 cm from the eye and it subtended a visual angle of 1.6°. Light flashes of controlled duration and repetition rate were delivered by means of an electronic shutter interposed in the optical path and driven by a pulse generator. The flash duration was 1 s, and the flash repetition rate one per 5 s. At the animal's eye the unattenuated intensity of the flash stimulus (designated as 0 log units) was 0.32×10^{14} photons·cm^{-2}·s^{-1} for UV light (353 nm), 0.51×10^{14} photons·cm^{-2}·s^{-1} for blue light (452 nm), and 0.56×10^{14} photons·cm^{-2}·s^{-1} for green light (552 nm). Intensities were measured using an IL 700 Research Radiometer equipped with an SEE 400D vacuum photodiode. Further details of the stimulus arrangement were as described in Matic and Laughlin (1981).

The moving grating was created by means of a specially-constructed template interposed between the animal and the tip of the light guide. The template was a radial grating composed of 16 opaque and 16 translucent sectors (i.e. 16 periods). The radial dimension of each sector was 3.0 cm. The grating was placed 4.0 cm from the eye and could be rotated clockwise or counterclockwise at any desired speed by means of an electronically-controlled motor. The light guide illuminated a 2.5 cm diameter circular patch of the grating near its circumference. This arrangement produced an approximately linear grating of contrast 1.0 and spatial frequency 0.035 c/deg within a circular patch subtending an angle of 35° at the eye. The rotating grating assembly was carried by the cardan arm, so that the stimulus could be presented in any desired region of the visual field. Furthermore, the rotational axis of the grating could be swivelled about the optical axis of the light guide, so that the orientation and direction of motion of the grating could be set as desired. The stimulus regime consisted of a 2-s motion in the preferred direction followed by a 2-s motion in the null direction, this cycle usually being repeated several times to obtain averaged responses. In all of the experiments reported here (except that of Fig. 5) the speed of the grating was set to produce a temporal frequency of 1.56 Hz, which was close to the frequency that elicited the strongest response to movement (see Fig. 5). The illuminating light from the light guide was left on continuously. The intensity and colour of this light were varied by filters as in the case of the flash stimulus. At the animal's eye, the unattenuated mean intensity of the grating (measured by recording the time-averaged output of the radiometer while the grating was in motion) was 0.27×10^{13} photons·cm^{-2}·s^{-1} for UV light (353 nm), 0.59×10^{13} photons·cm^{-2}·s^{-1} for blue light (452 nm), and 0.74×10^{13} photons·cm^{-2}·s^{-1} for green light (552 nm).

Spectral runs, both for flashes and movement, were conducted with a 2 log-unit neutral-density filter interposed in the stimulating beam. Thus, the intensities used during these runs were 2 log units below the maximum values specified above.

Preparation and recording. The lobula-plate region of the brain was exposed by removing a small section of cuticle from the back of the head. The characteristic branching pattern of the tracheae provided landmarks which assisted in positioning the tip of the recording electrode so as to find the desired neuron, e.g. H1 (see Dvorak et al. 1980). Recording was extracellular, using tungsten-in-glass electrodes (see Maddess and Laughlin 1985). Standard amplification techniques were used. Responses, stimulus monitor signals and voice commentary were stored on a multichannel Direct/FM tape recorder (TEAC R61) for subsequent analysis.

Data analysis. Recorded data was played back into a DEC 11/23 laboratory computer for analysis. The raw spike trains were passed through a Schmitt trigger, the output of which was fed into an analog filter which measured instantaneous spike-frequency. The filter consisted of a leaky integrator with an impulse response consisting of a single decaying exponential function with a time-constant of 125 ms. The output of the filter was an analogue voltage proportional to the instantaneous spike frequency averaged over 125 ms. The output of the monitor was sampled at a rate of 5 ms (for the flash responses) and 9 ms (for the moving-grating responses). Averaged responses were obtained by collecting, typically, 3 or 4 responses for the flash stimulus and 6 responses for the moving-grating stimulus.

Several response measures were employed. For the flash responses we used 4 measures: (i) the peak value of the 'on' transient, (ii) the integral of the 'on' response over the duration of the light flash, (iii) the plateau level of the 'on' response (i.e. the value of the response 1 s after the onset of the flash), and (iv) the peak value of the 'off' transient. For the moving-grating responses we employed two measures: (i) the peak value during motion in the preferred direction, and (ii) the integral of the response during motion in the preferred direction.

Spectral sensitivity functions were calculated from an intensity-response function, obtained at one or more wavelengths, and a spectral run. Details of the computer program employed for this purpose are given in Matic (1983).

Results

The results shown were obtained from 17 units in 12 different female preparations of *Eristalis tenax* L., and 11 units in 11 different female preparations of *Lucilia cuprina*. All of the units were of the 'optomotor' type (Bishop and Keehn 1967; Dvorak et al. 1975; Hausen 1976): they were directionally selective, had large visual fields (typically covering one entire eye), and showed sustained responses to movement.

Of the units that were investigated, 10 in *Eristalis* and 10 in *Lucilia* had a visual field in the contralateral eye, a preferred direction that was horizontal inward (toward the midline), and a region of highest sensitivity that was located about 20° below the equator and 20° lateral to the midline. Based on these characteristics and upon the position of the tip of the recording electrode, we are reasonably confident that these units represent a single neuron that is homologous to H1 in the other fly species (Dvorak et al. 1975; Hausen 1976; Dvorak et al. 1980). We shall refer to these units as 'H1'. 7 other units that were investigated in *Eristalis*, and 1 unit in *Lucilia* responded maximally to motion in the vertically-downward direction.

Unless specified otherwise, the results described below (and illustrated in Figs. 1–9) refer to *Eristalis*; experiments with *Lucilia* are described in a separate section, and illustrated in Figs. 10–12.

