

## 20. Vision during flight

T. COLLETT and A. J. KING (1975)

### 20.1. Introduction

AN insect must be able to detect and identify objects in its environment during flight. It can then approach or follow some objects and flee from others, while certain features of the terrain may provide guiding landmarks. When an insect moves the image of the surroundings flows across the eyes. Although this retinal image movement is an important cue for maintaining stable flight, it also disrupts the detection and analysis of particular features in the environment.

The problem of analysing visual stimuli against a moving background is common to most animals and many have adopted the strategy of making eye or head movements to minimize the disturbing effects of locomotion. Thus some birds perform a series of rapid forward head movements while walking; between each such saccade they keep the head still relative to the ground and the body moves forward to catch up with the head. So for most of the time the head is stationary; vision is only disturbed during head saccades. However, complete stabilization is rarely a feasible solution and for many animals just one part of the retinal image remains stationary, while the rest of the visual field moves about this point. The dogfish bends its head from side to side as it swims; at the same time it counter-rotates its eyes so that the eye on the inside of the curve fixates a vertical strip three feet away, and only this region of the visual field is stable (Harris 1965). In mammals, saccades enable selected parts of the surroundings to be viewed by the region of retina with greatest acuity. Eye and head saccades are also used during locomotion to point the fovea in the direction in which the animal moves, which helps keep the image stationary on the fovea.

Some insects make head movements during flight for the same kinds of reasons. Land (1973) has shown that if a blowfly is suspended so that movement is restricted to rotation about a vertical axis, changes of direction occur as the result of head and body saccades. In the intervals, despite fluctuations in the direction in which the body points, compensatory movements keep the head clamped with respect to the visual surroundings. The visual consequences of turns made by means of saccades will be brief. For a fly able to

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Head movements of flies during visually guided flight  
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move forwards, as well as turn, the situation will presumably be somewhat different. It will keep its head stationary relative to some point in front, and so only the images of very distant objects, or points directly in the line of flight, will be stationary. In this case the advantages of making saccades are twofold: it is easier to distinguish voluntary from involuntary turns, and at least for the front of the eye the retinal image will usually be almost stationary. Between saccades any movement of the image in this region can be attributed to unexpected perturbations, for instance a gust of wind. However, the moving background will still interfere with the detection of targets on the lateral retina.

In this chapter we consider some of the problems that flying insects must solve if they are to use their visual system effectively during flight. We present neurophysiological evidence from recent experiments on hoverflies for the existence of separate systems for feature detection and orientation. We then discuss some of the properties feature detectors must have if they are to be used during flight. Secondly, we consider the control of flight orientation by means of optomotor responses, and ways in which large-field motion detectors can generate optomotor torque to correct unintended deviation. Thirdly, we consider neurophysiological mechanisms enabling flying insects to track moving targets.

## 20.2. Feature detection in hoverflies

In the optic lobes of hoverflies we have recorded from two functionally distinct classes of movement detector. One class consists of directionally selective units with receptive fields (RFs) which cover most of one eye, with properties similar to those of large-field units in calliphorid flies described later. The other class are small-field units with properties which make it impossible for them to contribute to the responses of the large-field units and extremely unlikely that they play any part in a feedback system controlling orientation.

We have recorded the small-field units with electrodes placed in the medulla, external chiasm, and lobula. The units are not spontaneously active and give little or no discharge at on or off. Their RFs are approximately circular, *c.* 20° across. Strong responses are given to stimuli moving across the RF at more than *c.* 30° s<sup>-1</sup>, if the stimulus conforms to a set of requirements, which varies in detail from unit to unit. Many, but not all, units are directionally selective. Most of those that are have similar preferred directions, responding best to approximately backward movement (Fig. 20.1). Some units show strong preferences for dark patterns, with almost no response to light ones (Fig. 20.2). Others have weaker preferences, or none.

The units described here responded to small spots moving through their RFs, but not to the movement of long bars extending beyond the RF. They also failed to respond to gratings or single edges. Not all stimuli smaller than

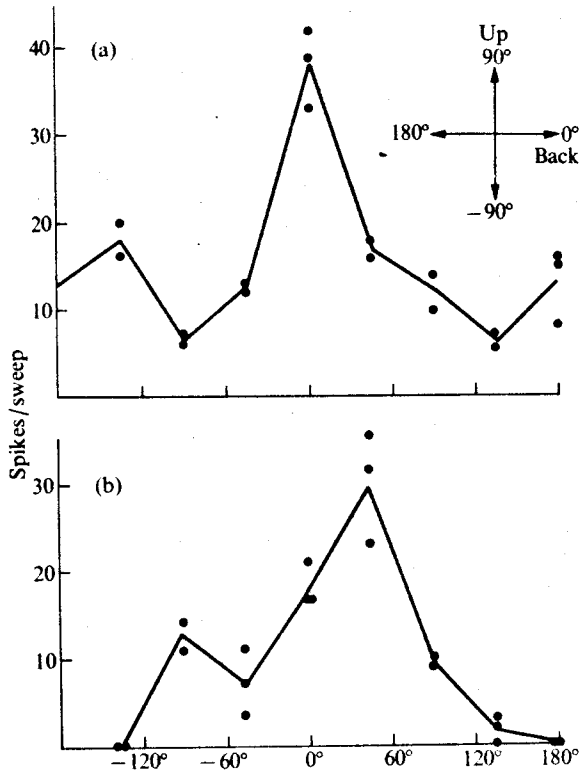


FIG. 20.1. Response of two directionally-selective units to movement of 2.5° dark spot through RF in various directions. Traverse starts and finishes outside RF. (a) Unit with weak directional selectivity. Spot moves 36°, at  $86^\circ \text{ s}^{-1}$ . Unit 12: *Syrphus* sp. RF is  $15^\circ \times 20^\circ$ , with centre at  $(0^\circ, +40^\circ)$ . (b) Unit with strong directional selectivity. Spot moves 37°, at  $134^\circ \text{ s}^{-1}$ . Unit 16: *Syrphus* sp. RF is  $15^\circ \times 20^\circ$ , with centre at  $(0^\circ, +55^\circ)$ . (RF dimensions are given throughout as horizontal and vertical angular extents, in that order. RF positions are given throughout as (azimuth, elevation) of the RF centre in the visual field. Azimuth is positive on the right of the mid-line, negative on the left. Elevation is positive above, negative below, the equator of the visual field. These are the co-ordinates used by Bishop, Keehn, and McCann (1968). 'Forwards' and 'backwards' refer to the visual field of one eye; so spots moving forwards are moving towards the mid-line. In Figs. 20.1–20.7, 20.9, 20.11, 20.12, there are two brightness levels: 'dark' is  $8 \text{ cd m}^{-2}$ , and 'bright' is  $25 \text{ cd m}^{-2}$ ).

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the RF were equally effective. We studied the effects of varying the contrast, velocity and size of the pattern, altering its horizontal and vertical extent independently.

Many units responded strongly to spots between  $2^\circ$  and  $4^\circ$  across, but not to smaller or larger ones (Figs. 20.2 and 20.3). In order to analyse this selectivity we compared the responses to spots of different diameters with the responses to bars of different heights but of constant width. Some units behaved in the way illustrated in Fig. 20.4b. Larger bars elicited smaller

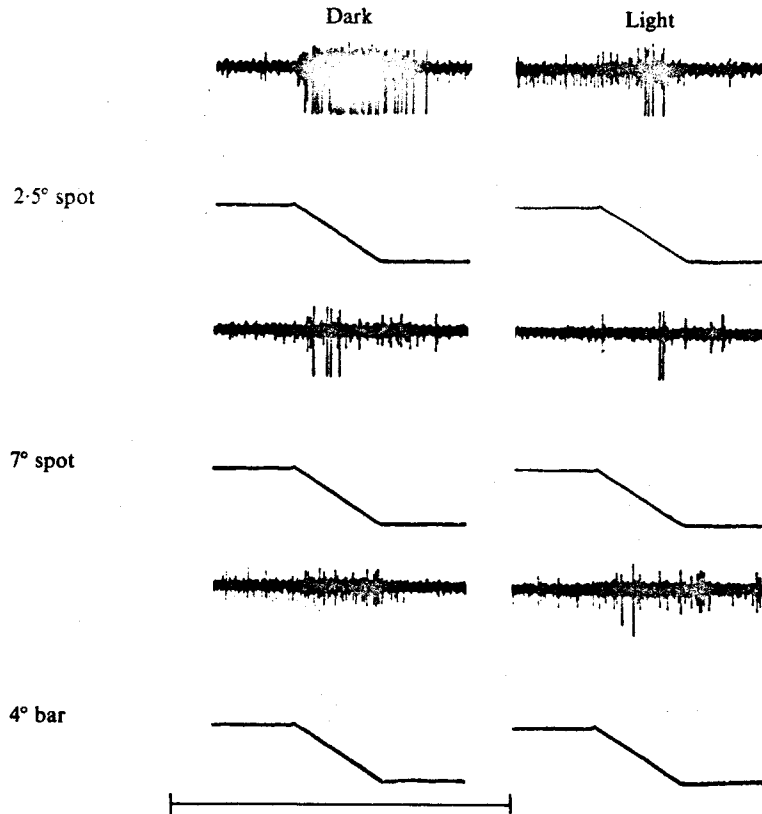


FIG. 20.2. Typical responses of unit which responds selectively to small dark spots. Unit has strong directional selectivity (same unit as Fig. 20.1b); no responses to any pattern for movement in anti-preferred direction. Responses shown for dark and bright patterns, moving backwards horizontally through RF. Patterns move  $37^\circ$ , at  $134^\circ \text{ s}^{-1}$ . Time mark: 1 s.

responses, and the response was roughly the same for bars and spots of equal height. These units were thus only excited if the extent of the stimulus perpendicular to the direction of motion was much smaller than the RF. Extent along the direction of motion was less critical, and these units responded well to  $3^\circ$  tongues.

