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# Colour inputs to motion and object vision in an insect

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## SUMMARY

Self-motion detectors of the dragonfly ventral cord have large fields that are sensitive to whole-field one-way motion with little habituation to the motion. In contrast, object-motion detectors have large fields, but their responses to the motion of small objects within the field habituate more easily and some are non-directional. Both types are large neurons that can be used for electrophysiological recording for long periods and are previously described in their anatomy and their responses to black and white moving patterns (Oldberg 1986). When tested with a flash of controlled intensity and wavelength, the self-motion neurons have a spectral sensitivity similar to that of photoreceptors with a peak in the green near 500 nm, but when tested with a moving edge, they have a single peak near 560 nm. They behave towards a pattern of two colours as if they are colour blind. Similar results are known for the bee and some butterflies.

Forward-looking object-motion neurons have a spectral sensitivity curve that is rather flat from 380 nm to 580 nm, some with a peak in the uv. When they are tested with a moving coloured pattern on a differently coloured background, there is no value of the foreground brightness, which gives a null response, however the brightness is adjusted. The optimum response to a coloured object appears when the background is green and the object is another colour; usually blue is the most effective. Discrimination of a small object is less effective when the object is green. These results suggest that colour vision is associated with object-vision; and that object-motion detectors are not colour blind, but do not necessarily discriminate colours.

## INTRODUCTION

The visual behaviour of insects depends on motion of the stimulus relative to the eye, and a good deal of the locomotory behaviour of the bee, such as the optomotor response (Kaiser 1975) and visual control of direction in flight (Lehrer *et al.* 1985, 1988, 1990), operates as if by monochromatic visual inputs only from those photoreceptors with a spectral sensitivity peak in the green. Much of the visual behaviour of insects, however, is directed towards coloured objects and the relation between colour vision and object vision is by no means clear. One intention of this paper is to explore whether colour coding can be used to investigate the processing mechanisms in object vision of insects. Colour vision is well documented in the bee, but less well-known in dragonflies, although these and many other insects have three or more spectral types of photoreceptors (Menzel 1979; Meinertzhagen *et al.* 1983).

Among the large descending neurons, with large fields, in the dragonfly ventral cord there is a group called self-motion detectors, which are related to the optomotor response, and another group called object-motion detectors, which respond to the movement of a small object, but not to motion of a large pattern that fills the field. The two groups have been characterized by Oldberg (1981, 1986). The self-motion detector neurons are directional in their responses and do not

easily habituate. The object-motion detectors respond well to small dark targets that move over a white or patterned background, but easily habituate. There are eight of the latter on each side, five of them directionally selective and six of them with large fields. In the directionally selective cells the movement of a patterned background in the null direction inhibits the response to the target. The object-motion detectors elicit wing movements and are thought to convey signals to the wings when objects move in the visual field, for either tracking or avoidance. We tested individual neurons of these two groups in the dragonfly *Hemianax* to establish their identities from the principal characteristics of their fields and then measured their spectral sensitivity with flashes.

The dragonfly self-motion detectors, like optomotor neurons of the bee, are colour blind and green sensitive. The other neuron type, the object detectors, prove to have a spectral sensitivity that is rather flat from 380 nm to 580 nm, as if inputs from several spectral types of receptors are summed, sometimes with a peak in the ultraviolet. There is nothing strange about these results, but there is a difficulty in finding an appropriate model for the patterns of inputs from the receptors. Lamina monopolar cell types I and II receive anatomical synapses from several receptor types (Meinertzhagen *et al.* 1983) and relatively flat spectral sensitivity curves from 317 to 614 nm have been measured for a selection of the dragonfly lamina

monopolar cells (LMC) (Laughlin 1976). The largest and most easily recorded LMC cells, with inputs summing several colour types of photoreceptors, could be on the pathway to the object-detector neurons, but not to the self-motion detector neurons. This, however, is an inference to be treated with suspicion because object vision by insects is associated strongly with colour discrimination, for which a mechanism that sums different colour types of receptors is not appropriate. The discrimination of coloured objects against background is improved by taking the differences between, and reduced by summing, receptor inputs. Having inputs only from green receptors, motion perception is not on the pathway of LMC cells, which merely sum the spectral types. It is very strange that the available spectral sensitivity data for the large lamina monopolar cells suggests that for a number of different reasons these cells are not on the pathway of motion detection or object detection in dragonflies, bees or the fly (Coombe *et al.* 1989). In the second part of the experiments, therefore, we turned to the detection of small moving coloured objects in front of a coloured background by object-motion detector neurons, and can conclude that in normal behaviour all these spectral sensitivities may change as the target changes.