Experiments with H1

Flash stimuli. The response of H1 to a 1-s flash of light from a point source consists of an initial burst of spikes ('on' transient), after which the spike frequency decays to a small plateau (Fig. 1). A second burst of spikes occurs at light-off ('off' transient).

Intensity-response relationships for the peak of the 'on' transient, the integral of the 'on' response and the peak of the 'off' transient are given in Fig. 2 for two

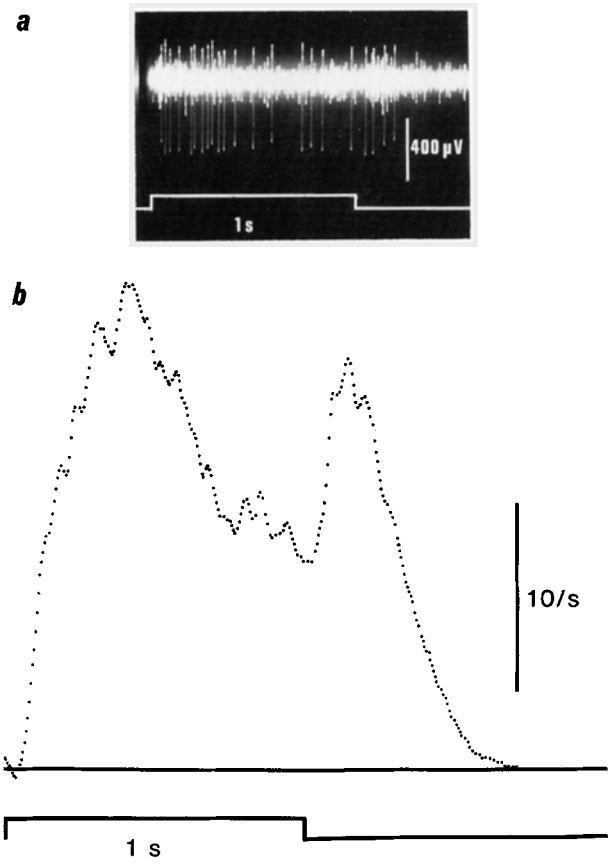

Fig. 1. **a** Extracellularly recorded response of H1 to a 1-s flash of light, depicted by the stimulus trace. Stimulus wavelength 452 nm, intensity 0 log units (see 'Methods'). **b** Time course of the response in **a**, showing instantaneous spike frequency versus time (see 'Methods'). Responses to 4 flashes were averaged

different H1 neurons. For each of the 3 components of the response, the intensity-response function shows a restricted dynamic range of ca. 2 log units between threshold and saturation. The intensity-response function for the 'off' transient is generally more variable.

Intensity-response functions were usually measured at a single wavelength (452 nm). However, on the occasions when they were measured at other wavelengths as well, the curves for different wavelengths exhibited similar shapes, but different intensity-thresholds (e.g. compare the functions obtained from unit 2 in Fig. 2, at 452 nm and 552 nm).

Average spectral-sensitivity functions for the 'on' transient and the 'on' integral, obtained from measurements on 10 different H1 neurons, are shown in Fig. 3. They are characterized by 2 peaks, one in the UV (at ca. 350 nm) and the other in the blue-green (at ca. 475 nm). There is some variability in the locations of the peaks and in the ratio of sensitivities at the 2 peaks, depending upon the particular cell and the response measure that is employed. The average value of the blue/UV sensitivity ratio is 1.11 ($\pm$0.37 s.d.) for the 'on' transient, 1.02 ($\pm$0.81 s.d.) for the 'on' plateau, and 2.11 ($\pm$1.52 s.d.) for the 'on' integral. A t-test on paired samples reveals that the blue/UV sensitivity ratio for