For reasons which are still uncertain, the size of the most effective spot is for some units (perhaps all) dependent on its velocity. One example is shown in Fig. 20.5. At  $70^\circ \text{ s}^{-1}$  the unit responded strongly to a backward moving  $2.5^\circ$  spot, but not to a  $7^\circ$  spot, but at higher velocities the  $7^\circ$  spot was preferred. The extent of a stimulus perpendicular to the direction of motion determines the number of subunits excited simultaneously, whereas extent along the direction of movement determines the time interval between the passage of the leading and trailing edges. Therefore units which are affected

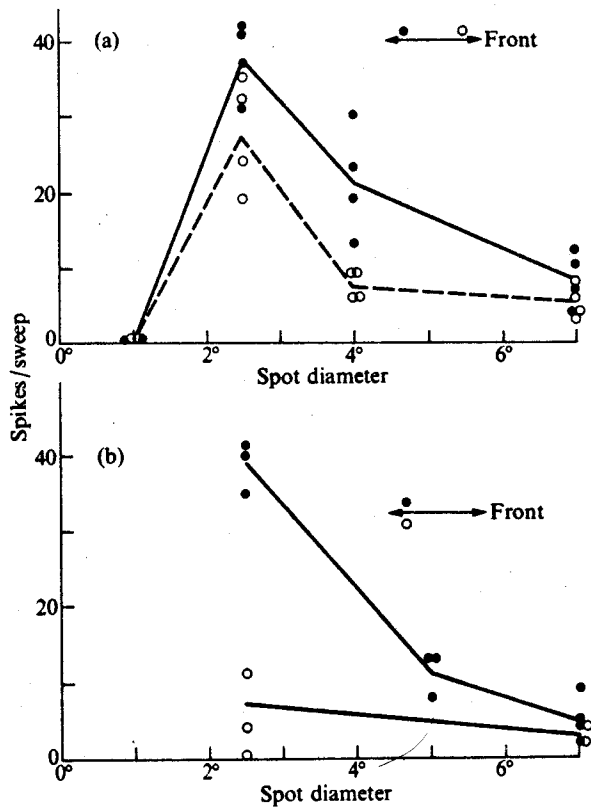


FIG. 20.3. Responses of two units to spots of various sizes. (a) Unit with weak directional selectivity. Spots move  $35^\circ$ , at  $65^\circ \text{ s}^{-1}$ . Horizontal movement through RF. Lines join the means of several responses for each spot size and direction of movement. Solid line: backwards movement; broken line: forwards movement. Unit 9; *Eristalis* sp. (b) Unit with strong directional selectivity. Same unit as Fig. 20.1b. Response to backward movement of dark and bright spots of various sizes; lines connect means of several responses. Solid circles indicate dark spots; open circles indicate bright spots.

by both leading and trailing edges may show some reciprocity between size and velocity. Whatever the mechanism responsible for this change in preference, it has a possible functional role. It enables the unit to recognize at different distances objects of a fixed size moving at a characteristic speed (e.g. other insects). This property may be more valuable than specificity for absolute retinal image size.

Other kinds of unit responded best to different features, or combinations of features. The unit of Fig. 20.4a was excited best by  $5^\circ$  spots and less by smaller or larger spots. No response was given to  $12^\circ$  spots. However, when tested with  $2.5^\circ$  wide bars of different heights, the response failed only for bars higher than  $20^\circ$ . The selectivity of this unit appears to be a function of both the horizontal and vertical extents of the stimulus.

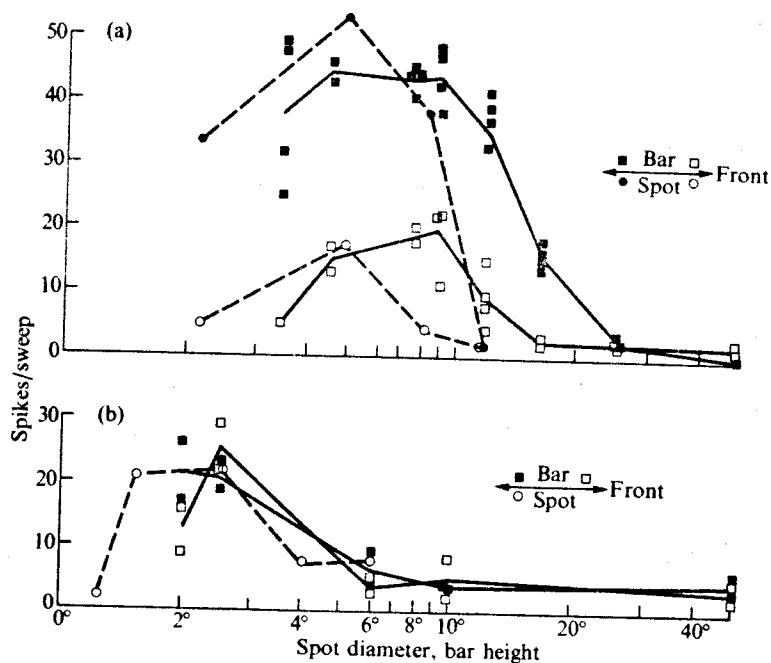


FIG. 20.4. Responses of two units to spots of different sizes and to 2.5° wide bars of different heights, moving horizontally through RF. Bars oriented vertically. (a) Unit with weak directional selectivity. Lines join the means of responses to several traverses. Solid lines indicate dark bar movement; broken lines indicate dark spot movement. Solid symbols: backward movement. Open symbols: forward movement; for bars symbols represent responses to single traverses; for spots symbols represent the mean response of several traverses. All stimuli move 40° at  $266\text{ s}^{-1}$ , starting and finishing outside RF. Unit 28; *Syrphus vitripennis*, ♂. RF is  $25^\circ \times 12^\circ$ , centred at  $(-12^\circ, +26^\circ)$ . (b) Unit with weak directional selectivity. Same unit as Fig. 20.3a. Bright spots and bars. Lines join means of several responses. Broken line and open circles represent spot movement (only backward movement shown: symbols represent means). Solid line indicates bar movement; solid squares, individual responses to backward motion; open squares, responses to forward motion. All patterns move through  $35^\circ$  at  $65\text{ s}^{-1}$ .

The units have inhibitory surrounds with properties different from those of the RF. The surround inhibition is not directionally or orientationally selective (Fig. 20.6) and it shows spatial summation: gratings have a more powerful inhibitory effect than a single edge or a bar. Rough plots of the size of the inhibitory region showed it was at least twice as large as the RF. The surround strength was graded, weakening with distance from the RF. Bars or edges moving through the RF at the same time as an effective spot abolish the response to the spot (Fig. 20.7). We do not know whether suppression under these circumstances can be attributed entirely to the non-directional surround mechanism.

The properties of the surround will prevent the unit from responding to effective features while large objects are moving close to the RF, or when the

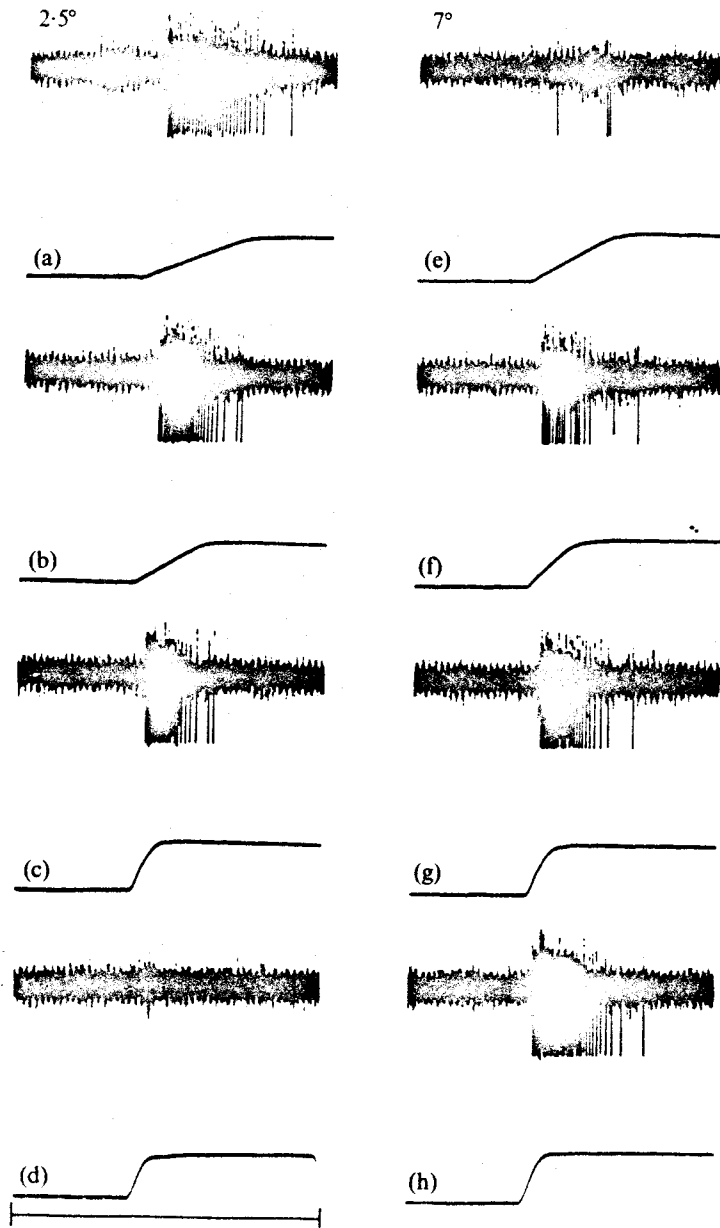


FIG. 20.5. Response to dark spots moving at different velocities. Directionally selective unit: spots move through RF in preferred direction (backwards, horizontal); no response to movement in anti-preferred direction. Unit did not respond to bright spots, or to bars of any size. (a)–(d):  $2.5^\circ$  spot; velocity changes from  $72^\circ \text{ s}^{-1}$  in (a) to  $430^\circ \text{ s}^{-1}$  in (d). (e)–(h):  $7^\circ$  spot; velocity changes from  $92^\circ \text{ s}^{-1}$  in (e) to  $370^\circ \text{ s}^{-1}$  in (h). Spots always move between same two points  $25^\circ$  apart. Unit 10; *Syrphus vitripennis*, ♂. RF:  $20^\circ \times 20^\circ$ , centred at  $(0^\circ, +65^\circ)$ . Time mark: 1 s.