#### METHODS

The dragonflies *Hemianax papuensis* (Burmeister) Odonata, were caught in the vicinity of the laboratory in Canberra as required. No differences in the spectral properties of the neurons were observed between males and females. A small hole was made in the neck and the connective was pierced with a tungsten microelectrode just anterior to the first thoracic ganglion (figure 1). The electrode was adjusted in its location within the

cord until the response of one neuron was isolated. Preparations lasted many hours, and the major problem is the habituation of the object-motion detectors, not the loss of the neuron.

The stimulus for the measurement of spectral sensitivity was either a flash or the motion of the edges of the arms of a 12-arm illuminated sector wheel seen against an illuminated background, beyond which the room was dark. Two beams of light from two xenon arc lamps were collimated, and the parallel beams each passed through a series of neutral density filters of metallized quartz, then through a selected narrow band interference filter. The coloured beams of controlled intensity and colour were each focused through a fast shutter upon the end of a quartz light guide that carried the light into the electrophysiology set-up. In one series of experiments, either beam was used directly as a 10 ms flash to measure spectral sensitivity; in another series one beam illuminated the moving sector wheel (26 cm diameter, one rotation in 3 s) while the other beam illuminated the coated white background seen between the sectors. These edges subtended 50° to 65° at the front of the eye, creating a large moving field. Tests were done with the preferred direction of edge motion. To stimulate self-motion detector neurons with chromatic contrast, the sector wheel was illuminated with one colour (the foreground) and the background was illuminated with the identical colour as a control, or with a different colour. Then the intensities were adjusted while the responses were recorded, in search of a relative brightness of the two colours that would yield a minimum response (as in figure 7). To reach a null in these experiments the geometry of the visual scene is not critical, but spurious shadows must be avoided. All reflecting surfaces were coated with flat-reflection white magnesium oxide paint (Eastman Kodak 6080, flat reflectance

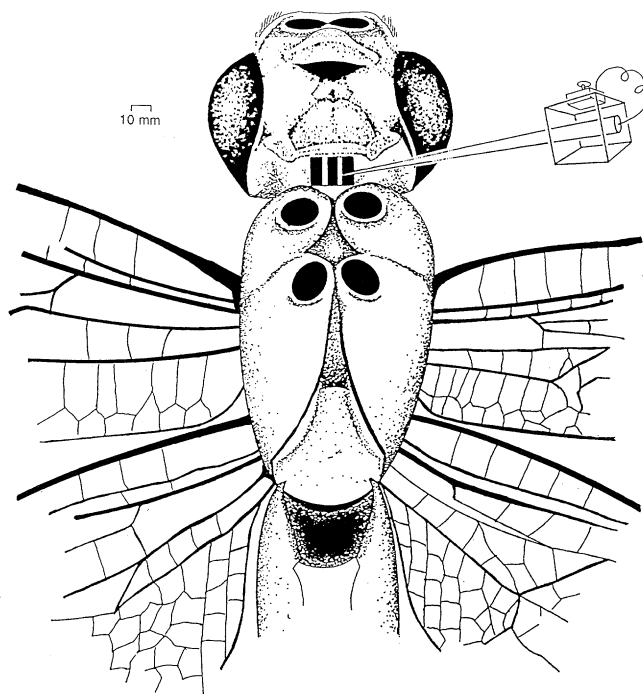


Figure 1. The preparation. A hole is made on the ventral side of the neck, through which an electrode is poked into the neck connective.