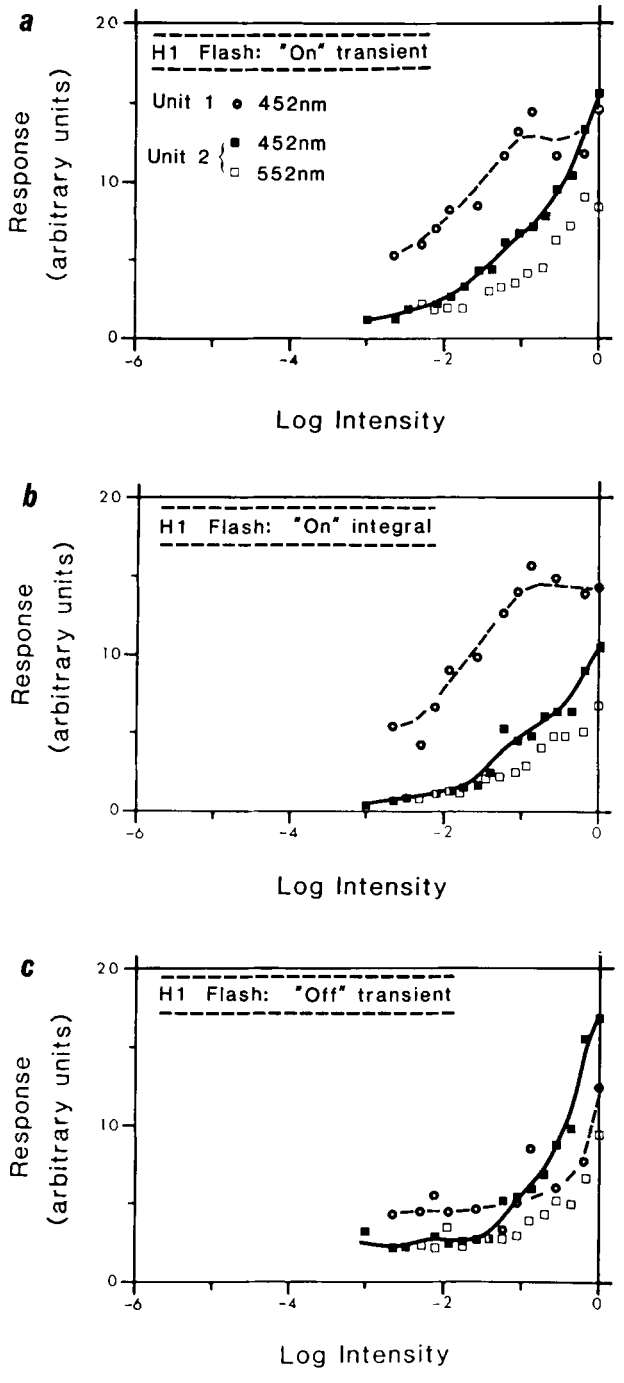

Fig. 2a–c. Intensity-response functions of the 'on' transient **a**, 'on' integral **b**, and 'off' transient **c** for two H1 units. One unit is symbolized by the circles (stimulus wavelength: 452 nm). The other unit is symbolized by the squares (stimulus wavelengths, filled squares: 452 nm; open squares: 552 nm)

the 'on' integral is significantly greater than that for the 'on' transient and the 'on' plateau ($P<0.05$ in each case), and that there is no significant difference between the measurements of this ratio for the 'on' transient and the 'on' plateau ($0.7<P<0.8$). Spectral-sensitivity functions for the 'off' transient tended to be very variable, consequently they were not investigated in detail.

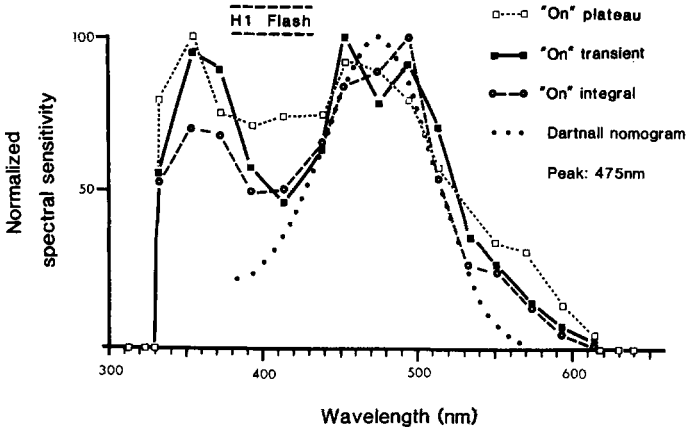

Fig. 3. Spectral-sensitivity functions of the 'on' transient (filled squares), the 'on' plateau (open squares) and the 'on' integral (open circles) for H1 neurons. The data represents measurements averaged from 10 cells. Overlapping data points are depicted by open squares. The dotted curve dipicts the theoretical Dartnall-nomogram for a visual pigment with peak absorption at 475 nm. It was calculated from Table 7.9 of Wyszecki and Stiles (1967)

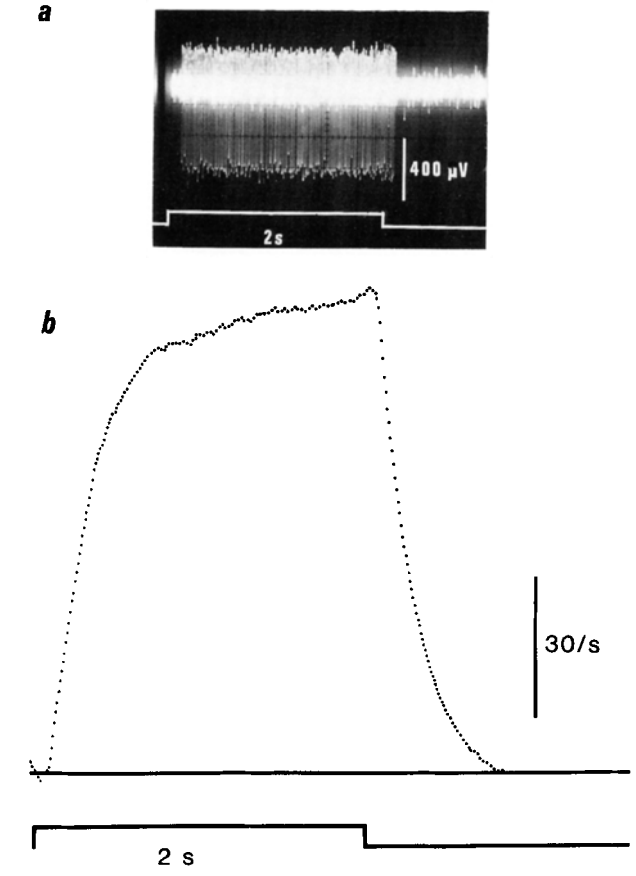

Fig. 4. a Extracellularly-recorded response of H1 to motion of a grating in the preferred direction for 2 s, followed by motion in the null direction for 2 s. The stimulus trace depicts the direction of motion (low: null direction; high: preferred direction). Stimulus wavelength 452 nm, intensity −0.87 log units. **b** Time course of the response in **a**, showing instantaneous spike frequency versus time (see 'Methods'). Responses to 6 cycles of preferred-null motion were averaged