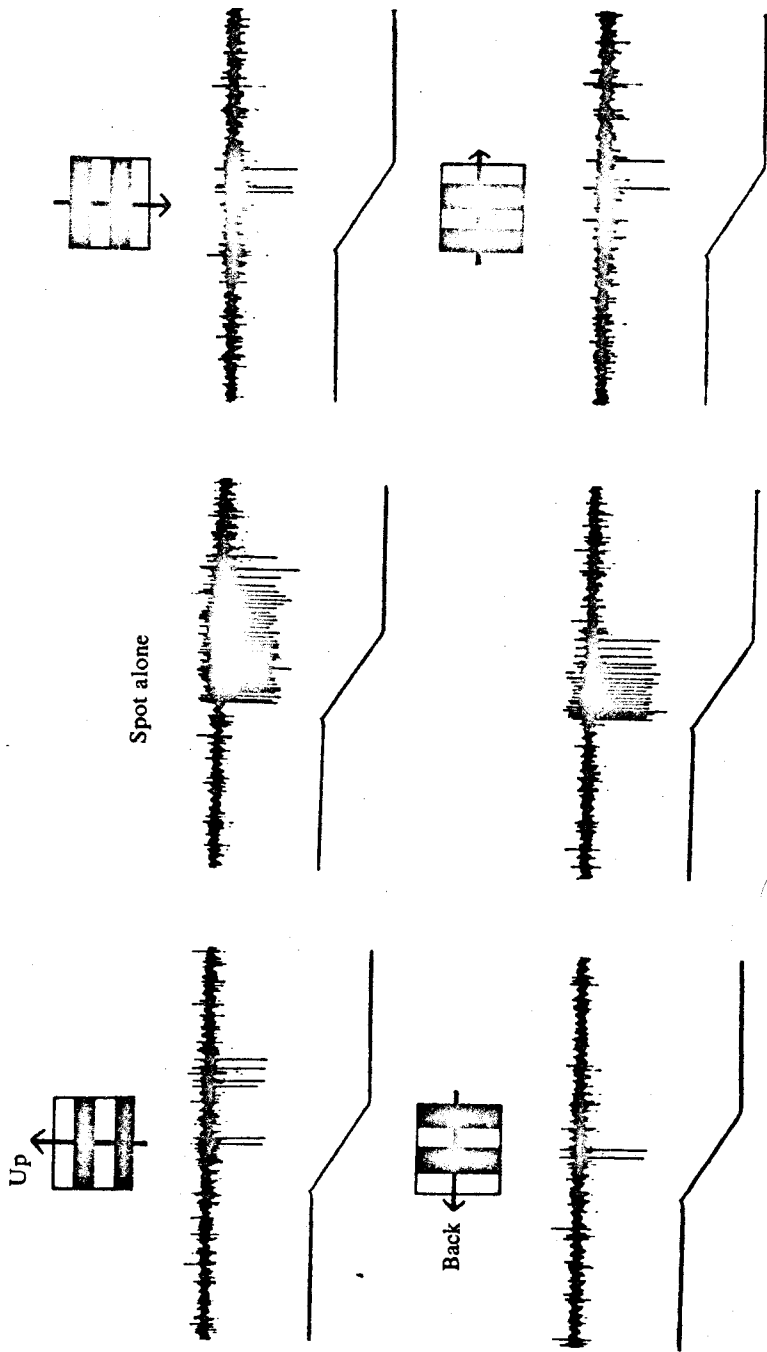


FIG. 20.6. Effect of grating moving outside RF on response to spot moving across RF. Spot always moves on same path: back wards, horizontal, between two points  $35^\circ$  apart, at  $195^\circ \text{ s}^{-1}$ . Monitor indicates stimulus movement. Grating is  $12^\circ$  square wave; driven by same waveform as spot, so monitor indicates movement of spot or grating. Directions of grating movement as indicated. Horizontal grating movement: grating moves in  $70^\circ \times 30^\circ$  region below RF. Vertical grating movement: grating moves in  $30^\circ \times 70^\circ$  region lateral to RF. Same unit as Fig. 20.1b.

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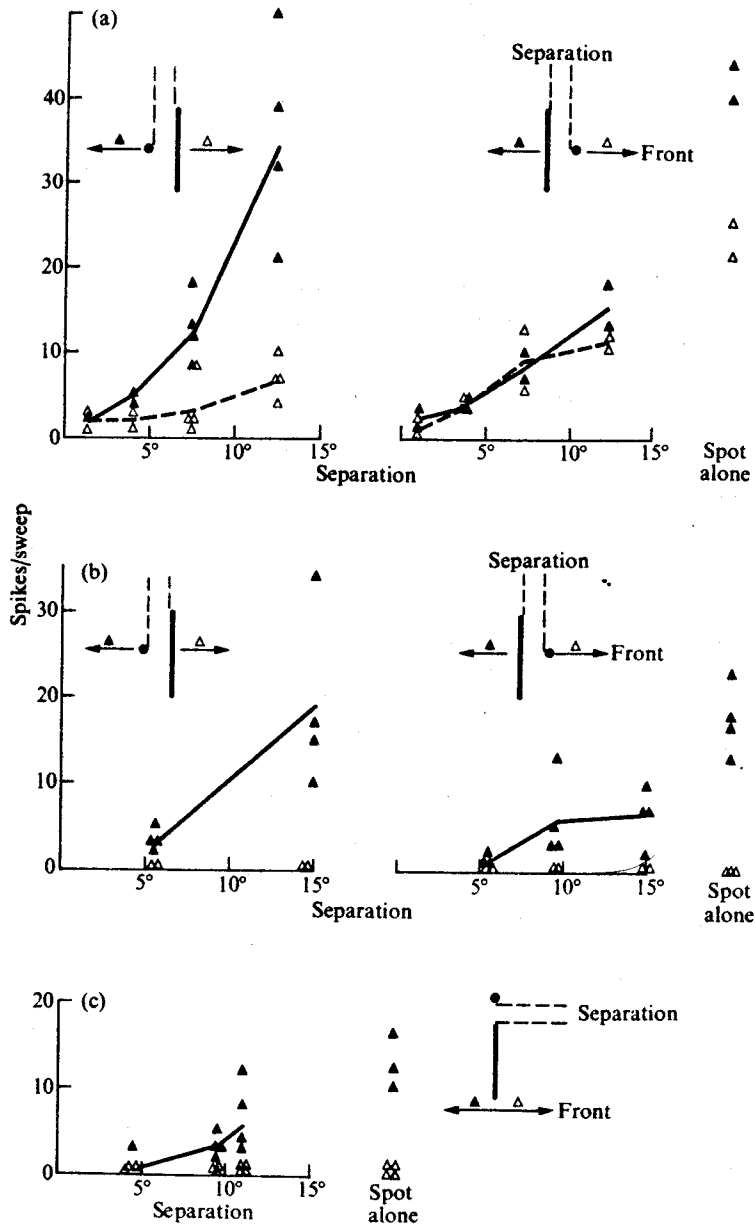


FIG. 20.7. Simultaneous movement of bar and spot at indicated separation in same horizontal direction between two points. Solid symbols: backward movement; open symbols: forward movement. Relative positions of bar and spot as indicated.  $2.5^\circ$  dark spot;  $2.5^\circ \times 50^\circ$  dark bar, with long axis oriented vertically. (a) Unit with weak directional selectivity. Same unit as Fig. 20.3a. Pattern moves through  $35^\circ$  at  $65^\circ \text{ s}^{-1}$ . (b) Unit with strong directional selectivity. Same unit as Fig. 20.1b. Pattern moves  $37^\circ$  at  $134^\circ \text{ s}^{-1}$ . (c) As (b) except that spot and bar separation varied vertically.