380–700 nm). The optics were all of quartz and the number of photons that passed through the light guides at each wavelength that was measured with a calibrating equipment (International Light Inc. SEE 400 photo-detector) was minimum detectable intensity  $6 \times 10^8$  photons  $\text{cm}^{-2} \text{s}^{-1}$ .

For the object-detector neurons the sector wheel was replaced by an illuminated disc with round holes, through which a translucent paper screen could be seen. The holes subtended  $6^\circ$  at the eye. The screen seen through the hole now becomes the object while the background is the area of the disc surrounding the holes (figure 2). The geometry of the stimulus was held constant for each series of tests, and to avoid intensity changes, the end of the light guide in figure 2 was not in line with the eye looking through the hole. For chromatic contrast with object-motion, the intensities at each wavelength were calibrated directly from the surface of the translucent screen.

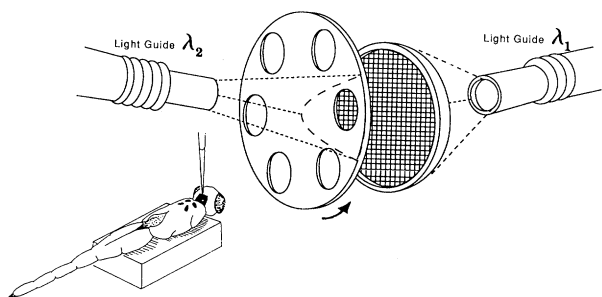


Figure 2. The apparatus to stimulate object-motion detectors. The rotating disc with six holes was covered with white reflecting magnesium oxide paint. The white translucent paper screen (cross-hatched in the diagram) could be seen through one moving hole at a time. The disc and the paper screen are illuminated separately by quartz-optics and obliquely placed light guides, with controlled wavelength and intensity. ( $\lambda_1$  = target, variable;  $\lambda_2$  = background.)

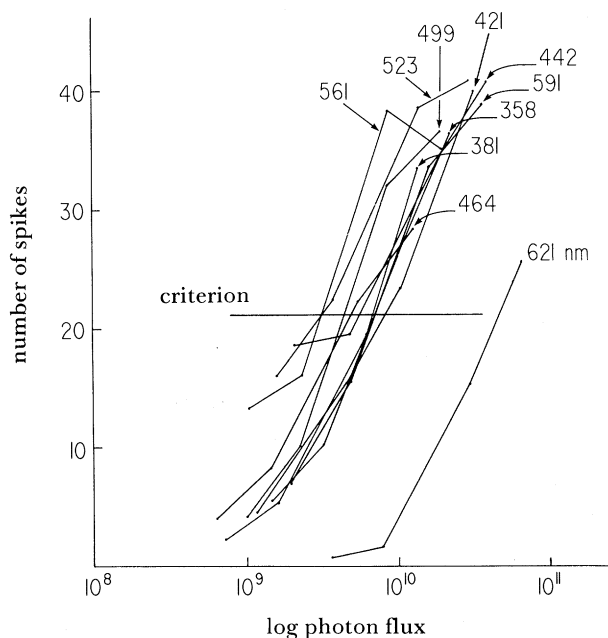


Figure 3. Responses (measured as number of spikes) plotted against intensity at 10 different wavelengths for a self-motion neuron of the dragonfly *Hemianax* ventral cord, showing the parallel curves and the criterion response for calculation of spectral sensitivity.

To measure the spectral sensitivity, the spike responses were recorded by computer and summed for 10 repetitions of the stimulus at each intensity at each wavelength, and then average spike counts were plotted as a function of log intensity at each wavelength (figure 3). From these sets of curves, the spectral sensitivity was calculated as the reciprocal of the number of photons at each wavelength required to give a constant number of spikes.

## RESULTS

### (a) Spectral sensitivity

#### (i) Self-motion detectors

The criteria for identifying the self-motion detector neurons were as tabulated by Oldberg (1981). In brief, these neurons are unidirectional, wide field, not easily fatigued or habituated, and they respond to large patterns that fill the field. Spike counts were plotted as a function of log intensity at each wavelength. The resulting S-shaped curves are consistently parallel over the range 358–621 nm so that there is no hesitation in calculating spectral sensitivity from a criterion response in the steepest part of the curves (figure 3). The curves in figure 3 are much steeper than the corresponding  $V/\log I$  curves for photoreceptors, suggesting a strong amplification and rapid saturation of the responses to transient stimuli. In this respect, they behave like lamina monopolar cells.