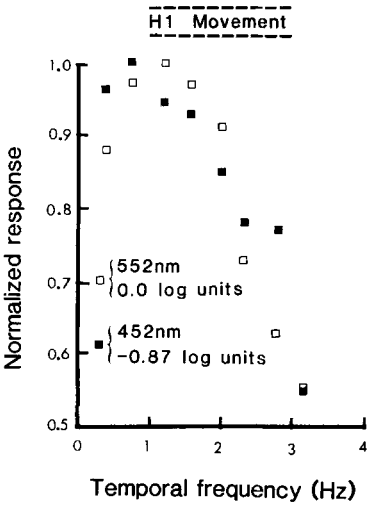

Fig. 5. Temporal-frequency dependence of H1 response to a grating moving in the preferred direction at various speeds. At each temporal frequency the response was measured by integrating (digitally) the voltage representing the instantaneous spike-frequency over the 2-s duration of motion in the preferred direction, and averaging the result over 6 cycles of preferred-null motion. Filled squares depict measurements conducted at a stimulus wavelength of 452 nm and intensity −0.87 log units; open squares depict measurements conducted at a stimulus wavelength of 552 nm and intensity 0 log units. For each stimulus condition, the data are shown normalized to the maximum response

Moving gratings. Movement of a grating in the preferred direction produces in H1 an increase in the mean discharge frequency (above the spontaneous rate), while movement in the null (opposite) direction causes the discharge frequency to be suppressed to nearly zero (Fig. 4). The strength of the response varies with the velocity of the grating (Fig. 5), attaining a maximum at a velocity corresponding to a temporal frequency of ca. 1.0 Hz, as in other fly species (Eckert and Hamdorf 1981; rev. Buchner 1984; Maddess and Laughlin 1985).

Intensity-response functions obtained using gratings moving in the preferred direction are shown for two different H1 units in Fig. 6. Two response measures were employed: peak spike frequency during grating movement, and average spike frequency during this period. The 2 measures give similar results. In comparison to the flash responses, intensity-response functions for movement display a much wider dynamic range (at least 4 log units), and the response amplitude is a much more linear function of log-intensity over this range. (The data shown in Fig. 6 was obtained from the same 2 H1 units as in Fig. 2, so as to enable a direct comparison.)

Intensity-response functions were usually measured at a single wavelength (452 nm). However, on the occasions when they were measured at other wavelengths as well, the curves for different wavelengths exhibited similar shapes, but different intensity-thresholds (e.g. compare the functions obtained from unit 2 in Fig. 6, at 452 nm and 552 nm).

Average spectral-sensitivity functions for movement, obtained from 6 spectral runs on 3 different H1 prepara-

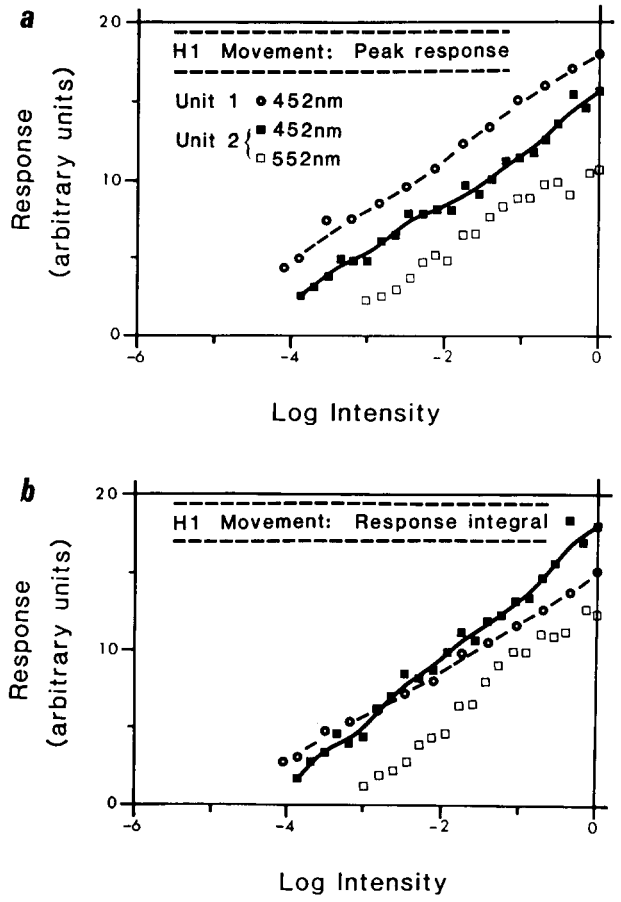

Fig. 6a, b. Intensity-response functions of H1 for movement. The data shows the peak response **a**, and the response integral **b**, for two H1 units. One unit is symbolized by the circles (stimulus wavelength: 452 nm). The other unit is symbolized by the squares (stimulus wavelengths, filled squares: 452 nm; open squares; 552 nm)

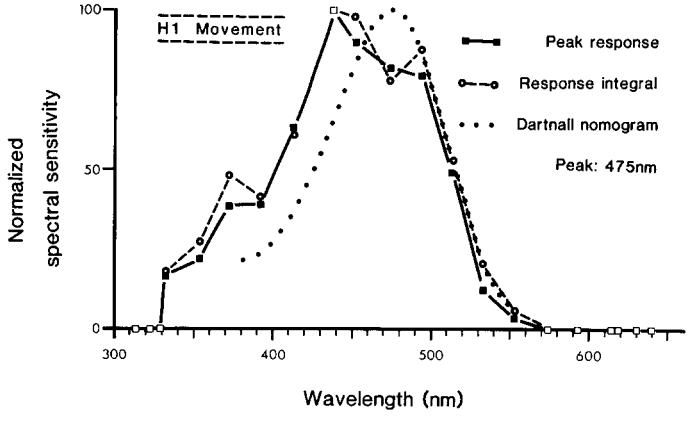

Fig. 7. Spectral-sensitivity functions of H1 for movement, for the peak response (filled squares) and the response integral (open circles). The data represents an average of 6 spectral runs on 3 units. The dotted curve is as in Fig. 3

tions are given in Fig. 7, for each of the two response measures indicated above. The 2 response measures yield similar results. However, in contrast to the flash responses, the spectral-sensitivity functions for movement are rarely dual-peaked: the average function is characterized by a single peak in the blue at ca. 450 nm. In general, responses to movement are characterized by a much lower sensitivity in the UV than at longer wavelengths. The average blue/UV sensitivity ratio measured for the response to movement was 5.01 ($\pm$2.21 s.d.), which was significantly greater than the value of 1.11 ($\pm$0.37 s.d.) measured for the transient component of the 'on' response to flashes ($P<0.01$, t-test).