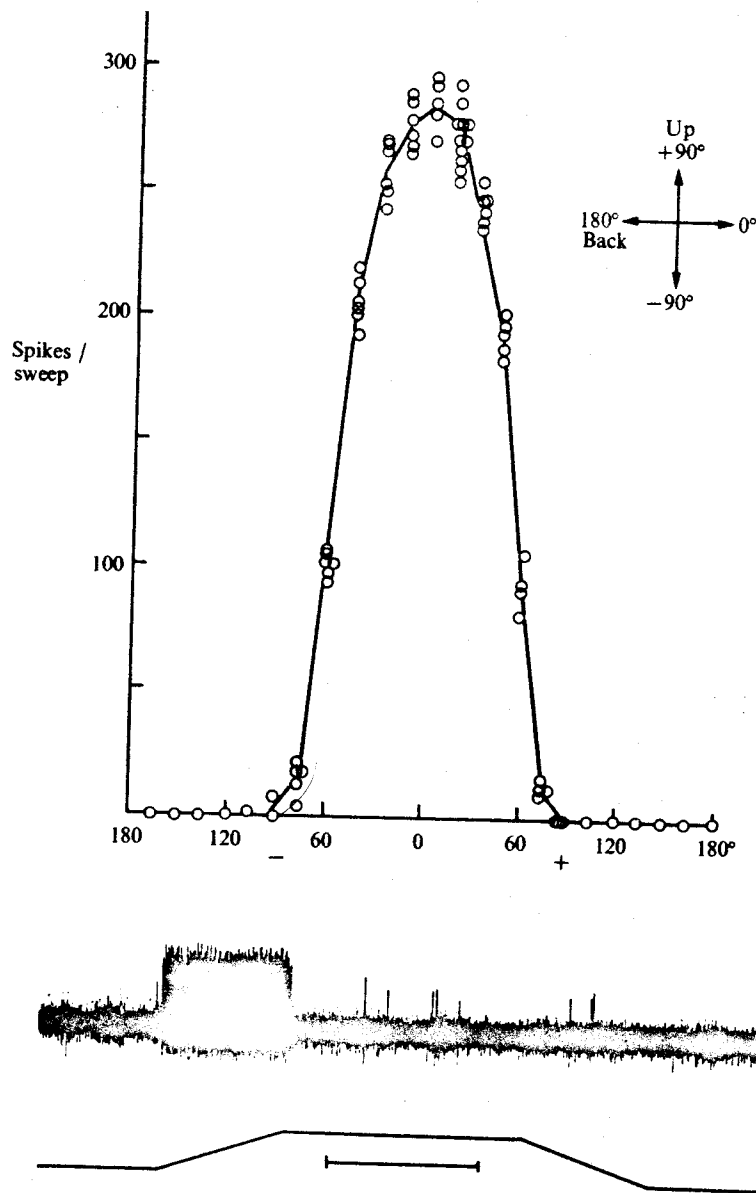


FIG. 20.8. Response of wide-field ipsilateral directionally selective movement detector, with no spontaneous activity to  $9.5^\circ$  square wave grating in  $40^\circ$  circular aperture centred at  $(+22^\circ, 0^\circ)$ . Grating moves at  $5.3^\circ \text{ sec}^{-1}$ . Bright bars are  $136 \text{ cd m}^{-2}$ , dark bars  $22 \text{ cd m}^{-2}$ , and surround  $8 \text{ cd m}^{-2}$ . Stimulus cycle composed of 1.7 s movement followed by 3.3 s no movement. Above: variation of response magnitude with direction of movement. Below: typical response to one cycle of horizontal movement. Time mark is 2 s. *Syrphus sp.*, ♂. Unit 1.

whole background is moving. We have not yet measured the velocity characteristic of the surround. The relation between the effect of velocity on the RF and on the surround will determine the extent to which the units are active during flight. We suspect the surround is activated at somewhat lower velocities than the centre. If the surround is sensitive to low velocity then the units will be shut off during flight, except perhaps for a small group in the direction of flight, for which, in an open environment, movement of the background across the surround would be very slow.

Several properties of these units make it impossible for them to contribute to the large-field movement detectors. Inhibitory surrounds prevent these feature detectors from responding to gratings and large bars, which are powerful stimuli for the large-field units. The feature detectors have little or no response at on or off, while the large-field units give powerful on and off responses. The feature detectors have a higher velocity threshold than the large-field units, which give a rather uniform response during movement, starting when the movement starts, stopping when it stops (Fig. 20.8), with little habituation. The feature detectors respond with a triggered burst, which often outlasts the presence of the exciting pattern in the RF (Figs. 20.2 and 20.6). When an effective pattern is presented to feature detectors several times in rapid succession (e.g. at 2 s intervals), the response is likely to be weak the second time, and to disappear by the fourth time; intervals of 15–20 s are required if the response is to be maintained. Units whose response is unreliable, and not related in any simple way to the duration or velocity of movement, are not suitable elements for closed-loop servo-control of orientation; they may trigger open-loop responses to objects that they recognize.

### 20.3. Object recognition during flight and the problem of relative movement

If objects can be identified by features independent of movement, then background movement during flight will not impede recognition. Colour is such a feature. Morpho butterflies will turn to a blue lure at a distance of 15–20 m (Swihart 1972). This response simply requires blue sensitive neurons which are not inhibited by relative motion.

In some circumstances movement itself may be a cue. Male grayling butterflies will pursue many passing objects in the hope that one is a female grayling. Experiments with dummies (Tinbergen 1972) showed that colour and shape are not important; pursuit is excited and possibly in part maintained by a dark object moving erratically. The irregular flight of both male and female will ensure that from moment to moment the speed and direction of the image of the female across the male's retina will differ from the background. This raises the problem of the detection of relative motion. To be sensitive to a moving butterfly during flight a detector should respond to the moving target but not to the moving background.

Neural basis of colour vision in the butterfly *H. erato*  
*J. Insect Physiol.* 18, 1015

"The animal's world"  
 George Allen & Unwin

Because movement in the surround inhibits their response, the units recorded in hoverflies can distinguish between target motion and image motion resulting from the insect's own movements. In this respect they are similar to visual cells in the ventral nerve cord of some Orthoptera (Palka 1969, 1972; Rowell 1971a). However, because the surround is activated by movement in any direction the hoverfly units do not detect relative motion; most will simply be shut off during flight.

Units which do detect the relative motion of a moving target against a moving background have been described in the anterior optic tract of the privet hawk-moth (Collett 1971a, 1972). These cells have directionally-selective excitatory centres and large directionally-selective inhibitory surrounds, so arranged that the centre response is only inhibited if surround motion is in the preferred direction of the centre. Consequently, the units will not respond to the motion of a large grating, or, presumably, to image motion of the environment when the insect moves. On the other hand they will respond if a target and grating move in opposite directions across the eye (see Section 20.6 on 'visual tracking' for a fuller description).

The anterior optic tract units are of little use if the background and target travel at different speeds in the same direction across the retina. Obviously, if the background moves very slowly and the target rapidly, units may respond to target motion, but not to the background, because the inhibition and excitation evoked by the moving background are both relatively weak. Indeed, Rowell (1971a) has shown for the orthopteran DCMD unit mentioned above that background motion at speeds of less than  $5^\circ \text{ s}^{-1}$  does not weaken the response to the target, and that above this lower threshold the strength of the inhibition increases with background speed. Whether there are neurons with more elaborate ways of detecting relative motion is not certain (but see Rowell 1971b).

The problem of recognizing the shape of a moving target has received little attention. In mammals the oculomotor system ensures that selected moving targets can be fixed on the retina. This may be true for insects as well, if saccades are used to bring selected stationary targets into the direction of flight. However, the images of objects not in the direction of flight will be distorted, as will all rapidly moving objects. If geometrical features are to be used for the recognition of moving images special tricks are needed. The behaviour of the hoverfly feature detectors suggests two possibilities.

- (1) Images of stationary objects and other moving insects will travel mainly horizontally across the retina. Thus vertical features will be less distorted than horizontal. Some of the hoverfly units fire to stimuli of any horizontal extent, but are only excited if the height of the image falls within a narrow range. Thus the specificity of these units is provided by vertical features.
- (2) Some units adjust their size preference according to the velocity of the image, and so are designed to recognise an object of a characteristic size

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Ann. Zool. 12, 497

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and speed at different distances. Here the specificity is given by the ratio of speed to size. The lesson to be learnt from these examples is that geometric features of moving images can be used for shape recognition provided that the image distortions can be predicted. One can either use some parameter that remains undistorted, or one can combine properties of the image in such a way that the combination is invariant with image motion. See Fig. 22.2 this volume.

#### 20.4. Orientation in flight: the role of the optomotor system

In addition to detecting targets during flight, an insect has to orient in its visual surroundings. In this section we discuss the role of the optomotor system in aerial navigation. A way in which it can act is seen clearly by considering the behaviour of hoverflies: they hang motionless in the air for seconds at a time. The optomotor system contributes to this hovering flight by providing an efficient velocity servo in which image motion in any direction across the retina produces a restoring force in the same direction, so minimizing the velocity of the image. The error signal for this servo could be provided by motion detecting neurons monitoring movement of the whole environment across the retina. Such neurons have been found in moths (Collett and Blest 1966), flies (Bishop and Keehn 1967), and bees (Kaiser and Bishop 1970). They are directionally selective to movement across the whole field of one or both eyes. Their preferred directions are either horizontal or vertical, so they are able to provide a combination of outputs signalling drift velocity of the eye. To give good stability the neurons providing the error signal should respond strongly at relatively low velocities (Fig. 20.9).