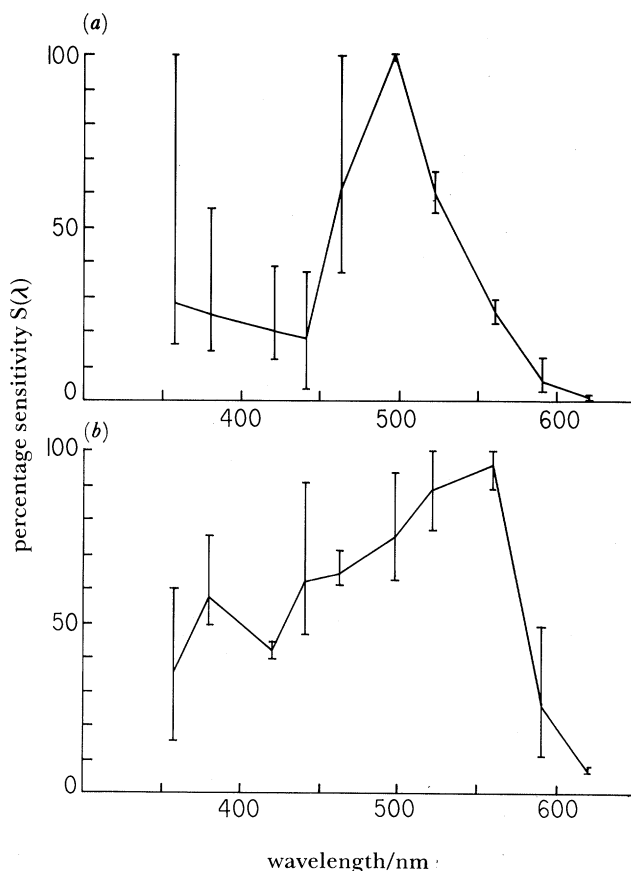


Figure 4. Average spectral sensitivity of three self-motion detectors measured with (a) a flashing point source (b) the rotating sector wheel. Error bars show standard deviations for  $N = 3$  neurons.



All of the neurons falling into the category of self-motion detectors (Oldberg 1981, 1986) have spectral sensitivity curves that resemble those of typical photo-receptors with peak near 500 nm in the green when tested with a flash (figure 4) but near 560 nm when tested with a moving pattern (figure 4*b*). Individual neurons respond to different directions with reference to the axes of the head, but we distinguished no corresponding differences in spectral sensitivity.

(ii) *Object-motion detectors*

The criteria for identifying the object-motion detectors were as tabulated by Oldberg (1981, 1986). In contrast to the self-motion detectors, they respond to movement of small objects, but are soon habituated and they do not respond to the motion of large patterns that fill their field. There are at least eight individually identifiable cells of this type. Six of the cells have large receptive fields, seven out of the eight prefer small targets, and five of them show some directional sensitivity. One has to be very patient with these neurons, sometimes allowing several minutes rest because they readily habituate to a repeated stimulus.

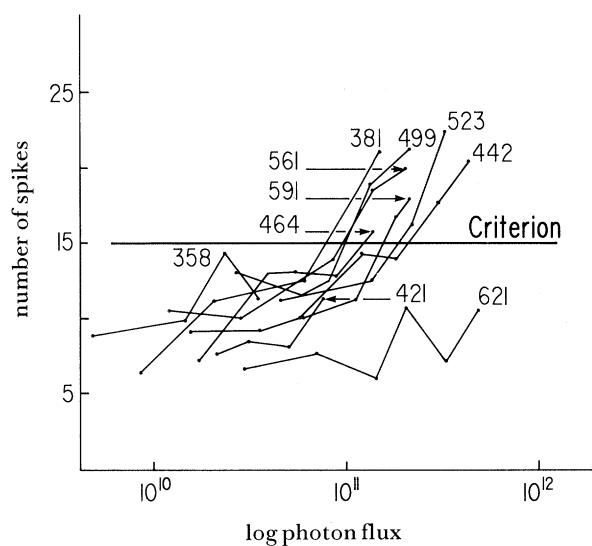


Figure 5. Responses of an object-motion detector plotted against intensity at 10 different wavelengths, showing the criterion response for calculation of spectral sensitivity.