Units sensitive to vertically-downward movement

It is not clear whether all of the 7 units that were investigated represent the same neuron, or class of neurons. Five of them had a visual field in the contralateral eye, 2 in the ipsilateral eye. All of the units were maximally sensitive to movement in approximately the same eye region as was H1. For all of the units, the flash response showed a spectral sensitivity with 2 peaks, one in the UV and the other in the blue, very similar to the situation in H1. Two contralateral units were tested with movement as well as flashes. The intensity-response functions and spectral sensitivity functions obtained from one of them, for flashes and for movement are shown in Figs. 8 and 9, respectively. The results are, on the whole, similar to those obtained with H1 (see Discussion).

Control experiments with Lucilia

In order to compare the findings in *Eristalis* with those in a more 'conventional' species of fly, we measured responses of homologous movement-detecting cells in the Australian Sheep Blowfly *Lucilia cuprina* to flashes and movement, using the same apparatus and identical conditions of stimulation.

Spectral-sensitivity functions for flashes ('on' transient and plateau) and movement (average response) are shown for two H1 preparations in Figs. 10 and 11. In both preparations, the spectral sensitivity of the flash response as well as that of the movement response are clearly dual-peaked, with one peak in the UV and the other in the blue-green region of the spectrum.

Spectral-sensitivity functions for movement were measured in 8 other H1 preparations of *Lucilia*, using the average response criterion (Fig. 12, filled circles). The resulting average spectral-sensitivity function is clearly dual-peaked. The mean blue/UV sensitivity ratio is 1.21 ($\pm$0.19 s.d.), which is significantly lower than the value of 5.01 ($\pm$2.21 s.d.) measured for the movement response in *Eristalis* ($P<0.01$, t-test). The spectral sensitivity of the movement response was also measured in a *Lucilia* cell that was sensitive to vertically-downward movement in the contralateral eye. The resulting function was also dual-peaked (Fig. 12, open circles).

In summary, large-field movement-detecting neurons in the lobula plate of *Lucilia* exhibit a spectral sensitivity function that is dual peaked, not only with respect to flashes, but also with respect to movement.

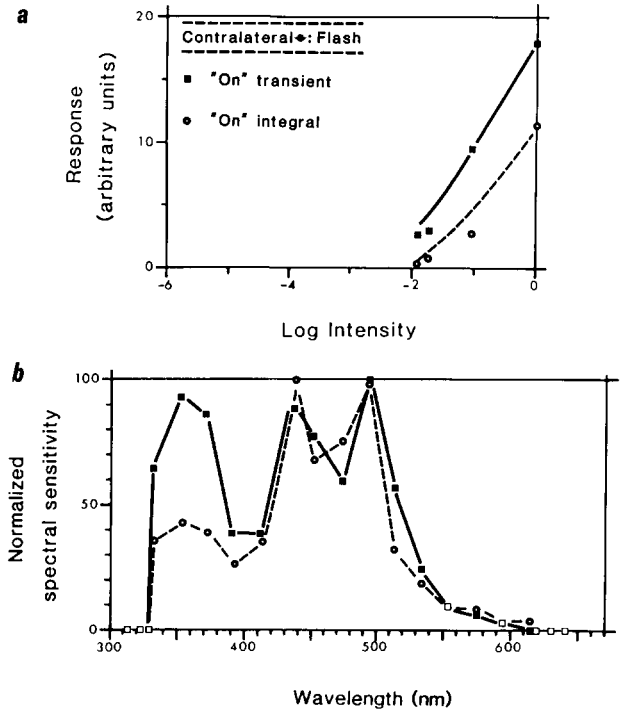

Fig. 8a, b. Flash responses from a unit whose preferred direction was vertically-downward, in the contralateral eye. **a** Intensity-response functions for the 'on' transient (filled squares) and the 'on' integral (open circles). Stimulus wavelength: 452 nm. **b** Spectral-sensitivity functions for the 'on' transient (filled squares) and the 'on' integral (open circles). Overlapping data points are depicted by open squares

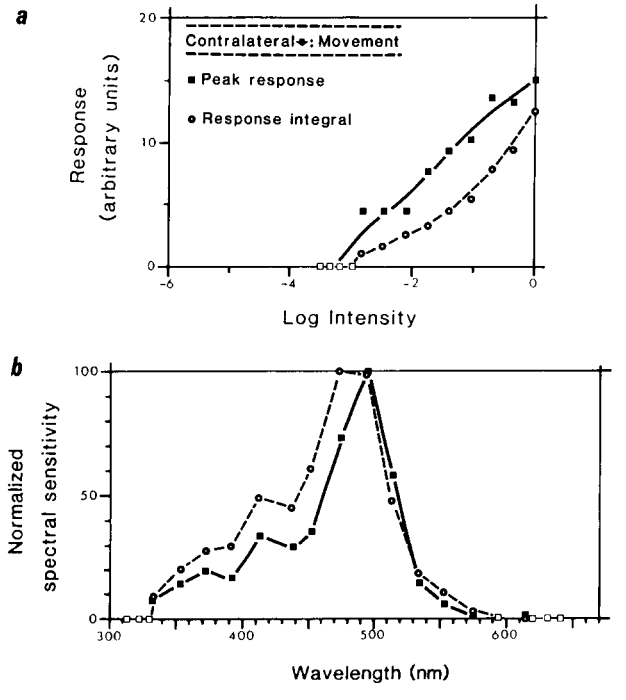

Fig. 9a, b. Responses to movement from the same unit as in Fig. 8. **a** Intensity-response functions for the peak response (filled squares) and the response integral (open circles). **b** Spectral-sensitivity functions for the peak response (filled squares) and the response integral (open circles). In each panel, overlapping data points are depicted by open squares