The optomotor system also helps to stabilize locomotion. Experiments by Wilson and Hoy (1968), for example, suggest strongly that the optomotor system can keep an insect on a straight course. In the dark, or in the light under open-loop conditions, the bug, *Oncopeltus*, tends to walk in circles, which for an individual bug are likely to be always in the same direction. However, when the bug walks freely in the light, it can maintain a straight course. In this case the optomotor system apparently corrects an inherent asymmetry in the locomotor system. For a hovering fly the optomotor reflex will tend to reduce the output of the movement detectors to zero, assuming for simplicity that the spontaneous rate of the movement detectors induces negligible torque. In the second example, where the system acts to keep the bug on a straight course while moving forwards, the situation is more complicated. It is this situation we wish to discuss here.

Consider an insect moving within an environment in which objects are uniformly distributed. When the insect moves forwards the images of objects will tend to travel backwards across the retina. The speed of retinal image motion will depend on both the distance of the objects from the fly and the

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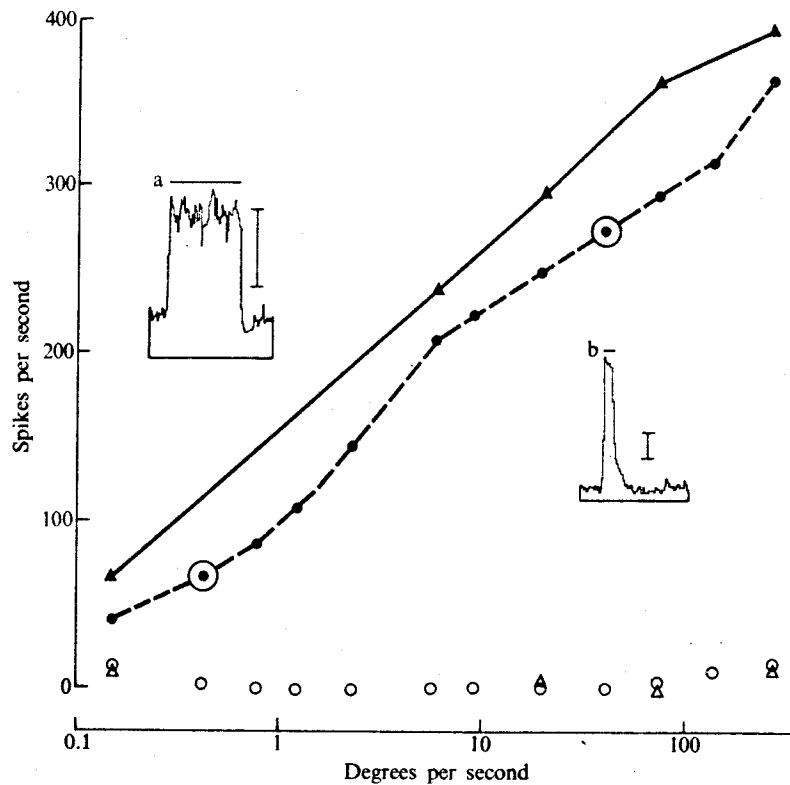


FIG. 20.9. Response of wide-field contralateral movement detector with forward preferred direction to stimuli moving at different velocities. Patterns projected on to a  $70^\circ \times 70^\circ$  tangent screen. Circles represent responses to  $5^\circ \times 36^\circ$  bar which moves through  $25^\circ$  between  $-30^\circ$  and  $-5^\circ$ . Bar extends vertically from  $+32^\circ$  to  $-4^\circ$ . Triangles indicate responses to  $12^\circ$  period square wave grating. Grating covers screen and moves  $25^\circ$ . Solid symbols indicate forward motion, open symbols backward movement. Data points represent average firing rate over five sweeps. Insets show computer print-outs of the response to bar movement at two velocities, averaged over five sweeps. The means of these responses are indicated by the encircled symbols. Time calibration for (a) is 59 s, for (b) 625 ms. Vertical calibration 50 spikes  $s^{-1}$ . *Calliphora erythrocephala*, ♀. Unit C31.

region of retina they stimulate. Thus the images of near objects will move faster than more distant ones, and images will move more rapidly across lateral than across anterior or posterior retina. However, if an insect is stationary, except for rotation about a vertical axis, the velocity of image movement will depend only on the angular velocity of the insect. These two situations are combined when an insect flying forwards deviates from a straight course and the image movement generated by the turn is superimposed on that due to the forward component of movement. The eye on the outside of the turn usually sees images moving backwards, whereas the

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eye on the inside of the turn sees images moving both backwards and forwards. The exact distribution of image movement will depend on the translational and angular velocities of the insect with respect to the world, and on the distribution of objects in it. However, for the eye on the inside of the turn there will always be some forward motion in the front and the back, whereas lateral retina will predominantly be stimulated by backward motion. The velocity feedback signals are therefore derived from the sums and differences of forward and backward movement across the two eyes. The situation is slightly more complicated if translatory motion has a transient sideways component, caused for instance by a sudden cross-wind. However, in some Diptera at least, the present analysis is unaffected by this extra degree of freedom, as the resulting image movement over the front of the eye generates appropriate compensatory torque, whereas image movement over the back of the eye can be neglected because in this region the sensitivity of the optomotor system is weak (McCann and Foster 1971). *Kybernetik* 8, 193

The feedback signals are separated in that they come from neurons with forward and backward preferred directions. There is little doubt that both classes of neurons can contribute to optomotor torque. A variety of flying insects when stimulated with backward (or forward) movement across one eye produce torque that makes the insect turn to the same (or opposite) side. Goetz (1972) has investigated the optomotor behaviour of walking *Drosophila* under open-loop conditions. If the two eyes are presented with similar stimuli moving backwards at different velocities, the insect turns to the side of the faster stimulus (but see Section 20.4.4 on anomalous torque). In this case torque is generated because of a difference in the speed of backward motion across the two eyes.

In some Diptera the neurons which probably mediate optomotor torque are most sensitive to movement in a frontal region of the eye, centred some 20° from the mid-line (Bishop, Keehn, and McCann 1968). Consequently, during forward flight the image of the background will travel relatively slowly across the region of highest sensitivity. Therefore, should the insect deviate from a straight course, the visual feedback resulting from the turn is, in the region of highest sensitivity, superimposed upon a relatively weak level of excitation resulting from the forward movement of the insect. It is thus likely that over part of the region of highest sensitivity there will be a net forward component to image movement for the eye on the *inside* of the turn.

Thus corrective torque during flight can be generated in two different ways: (1) the difference in the speed of backward motion across the two eyes; (2) the presence of forward motion across one eye. Our problem is to determine the relative contributions of the forward and backward motion detectors under normal conditions. To make accurate measurements of differences in the speed of backward motion across the two eyes requires more sophisticated neural equipment than a system which simply detects

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and eliminates forward motion. It is worth considering some of the difficulties that arise if flight is to be stabilized by equalizing the responses of backward sensitive neurons.

#### 20.4.1. *Asymmetries in signal transmission*

If the neurons with backward preferred direction make a substantial contribution to stabilization during flight, it becomes essential to eliminate any inherent asymmetry that may exist in the transmission of signals from the two eyes. As Horridge (1966) emphasized, in feedback circuits which reduce the retinal slip speed to zero, good stabilization is achieved without any great accuracy in the open-loop gain, provided that it is high. But if optomotor torque is controlled by the difference in the speed of backward movement across the two eyes, to keep the insect on a straight course the forward gain must ideally be the same on both sides.

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#### 20.4.2. *Saturation*

Clearly, if velocity differences between the two eyes are to be compared, the responses of the wide-field units mediating the optomotor response should vary with image speed over a suitable range of speeds. Figure 20.9 shows the responses of a movement detector with forward direction (type 2al of Bishop, Keehn, and McCann 1968) to a black bar  $36^\circ$  high and  $5^\circ$  wide moving horizontally through  $25^\circ$  at different speeds. The bar swept through the most sensitive region of the unit's receptive field, and the cycle times used gave at least 15 s interval between each traverse. The firing rate varies linearly with the logarithm of the velocity over three orders of magnitude. Very much the same relation was obtained when the stimulus was a  $70^\circ \times 70^\circ$  vertical grating of  $12^\circ$  period. This evidence (see also Fig. 6 of Bishop and Keehn 1967) suggests that wide-field movement detectors are sensitive indicators of stimulus velocity both for large and relatively small stimuli over a wide range of speeds. On the other hand the data of Fermi and Reichardt (1963) using optomotor torque as an indicator of the velocity response shows that the torque generated by a fly (*Musca domestica*) placed in the centre of a rotating striped drum may (depending on the number and width of stripes) saturate at much lower velocities than Fig. 20.9 indicates.

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#### 20.4.3. *Movement detectors confound stimulus parameters*

If flight is to be stabilized accurately by neurons with backward preferred direction, then the neurons should act as reliable velocity sensors, that is, their responses should ideally vary with velocity and nothing else. However, it is known that the response of some movement detectors varies with the brightness and contrast of a stimulus (Bishop and Keehn 1967), as well as with its size and velocity. If movement detectors confound stimulus parameters, insects would automatically tend to turn towards objects which



because of their contrast or size stimulate the neurons particularly strongly, and this may not be where the insect wishes to go.

#### 20.4.4. *Anomalous torque*

Measurements of the optomotor torque generated by stationary flies placed inside a moving drum (e.g. Fermi and Reichardt 1963) show that as the velocity of a moving stimulus is increased the torque rises to a peak and then falls. If the units with backward preferred direction are the principal contributors to torque during normal flight, the system will behave anomalously for stimuli moving faster than the optimal velocity.