Spectral sensitivity was measured with 10 ms flashes at long intervals on the translucent screen on a dark background. Spike counts were plotted as a function of log intensity at each wavelength (figure 5). The resulting S-shaped curves are not so consistent, and not so obviously parallel as those for self-motion detectors (figure 3). The easy habituation of these neurons makes it difficult to obtain reliable results. After the measurements are made, it is sometimes difficult to find a criterion response in a region where the curves are sufficiently parallel to give a spectral sensitivity curve. When the curves are not parallel they will give a different spectral sensitivity curve for each criterion response. Despite these reservations, the object-detector neurons have rather flat spectral sensitivity curves, sometimes with a sharp peak in the uv (figure 6).

With differences due to errors of measurements, we

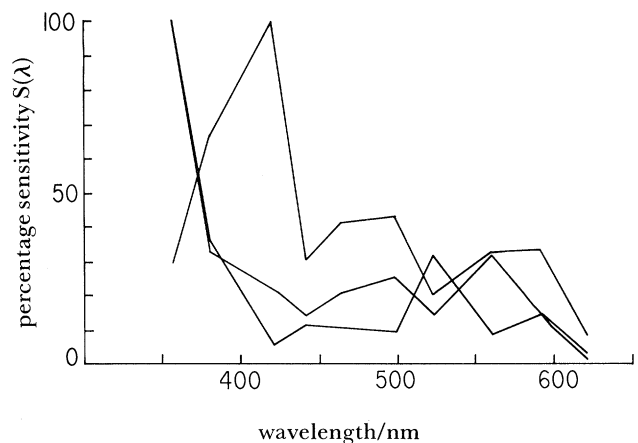


Figure 6. Spectral sensitivities of three object-motion detectors of the dragonfly tested with the rotating disc with holes, as in figure 1.

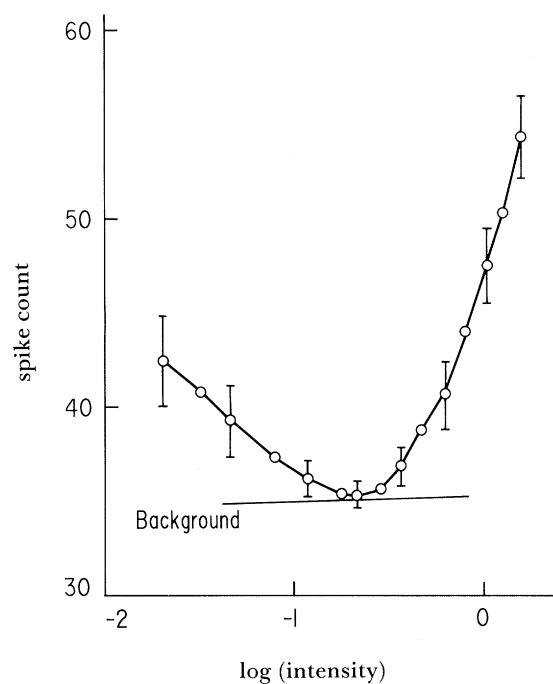


Figure 7. A test for monochromatic input of a self-motion (optomotor) ventral cord neuron of the dragonfly, with a white sector wheel illuminated with monochromatic light at 470 nm moving against a white background illuminated at 570 nm. Adjustment of the relative intensity (horizontal scale) brings the response rate down to the spontaneous background level that is seen with no motion. Error bars show standard deviations for three sets of measurements on the same neuron.

are not certain that the object-motion detectors all have the same spectral sensitivity, or whether these neurons consistently differ as individuals. It is clear, however, that apart from some with a peak in the ultraviolet, the spectral sensitivity curves are usually flat, from 380 nm to 580 nm and that small peaks in this range are not consistent from cell to cell (figure 6). The differences can be attributed to different weighting of inputs either in individual animals or in neurons, because usually only one neuron was measured in each animal.