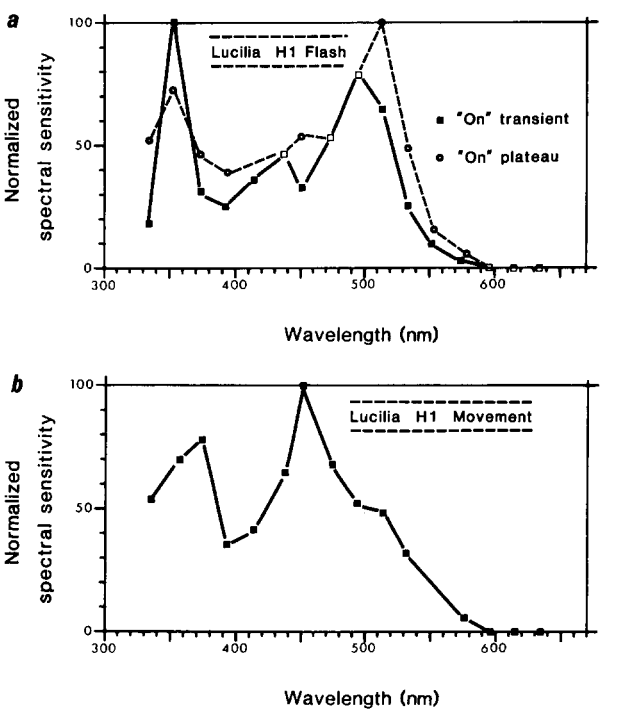

Fig. 10a, b. Measurements of spectral sensitivity of a H1 unit in *Lucilia*. **a** Spectral-sensitivity functions for the 'on' transient (filled squares) and the 'on' plateau (open circles). Overlapping data points are depicted by open squares. **b** Spectral-sensitivity function for movement

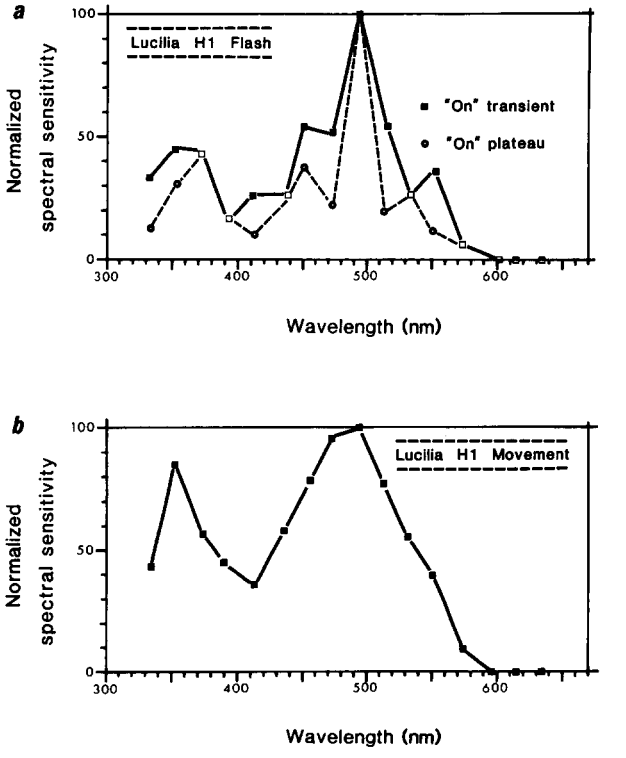

Fig. 11. Measurements of spectral sensitivity of a H1 unit in another preparation of *Lucilia*. Details as in Fig. 10

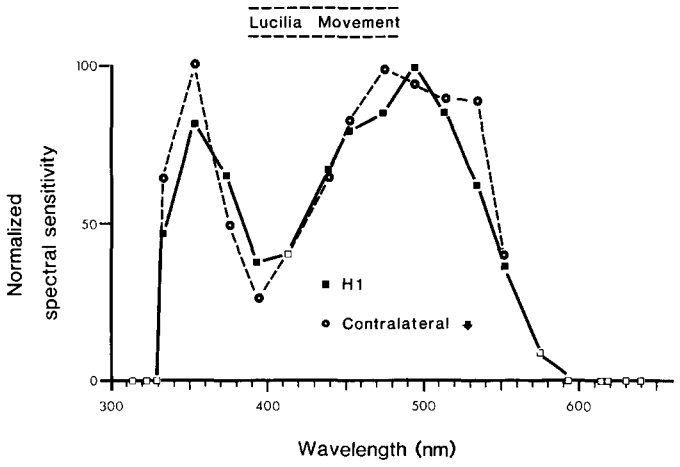

Fig. 12. Spectral-sensitivity functions for movement, measured from units in *Lucilia*. Filled squares: H1, average of 8 units; Open circles: a unit sensitive to vertically-downward movement in the contralateral eye

Discussion

Our results in *Eristalis* show that the intensity-response function for the flash response possesses a dynamic range of only ca. 2 log units of intensity, differing substantially from that for the movement response which exhibits a dynamic range of ca. 4 log units. This discrepancy, however, does not necessarily imply that the responses to flashes and movement are mediated by different neural pathways: the underlying reason could be the difference in the stimulus protocols that were used in the 2 cases. The flash stimuli were applied to the dark-adapted eye. The movement stimuli, on the other hand, were presented with the rotating grating illuminated continuously, and the responses were measured for various intensities of the illuminating beam. The protocol used in conjunction with the moving stimuli could have adapted the system to each intensity, and thus expanded the effective intensity range of the response. (Continuous, rather than flashed illumination was deliberately employed with the moving grating in order to prevent the movement response from being contaminated by a flash response.) In any event, the differences in the intensity-response functions and the underlying reasons are not central to the theme of this paper, and we have not investigated them further experimentally.