During flight the background passes backwards over the retina. If the insect veers to the left, the background will travel more rapidly across the right eye than the left. At relatively low speeds, backward-sensitive movement detectors with visual fields in the right eye will respond more strongly than those with left visual fields. As a consequence the torque induced by the backward units will tend to make the insect turn to the right, thus helping it keep to a straight course. Suppose now that the insect is blown by a strong wind or flies so fast that the image of the background travels across the eye at a greater speed than the peak velocity of the optomotor system. Now any tendency to turn to the left will mean that movement detectors with left visual fields will respond more strongly than those with right visual fields, so making the insect turn even further to the left. This unstable situation would lead to an insect flying upwind, or erratically, if its forward velocity is high. Kennedy (1939) gave a rather similar account of a mechanism which would make mosquitoes fly upwind, and more recently Goetz (1972) has considered the same problem.

None of the problems listed above arise if only the forward sensitive neurons are responsible for controlling torque during flight. If both sets of neurons are active, those with forward preferred direction will tend to reduce any deviation in flight path caused by the asymmetrical response of the backward sensitive ones. Although the relative contributions of the forward and backward motion detectors to flight stabilization have not been assessed under natural conditions, there are some indications that the forward-sensitive neurons may play the more important role.

- (1) During flights which last more than a few seconds the response of neurons with backward-preferred direction will be partially adapted, whereas the forward-sensitive neurons which only respond during turns will be relatively fresh.
- (2) In the privet hawk-moth, neurons with forward- and backward-preferred direction behave differently when presented with two moving stimuli, one travelling in the preferred direction, the other in the anti-preferred direction (Collett 1971*b*). Forward motion across the

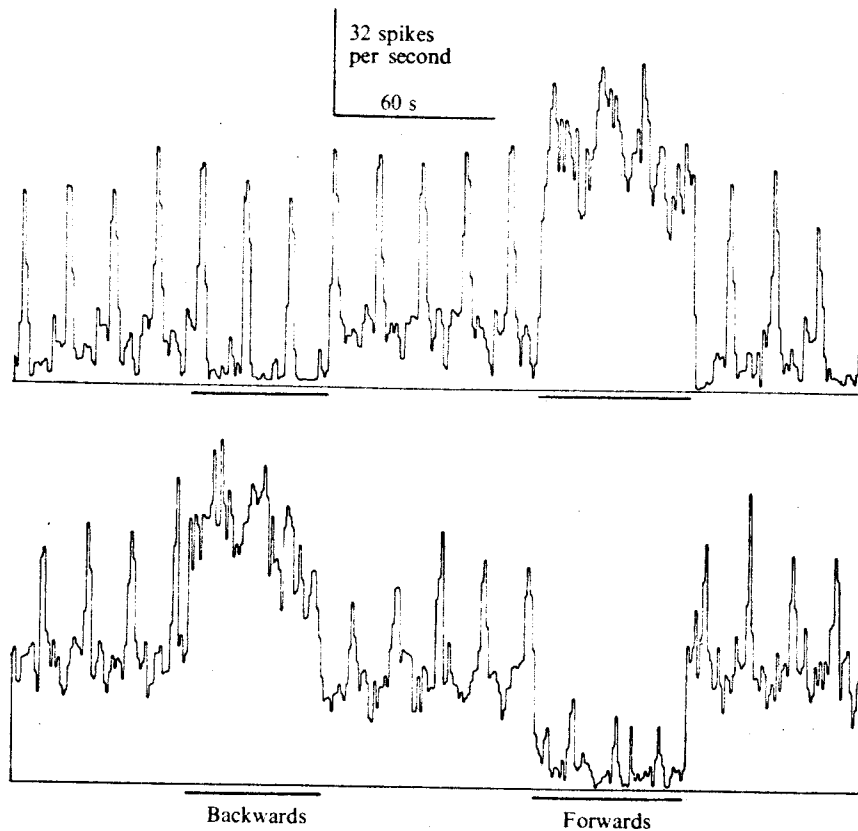


FIG. 20.10. Responses of two wide-field movement detectors projecting from the optic lobe of the privet hawk moth recorded simultaneously. The preferred direction of the unit in the top trace was forwards, the bottom trace backwards. A  $40^\circ$  high,  $3^\circ$  wide light bar moves back and forth through  $40^\circ$  in 3 s in an anterior region of the field. The peaks in firing rate are caused by bar movement in the preferred direction, the troughs by movement in the anti-preferred direction. When indicated by the bars beneath the traces, a grating of  $30^\circ$  period moved at about  $30^\circ \text{ s}^{-1}$  horizontally, backwards or forwards, in the posterior half of the field. Firing rate is averaged over 1 s bins. Reproduced from Collett (1971b).

receptive field of a neuron with backward-preferred direction suppresses the response to a target moving in the preferred direction elsewhere, but backward motion has no effect on the response of a neuron with forward-preferred direction to a second target moving in the preferred direction (Fig. 20.10). In blowflies, movement detectors with forward-preferred direction across one eye enhance the response of movement detectors with backward-preferred direction across the other eye, but the backward-sensitive neurons do not affect the forward-sensitive ones (McCann and Foster 1971). Both features will tend to amplify the effect of a forward-moving stimulus by suppressing

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the activity of units responding to backward movement on the same side, or enhancing the activity of the backward-sensitive neurons on the opposite side. However in *Drosophila* behavioural experiments suggest there is no such asymmetry (Goetz 1964).

- (3) Most measurements of torque generated during flight have failed to separate the torque due to the optomotor system from that generated by the saccadic system. Since there is evidence that saccades may be visually triggered (Fig. 12 of McCann and Fender 1964; reproduced by Land in Chapter 21), statements about the relative strengths of optomotor torque resulting from forward and backward motion are difficult to interpret. It has recently been reported that, in some flies, backward-stimulus motion generates more torque than forward motion (Heisenberg 1972; Reichardt 1973). This difference could be the result of asymmetries in the saccadic or optomotor systems, or simply because during backward motion the optomotor and saccadic systems cause the fly to turn in the same direction, whereas during forward motion the torques generated by the two systems are of opposite sign. Land discusses this question in more detail in Chapter 21.

Thus the optomotor system provides some stability in flight, but it is supplemented by other visual and non-visual control mechanisms which may in addition determine the *direction* of flight. Bees and ants, for instance, are able to orient by maintaining a constant angle with respect to the sun. von Frisch's classical experiments (von Frisch 1967) have shown that foraging bees can use colour as a cue to a good feeding place, so in some way the colour of a target must be used to control the direction of flight. However, recent experiments by Kaiser (1972) and Kaiser and Liske (1972) argue compellingly that the bee optomotor system receives inputs principally from green receptors and is therefore colour blind. In these circumstances the optomotor system is unlikely to control the direction of flight, but merely stabilize a course determined in other ways. Land's (1973) studies of head saccades in blowflies suggest that flies may make rapid saccades towards particular features in the environment in order to change course, and between turns stabilize their flight course partly by means of the optomotor response. Furthermore, the saccadic system can prevent the fly from being pulled in the direction of irrelevant features which stimulate the optomotor system asymmetrically.

### 20.5. Directionally-selective units as velocity detectors

The questions raised in the previous section prompted us to examine how accurately the wide-field directionally-selective units of the blowfly serve as velocity sensors. Features in a natural environment will be of varying sizes and shapes, so to act as a reliable monitor of the speed of background movement the wide-field units should ignore the spatial properties of the

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stimulus. It was interesting, therefore, to find that the relation between firing rate and stimulus velocity is largely unaffected by the form of the moving stimulus, provided that the stimulus passes through the RF region of peak sensitivity.

Units sensitive to forward motion were the most convenient to work with. To minimize damage motion detectors with left visual field were usually recorded in the right optic lobe. Data from units were discarded if the spontaneous firing rate was more than *c.* 10 spikes per sec, since higher rates were associated with unreliable and weak responses. The number of tests that could be performed on a single unit was limited by the gradual deterioration of the preparation and because of the 15 s interval between each traverse of the stimulus necessary to make all the responses independent of each other.

In Figs. 20.9, 20.11, 20.12, and 20.13 the firing rate of a forward-sensitive unit is plotted against stimulus velocity for different patterns. In all cases the stimulus passed through the most sensitive region of the RF. Each point is the average firing rate during five sweeps of the stimulus. The slope of the relation does not vary greatly with the number of bars (Fig. 20.9), or with

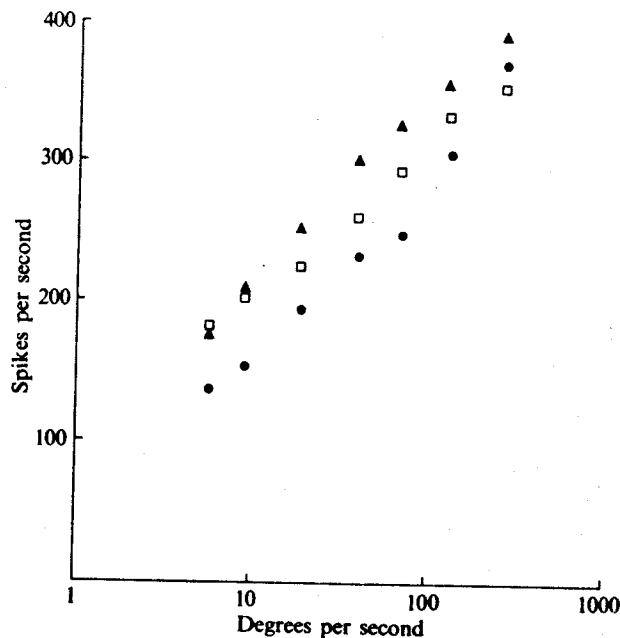


FIG. 20.11. Velocity characteristic of contralateral wide-field movement detector with forward preferred direction to single  $36^\circ$  high bars of different widths moving horizontally between  $-25^\circ$  and  $0^\circ$ . Circles indicate bar width is  $1.5^\circ$ , squares  $7^\circ$ , and triangles  $17^\circ$ . Only responses to forward motion are shown. *Calliphora erythrocephala*, ♂, unit C32.