**(b) Tests with chromatic contrast****(i) Self-motion detectors**

By using the rotating sector wheel, the background was illuminated by light of one colour and the sectors by a different colour. A useful control against the effects of shadows is to test with two lights of similar wavelength. The background response is the spike rate when there is no motion. To do the experiment, one light is adjusted to various values of intensity while the other is held at one convenient intensity that gives a balance in the middle of the range.

With self-motion detector neurons, there is always an intensity ratio at which the two colours are not distinguished and the response falls to the background (no motion) level (figure 7), showing that self-motion detectors are colour-blind.

**(ii) Object-motion detectors**

The object-motion detectors behave quite differently. When the moving hole and its background are illuminated by the same colour, their brightness can be adjusted so that there is no response (figure 8, curve *a*). This control provides a measure of the spontaneous activity plus the lowest response that the equipment allows, despite the effects of shadows and possible artefacts at edges; in fact, it establishes that a null can be achieved by suitable adjustment of intensity. When the moving blue (442 nm) object is given on a yellow (573 nm) background, however, there is a response at all adjustments of the intensities (figure 8, curve *b*). A blue object moving on a green background is one of the

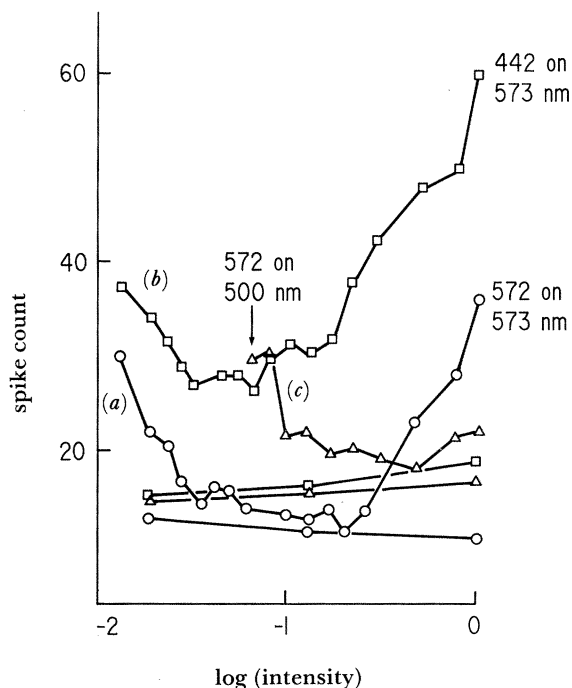


Figure 8. Responses of an object-motion neuron of the ventral cord of the dragonfly *Hemianax*. (*a*) With the object at 572 nm on a background at 573 nm, the response can be brought down to the spontaneous (no motion) level by adjustment of the relative intensity. (*b*) With a combination of 442 nm object on 573 nm background, or not so clearly (*c*) with 572 nm on 500 nm, no match of the moving object against the background is possible.

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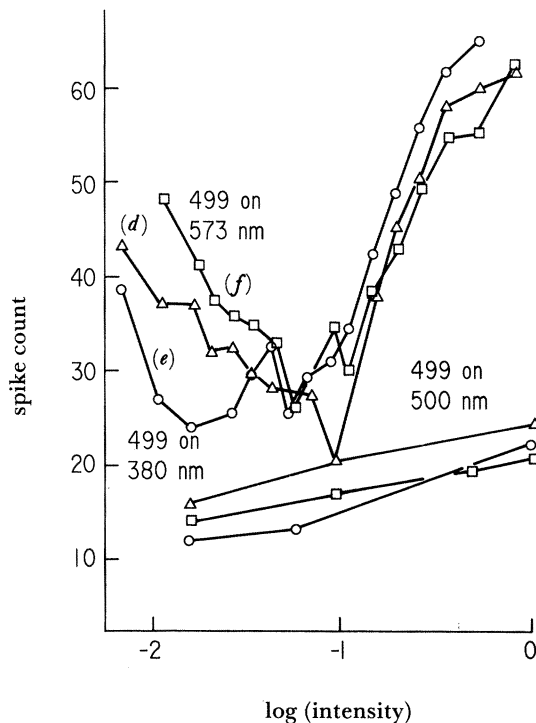