It is clear from the results that, in *Eristalis*, the spectral sensitivity of the flash response is substantially different from that of the movement response. We consider below two possible reasons for this.

Firstly, it is known that the spectral sensitivity of the major class of photoreceptors in the eye (R1–6) varies slightly with the state of adaptation of the eye, or, more specifically, with the degree of activation of the intracellular 'longitudinal pupil' that is associated with each photoreceptor (Hardie 1979; Vogt et al. 1982). Thus, given that the spectral sensitivities of the flash and movement responses were measured using different stimulus protocols, could the observed differences in spectral sensitivity be attributed to different degrees of activation of the pupil? We feel that this is unlikely for 2 reasons: (i) In *Calliphora* (Hardie 1979) and *Musca* (Vogt et al. 1982) it has been shown that the pupil is relatively transparent in the UV and that the primary effect of its activation is to shift the peak of sensitivity in the visible region (blue-green) toward slightly shorter wavelengths, and to depress slightly the sensitivity at this peak relative to that at the UV peak. Our experiments, on the other hand, show that the main difference between the spectral sensitivities of the flash and the movement responses is an almost complete absence of the UV peak in the latter case. It is difficult to account for this change purely in terms of differences in pupillary activation, unless one makes the rather unlikely postulate that the absorption spectrum of the *Eristalis* pupil is very different from those of other flies. (ii) In *Calliphora*, it is known that, for illumination at wavelengths near the peak of sensitivity in the visible range, the pupil is fully activated at an intensity of ca. 10^{12} photons $\cdot$ $cm^{-2} \cdot s^{-1}$ (Dr. R. Hardie, pers. comm.). If we assume that the *Eristalis* pupil operates over a similar intensity range, and that the time constant of its closure is comparable to that of the *Calliphora* pupil (ca. 1 s; rev. Stavenga 1979) it follows that, with the intensities that we used in the spectral runs for the flash response (see 'Methods'), the pupil should have been nearly fully open at the peak of the 'on' transient of the flash response, and nearly fully closed at the end of each flash. The discrepancy between the spectral-sensitivity profiles for the 'on' transient and 'on' plateau responses should reflect the change in spectral sensitivity due to the closure of the pupil (compare filled squares with open squares in Fig. 3; note, however, that each of these curves has been separately normalized to unity). We see that there is only a small change, if any, in the ratio of UV/blue sensitivity between the 2 curves. Since the spectral runs for the movement response were carried out at a somewhat lower intensity than those for the flash response (see 'Methods'), it follows that, during the movement runs the state of activation of the pupil would have been one that was inbetween that corresponding to the dark-adapted state (fully open) and that corresponding to the end of each flash (nearly fully closed). Given this, it is difficult to account for the presence of a strong UV peak in the 'on' transient as well as the 'on' plateau of the flash response on the one hand (Fig. 3), and the virtual absence of a UV peak in the movement response, on the other (Fig. 7), purely on the basis of differences in the degree of pupillary activation. (It is conceivable, however, as suggested by one of the referees, that the pupil is responsible for the slight shift of the visible peak toward shorter wavelengths in the data of Fig. 3 for *Eristalis* and Fig. 10 for *Lucilia*; however, more data is needed to establish this with certainty.)

A second, more likely explanation for the large difference in UV sensitivity between the responses to flashes and movement, is that each of the large-field movement-detecting pathways receives input from more than one

spectral class of photoreceptor, and that different classes, or combinations of classes are responsible for mediating the 2 kinds of response. It is of interest to consider which of the known spectral classes of photoreceptor in *Eristalis* could be contributing to the inputs.

Bishop (1974) observed 2 spectral classes in the dronefly retina, one with peak sensitivity in the UV (ca. 350 nm) and the other in the blue (ca. 450 nm). In a later study Horridge et al. (1975) confirmed the existence of these 2 types, and reported a third type which they encountered far more frequently. This third class had two peaks, one in the UV (at ca. 350 nm) and the other in the blue (at ca. 470 nm). It is probable that the UV peak in this class arises from an 'antenna' pigment, as in other flies. (They also documented a 4th, very rare class with triple peaks, one near 520 nm.)

For all of the *Eristalis* movement-detecting neurons that we have examined here, the flash responses show a twin-peaked spectral sensitivity closely resembling that of the third category of receptor cells mentioned above (UV-blue; see Figs. 3, 8b). Thus, the flash responses are in all probability driven by this class of receptors. A comparison of the spectral sensitivity of the flash response of H1 (Fig. 3) with that of the UV-blue receptors as given by Horridge et al. (1975) reveals that the 2 curves match very well at all but the longest wavelengths (530–620 nm), where H1 exhibits a greater sensitivity. This shoulder of enhanced response may reflect a small, additional contribution from a 'green' receptor, whose existence has been suggested by other experiments (Horridge et al. 1975; Tsukahara and Horridge 1977; Horridge and Marcelja, unpublished). The dotted curve included in Fig. 3 is a theoretical Dartnall-nomogram for a visual pigment with peak absorption at 475 nm. It indicates that, in the region to the right of the blue peak, the shape of the spectral sensitivity functions of the H1 flash response (the 'on' transient, 'on' plateau, and 'on' integral) cannot be easily explained in terms of a single pigment: it is necessay to invoke an additonal 'green' pigment to account for the long-wavelength shoulder.