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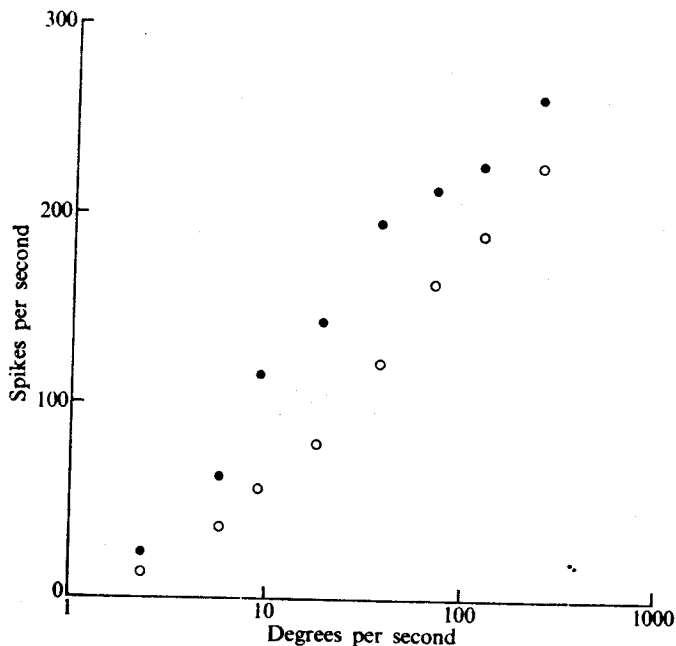


FIG. 20.12. Velocity characteristic of contralateral wide-field movement detector with forward preferred direction for bars  $1.5^\circ$  wide and of different heights. Open circles indicate bar height is  $3^\circ$ , solid circles a bar height of  $39^\circ$ . Bars move  $25^\circ$ , between  $-25^\circ$  and  $0^\circ$ . *Calliphora erythrocephala*, ♀. Unit C33.

the width (Fig. 20.11), or height (Fig. 20.12) of individual bars. In the experiment of Fig. 20.13 the unit was stimulated by a single vertical bar,  $16^\circ$  wide by  $36^\circ$  high, on a light background, or by a light bar of the same dimensions on a dark background. It is clear that for these parameters contrast reversal has a negligible effect on the unit's velocity characteristic.

These findings suggest that the response of the unit is principally determined by stimulus velocity. However, more complicated results are obtained if stimuli do not pass through the most sensitive region of the RF. The velocity characteristic of the upper part of the eye differs considerably and consistently from that of the lower; the upper responds better than the lower to high speeds, whereas the converse holds for low speeds (Fig. 20.14). Despite these complications it is true to say that, for stimuli passing through the region of peak sensitivity, the unit acts as a remarkably faithful velocity sensor, ignoring other aspects of the stimulus.

In the previous section we argued that it is of little consequence if the velocity information gathered by motion detectors is distorted by other stimulus parameters, so long as the units do no more than participate in a velocity servo which drives their output to zero. However, the behaviour of

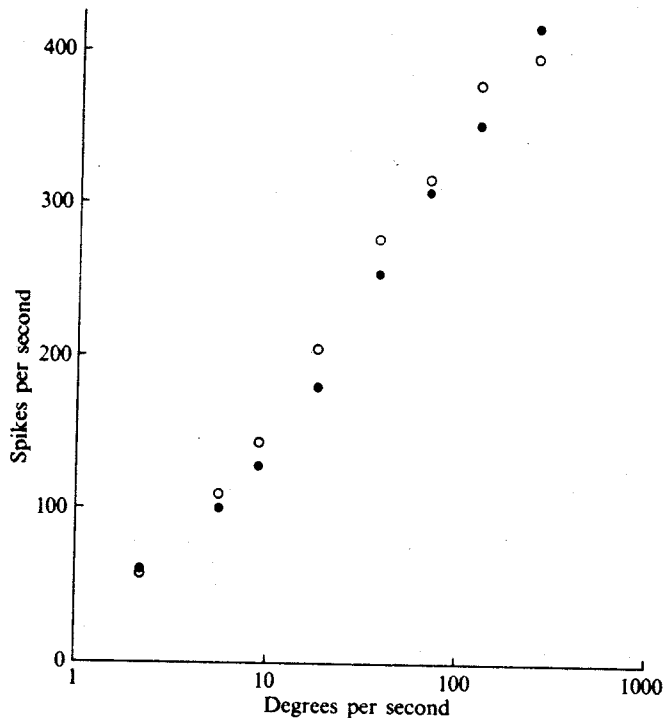


FIG. 20.13. Velocity characteristic of contralateral wide-field motion detector with forward preferred direction to a single light bar (open circles), or dark bar (solid circles). Bar moves  $25^\circ$  horizontally between  $-30^\circ$  and  $-5^\circ$ . *Calliphora erythrocephala* ♂. C35.

the units in the present experiments suggests they might contribute to a more sophisticated control system; one, for example, in which motor commands are generated to make the insect turn at a specified velocity. The optomotor system might then be part of a velocity servo which enables the commands to be executed accurately, in addition to its role in stabilizing locomotion.

However, this suggestion must be considered in the light of experiments on the velocity response of motion detectors when the stimulus is a rotating, striped drum. In this situation, unlike ours, the velocity characteristic of the optomotor response, measured behaviourally (Fermi and Reichardt 1963), and of motion detectors (Bishop and Keehn 1967) depends strongly on the spatial wavelength of the stimulating pattern. The response of the unit partially adapts to continuously moving stimuli (e.g. Bishop, Keehn, and McCann 1968) and the state of adaptation is very likely to be a function both of the velocity and of the spatial characteristic of the pattern. Whether the difference between our experiments and those of Bishop and Keehn can be explained in this way, and whether the effect of spatial wavelength on the

FIG. 20.12. Preferred direction of motion detector in three different responses.

velocity cannot be explained in this way.

## 20.6.

Some of the units in the present experiments suggest we will contribute to a visual system.

To understand animal movement, we need to understand the underlying mechanisms. This is a high-level problem, and it is a kind of self-referential problem, or optomotor system.

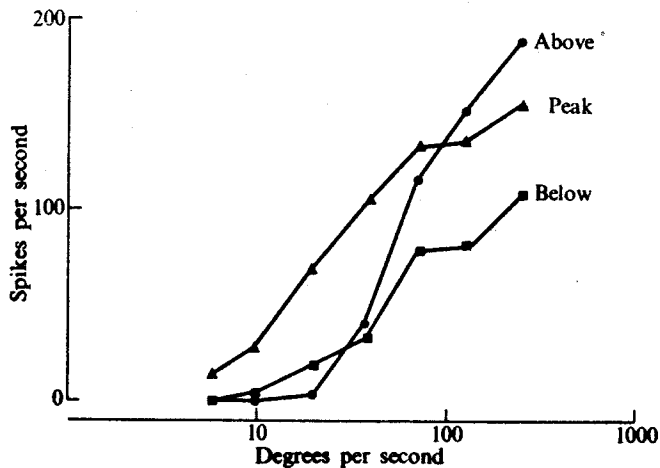


FIG. 20.14. Velocity characteristics of contralateral wide-field motion detector with forward preferred direction to light  $4^\circ$  diameter spot moving horizontally between  $-30^\circ$  and  $-5^\circ$  in three different vertical positions. The vertical coordinate of the centre of the stimulus for the response labelled peak is  $-3^\circ$ , for that labelled above  $+13^\circ$ , and for that below  $-19^\circ$ . *Calliphora erythrocephala* ♂. C37.

velocity response is important under natural conditions are questions we cannot yet answer.

## 20.6. Visual tracking

Some insects are able to track moving targets during flight. In this section we will describe in more detail the behaviour of neurons in the anterior optic tract of the hawk-moth, since these neurons are well suited to play a role in a visually-guided tracking system.

To track accurately targets which subtend a small angle on the retina, animals presumably require a system additional to the optomotor system. Indeed, the optomotor system would be expected to work against any attempt to track with smooth pursuit movements a small moving target against a featured background, for the image movement of the background during any tendency to track will result in an opposing optomotor response. Thus rabbits will follow small moving targets with their eyes only if the background does not elicit an antagonistic optomotor response (Rademaker and ter Braak 1948). In flies, where the sensitivity of the optomotor system is highest towards the front of the eye, it may well be that so long as the moving target is large and stimulates large-field movement detectors strongly, a kind of transient tracing can be achieved by the optomotor system by itself, once the target is fixated by the front of the eye. In this case the opposing optomotor torque generated by the background would make the fly follow

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the target with a velocity error which would depend on the nature of the background and the position of the target on the retina. But for short periods, at least until the target was carried beyond the sensitive frontal region, the fly would tend to follow it. Preliminary experiments by Virsik (cited by Poggio and Reichardt 1973) suggest that this may be so for the house-fly, which follows a moving stripe against a featured background with the sort of lag expected, were the optomotor system responsible for the behaviour. Presumably under normal circumstances, head saccades could periodically abolish the position error, as do saccadic eye movements generated by the primate oculomotor system.