Figure 9. The same object detector neuron as in figure 8. (*d*) With an object of 499 nm on a background of 380 nm, or (*e*) an object of 499 nm on a background of 573 nm, no match is possible. As a final control at the end of the experiment, (*f*) an object of 499 nm can be matched against a background of 500 nm.

preferred stimuli for this neuron. A yellow object (572 nm) on a green background (500 nm) gave a null (curve *c*). A green object (499 nm) on a yellow background (573 nm) could not be adjusted to a null (figure 9, curve *f*) and there was a similar result with a uv background (380 nm) on the same neuron (figure 9, curve *e*). As a control against shadows in the stimulus at the end of this long run on one neuron, an object at 499 nm could be balanced completely by a background at 500 nm (figure 9, curve *d*). With other object-motion neurons we also found that a blue object could always be seen on a green background, but so far we have not found different types of sensitivity to coloured backgrounds in individually identified object-motion detector neurons. We did not test small uv-coloured objects, and for obvious reasons we could not use black objects, which are perhaps the optimum stimulus for these neurons.

**DISCUSSION**

The self-motion detectors proved to have inputs only from green-sensitive receptors, in agreement with the spectral properties of the optomotor response in other insects with several types of colour receptors. It must be remembered, however, that the bee has some behaviour patterns that appear to have only green inputs, but which require neurons other than large-field optomotor or self-motion detectors. Examples are the scanning behaviour of the worker bee (Lehrer *et al.* 1985), the measurement of range (Lehrer *et al.* 1989) and landing at right angles to an edge (Lehrer *et al.*

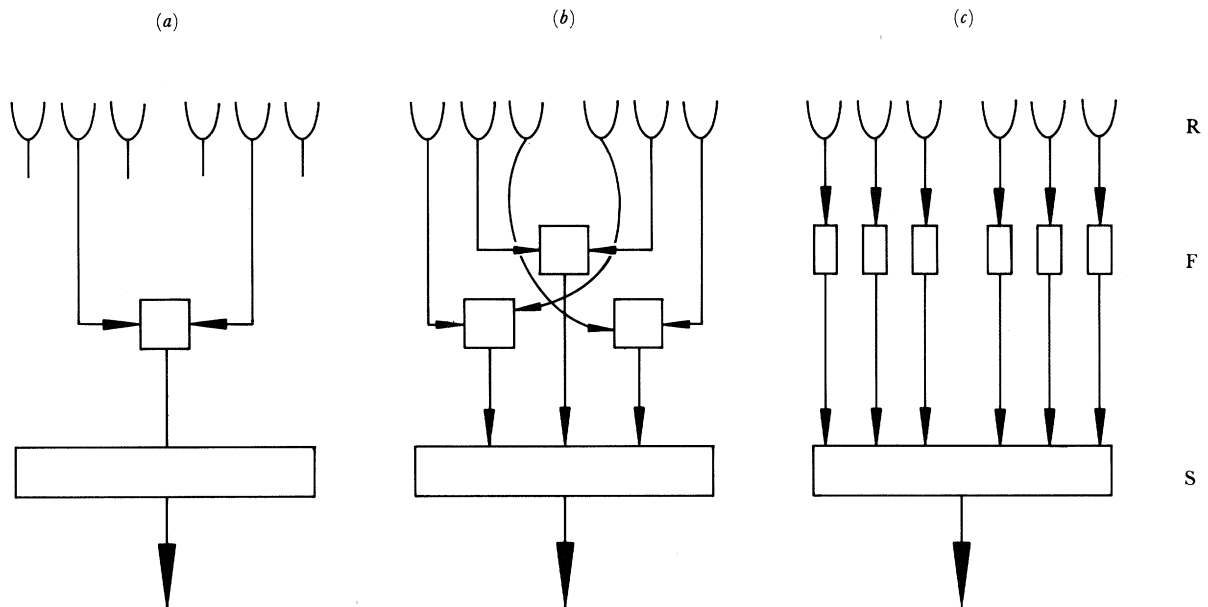


Figure 10. Model connections for coding colour and motion. (a) Monochromatic inputs to the elementary motion detectors. (b) Receptors of different colour peaks feed into different elementary motion detectors. (c) Without directional motion perception, the receptors feed into different non-linear filters (F) to produce a total response (S) that is not necessarily equal to the sum of its parts.