In contrast to the flash response, the movement response in *Eristalis* shows no UV peak, only a single peak in the blue (Fig. 7). In the region to the right of the peak, the shape of the spectral-sensitivity curve is well approximated by the same Dartnall-nomogram with peak absorption at 475 nm, with no evidence of an additional contribution from a 'green' receptor.

It is well accepted that, in most of the flies that have hitherto been examined (e.g. *Musca, Calliphora, Drosophila*) the major retinal input to H1 (and other large-field motion detecting neurons in the lobula plate) comes from the R1–6 class of receptors, whose rhabdomeres are located peripherally within each ommatidium (McCann and Arnett 1972; rev. Kaiser 1975; Heisenberg and Buchner 1977; rev. Wehner 1981). These receptors, which are the largest, most abundant, and most frequently encountered by the recording electrode (Hardie 1985), invariably possess a spectral sensitivity with 2 maxima, one in the UV and the other in the blue-green. Receptor classes R7 and R8 possess rhabdomeres which are located centrally within each ommatidium. R7 exhibits a single peak in the UV, and R8 a single peak in the blue or green (rev. Hardie 1985). These receptors are smaller and less abundant than those of the R1–6 class. By analogy with these findings, it is not unreasonable to postulate that the most abundant recordings from *Eristalis* photoreceptors, which are also twin-peaked with one peak in the UV and the other in the blue-green (Horridge et al. 1975) represent the R1–6 receptor class, and that this class provides the major excitatory input to H1 in this insect as well. If we accept this propositon, then it follows that the flash response in *Eristalis* is mediated by R1–6 receptors. It also follows that the absence of the UV peak in the movement response of *Eristalis* must be the result of an inhibition of the R1–6-mediated response by a UV channel, possibly driven by R7, assuming that the latter possesses a spectral sensitivity similar to that observed in the other fly species. A similar explanation was proposed by Hardie (1979) to account for the suppression of the UV sensitivity in the optomotor response of *Musca* at high levels of light adaptation (Eckert 1971). Our data on the spectral sensitivity of the flash response in *Eristalis* (Figs. 3, 8b) suggests that the blue/UV sensitivity ratio for the 'on' integral is higher than that for the 'on' transient or the 'on' plateau. This is consistent with what one might expect from a transient, UV-driven inhibition, but further work is necessary to ascertain whether this is indeed what occurs.

Independent evidence for the inhibition, by the central photoreceptors (R7 and/or R8), of the excitation produced by the peripheral photoreceptors (R1–6), comes from the experiments of Kirschfeld and Lutz (1974). They found that in *Drosophila* the optomotor response that is elicited by sequential stimulation of two R1–6 photoreceptors within an ommatidium can be inhibited by illumination of the central rhabdomere within the same ommatidium or in neighbouring ommatidia. Immunohistochemical studies on *Calliphora* reveal the presence of the transmitter histamine in the terminals of receptors R1–6 and R8 (Nässel et al. 1988), but of the inhibitory transmitter GABA in the terminals of R7 (Datum et al. 1986). This is consistent with the notion that signals originating from R7 act in an inhibitory fashion upon the signals originating from R1–6.

In most of the fly species that have hitherto been examined (*Musca, Calliphora, Drosophila* and *Phaenicia*) the spectral sensitivity of movement detection is characterized by 2 peaks, one in the UV and the other in the blue or green (revs. Kaiser 1975; Wehner 1981; Tinbergen and Abeln 1983). This is now confirmed and extended by our own data in *Lucilia* (Figs. 10–12). In the honeybee, on the other hand, the spectral sensitivity of movement detection has a single peak in the green at ca. 550 nm (Menzel 1973; Kaiser 1975). Thus, our findings indicate that the spectral sensitivity of movement detection in the dronefly *Eristalis* bears a closer resemblance to that of the honeybee, than to that of other flies. This similarity to the honeybee may arise from the fact that the dronefly and honeybee occupy similar

ecological niches, both foraging for nectar in flowers. Other fly species such as *Musca, Calliphora, Sarcophaga, Lucilia, Phormia* or *Drosophila* do not visit flowers regularly. It is quite conceivable that the suppression of the UV peak increases with the extent of light-adaptation in all flies, but that the strength of this suppression varies in different species, with *Eristalis* representing an extreme case of complete suppression. There is evidence for partial suppression of UV sensitivity in *Phormia* (Kaiser 1975).

Is there an advantage to eliminating the UV peak in a nectar-feeding species? When a flying insect approaches a flower to land on it, the left and right boundaries of the flower can be separated by quite a large visual angle when the insect is close to the flower. Each eye would then see – in addition to any structure within the flower – a single, vertically-oriented moving edge corresponding to the boundary of the flower, which can produce a strong response in H1. In viewing a UV-reflecting flower against a background of green foliage, it is likely that a spectral channel with a single peak in the green or blue-green would register a much greater contrast at the border between the flower and the background, than would a channel with two peaks, one in the UV and the other in the green. Thus, if signals from the movement-detecting neurons are to be used to stabilize a flying insect's approach to a flower, it may be desirable to have a single peak of sensitivity in the blue or green, without a second peak in the UV. It is possible that the rigid dipteran ancestry of *Eristalis* has forced upon it a retina whose structure and visual pigments resemble those of other flies, but that the neural processing of the retinal signals has evolved to compensate for this and rendered vision in this fly species more akin to that in the honeybee, and therefore better adapted to its lifestyle.

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