1990), all of which require something more than the optomotor neurons. For these behaviour patterns, therefore, there must be other types of colour blind motion-sensitive neurons with spectral sensitivity peak in the green.

The dragonfly self-motion detectors must have a pattern of inputs from only the receptor types with green peak near 500 nm when tested with a flash, and the part of the motion detection that responds to flicker must arise from interactions that are limited to these receptors (figure 10*a*). Dragonfly neurons on this pathway, when tested with a moving stimulus, have a spectral sensitivity with peak near 560 nm (figure 4), showing that the directional component of motion detection has summation of inputs from other receptors or with the spectral peak pushed to a longer wavelength by antagonism from blue receptors. As there are four different preferred directions for the self-motion neurons, there are presumed to be four of these directional circuits. For the distinction between directional and flicker components of motion perception in insects, see papers on the template theory (Sobey & Horridge 1990). Similar results with moving and flash stimuli have been found in the dronefly (Srinivasan & Guy 1990). We do not yet understand the functional significance of this spectral shift depending on the stimulus, but in some way it must be adapted to motion perception in natural green surroundings.

The responses to moving coloured spots help us to distinguish some theoretical models of the input channels of object vision, but combined data on the optic lobe neurons of dragonflies are hard to fit into any scheme. Five different spectral types of photoreceptor are known in the dragonfly *Sympetrum* with peaks at 340, 410, 490, 540 and 620 nm (Meinertzhagen *et al.* 1983). The lamina ganglion cells are also of several colour types, with various combinations of

inputs from different receptor types (Meinertzhagen *et al.* 1983, figures 19 and 20). Some of the lamina cells have inputs only from receptors with peaks in the green, others appear to sum more than one receptor type, but only from one ommatidium as shown by their very narrow angular sensitivity. There is no suggestion that different colours are line-labelled in the lamina by neurons with narrow, but different spectral sensitivity curves.

The object-motion detector neurons of the lobula behave as if they have inputs from many small-field on-off units of the medulla at synapses that rapidly adapt, and the responses to moving coloured spots on a coloured background show that the small-field medulla units must have a diversity of inputs from different types of receptors. Their spectral properties must also represent the distributions of the receptors in the part of the eye that we used. In the dragonfly medulla there are in fact small-field non-directional motion sensitive units that respond with spikes to small moving targets that move, and also at 'on' and at 'off' (O'Carroll, unpublished data). These neurons behave as if they have rectified the responses of several lamina ganglion cells, but their spectral properties have not yet been measured. The non-directional object-detector neurons that we tested in the dragonfly apparently sum the inputs from several receptor types, but their very wide spectral sensitivity shows that they are unlikely to signal the actual colour of a small object. To model a system with these properties requires either a summation of small-field colour-coded unit-motion detectors (figure 10*b*), or a non-linear summation of small-field colour-coded on-off units (figure 10*c*). The summation must be of a kind that yields a large field, but sensitivity only to small objects within that field, with habituation added.

If the object-detector neurons are part of the motor

output from the brain controlling locomotion towards an object, they would perhaps have flexible spectral sensitivity, in that the object is detected in any direction, but discrimination of colour is completed by a separate circuit and only the final steering instructions are passed down the ventral cord. Clearly, such behaviour must be flexible with reference to colour. If so, the spectral sensitivity curves that we have measured, besides depending on the eye region, might be flexibly narrowed down to selected wavelengths by neural interaction. A directional and adaptive control of the spectral sensitivity of the descending neuron may in fact start at the lamina level, which would explain the curious discrepancy between the broad spectral sensitivity curves of the lamina and object-detector neurons and the discrimination of colour in visual behaviour of whole animals towards objects.

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