The behaviour of some neurons in the anterior tract of the privet hawk-moth suggests that possibly some insects may have a more sophisticated system for visual tracking. The receptive fields of these neurons are typically  $30^\circ$  or more across and located in the antero-ventral quadrant of the eye ipsilateral to the recording site. The neurons respond optimally to stimuli moving forwards over the eye, backward movement suppressing the resting discharge. They respond to light or dark targets of any shape or size so long as the target is not appreciably larger than the field. Forward motion over the rest of the eye, provided that the speed of the surround stimulus is greater than  $3^\circ \text{ s}^{-1}$ , suppresses the centre response, but backward motion does not. Across the contralateral eye backward, but not forward motion inhibits the response to movement within the receptive field (Fig. 20.15). Directionally-selective inhibition of this kind allows the unit to respond to a target moving in the preferred direction, when the insect is still, or when the insect turns in the same direction, but more slowly than the target. And this is what happens during tracking.

When a grating in the surround moves backwards across the ipsilateral eye, or forwards across the contralateral eye, at speeds of more than  $3^\circ \text{ s}^{-1}$ , the velocity characteristics of the centre region are changed. With no surround motion most of the units investigated only responded to target speeds above  $2^\circ \text{ s}^{-1}$ , the response magnitude increasing with the velocity up to  $20^\circ \text{ s}^{-1}$  (Fig. 20.16). However, with such facilitatory surround movement they are sensitive to targets moving as slowly as  $0.06^\circ \text{ s}^{-1}$  within the centre region, while responses to higher speeds are enhanced (Fig. 20.17). Such behaviour would be appropriate for neurons which form part of a velocity servo for tracking a moving target, with the output of the neurons providing a command signal to torque generators.

Consider an insect starting to track an object moving at a constant speed. As the insect begins to follow the target, the slip speed of the target image across the eye decreases, and the image of the background moves in the reverse direction. When the target image is effectively stabilized on the retina, its slip speed approaches zero, while the background now moves across the retina at a rate equal to the eye speed. If the neurons are to respond



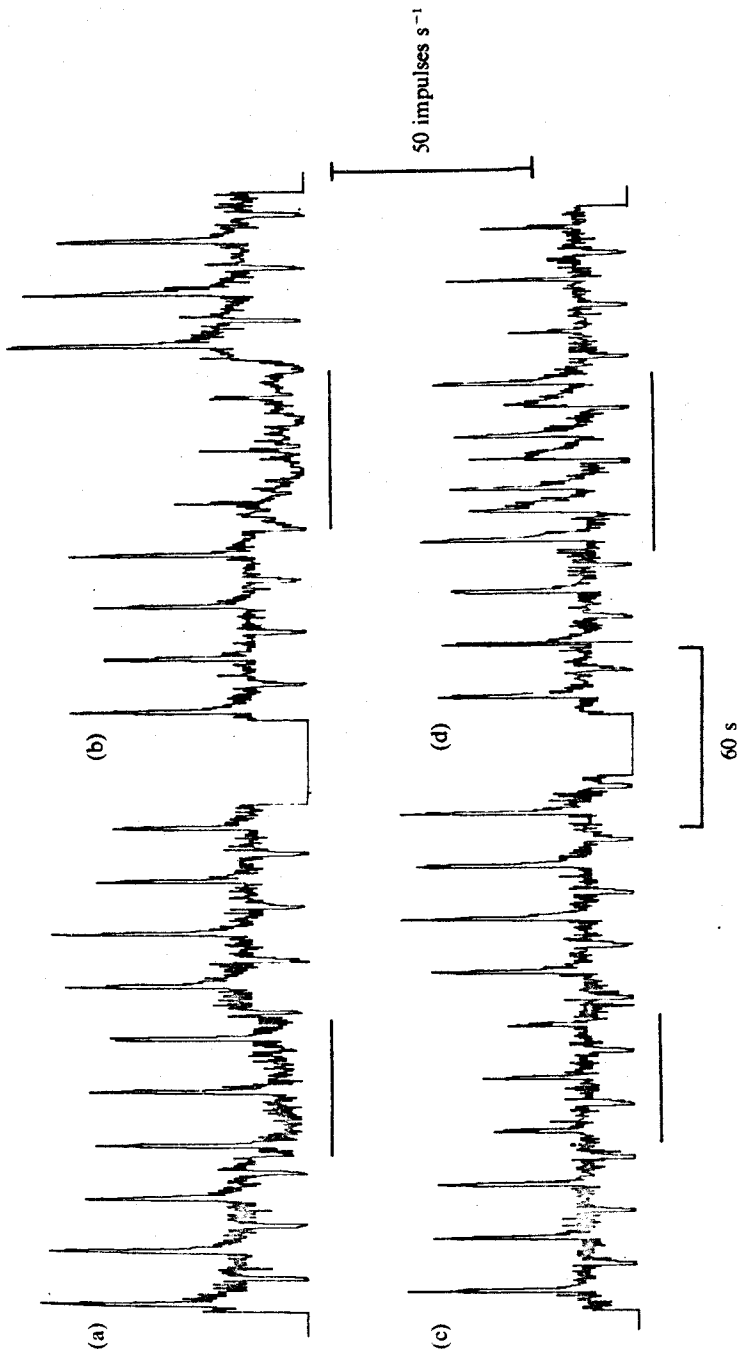


FIG. 20.15. The effect of gratings of 30° period, moving at 30 s<sup>-1</sup> outside the RF centre of the right eye, or across the left eye, on the response of a unit to a vertically oriented bar moving 20°, at 16 s<sup>-1</sup>, forwards and backwards within the RF centre. This unit, like those of Figs. 20.16 and 20.17, has forward preferred direction, was recorded in the right anterior optic tract (AOT) of a privet hawk-moth, and had a roughly circular RF centre, 30° across, situated in the anterior ventral quadrant of the right eye. The peaks in firing rate, reproduced from a computer print-out, are caused by forward bar motion, the troughs by backward motion. The lines beneath the traces indicate when the left or right grating was moving. In (a) and (b) the right grating travelled, respectively, backwards and forwards. In (c) and (d) the left grating travelled, respectively, backwards and forwards. Firing rate is averaged over 250 ms bins. Reproduced from Collett, 1972.

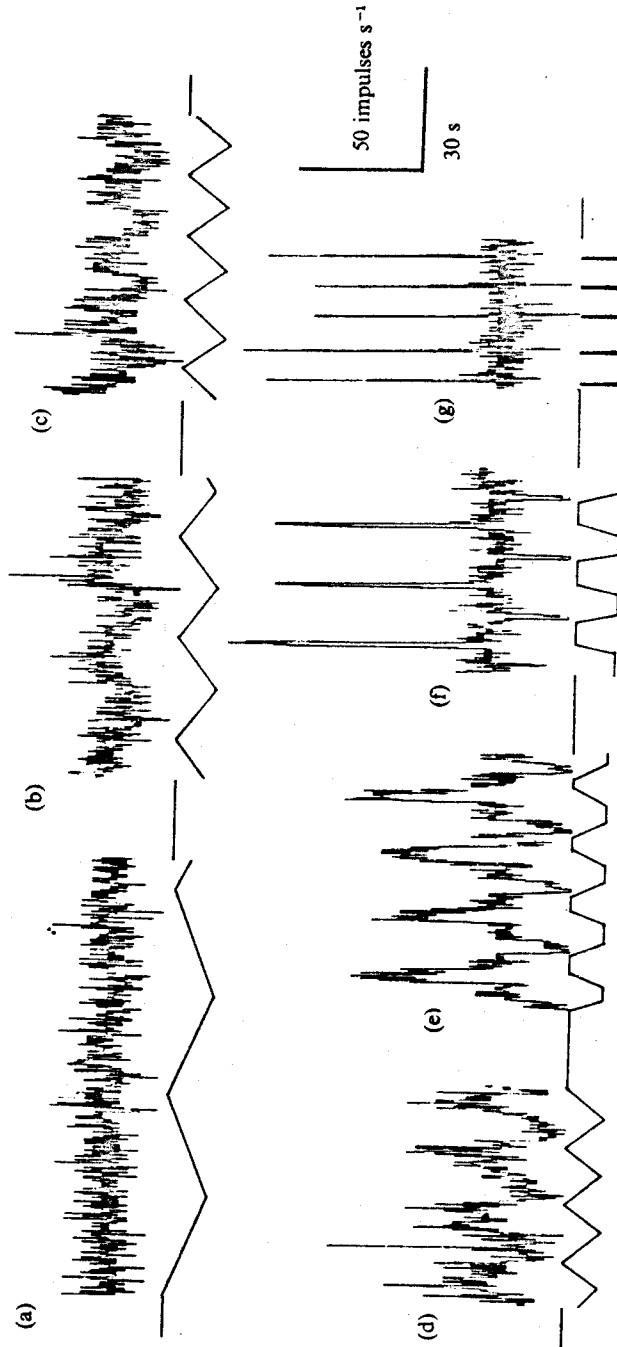


FIG. 20.16. Response of AOT unit to a bar,  $15^\circ$  high by  $5^\circ$  wide, which moved horizontally, backwards and forwards, at different speeds. The  $25^\circ$  sweep of the bar lay within the RF centre. The bar speeds were: (a) 0.8; (b) 1.7; (c) 2.8; (d) 3.6; (e) 6.2; (f) 20.8; (g)  $100^\circ \text{ s}^{-1}$ . The stimulus monitor below the computer print-out of firing is a diagrammatic indication of the movements of the bar. Upward excursions signify forward movement. Firing rate is averaged over 250 ms bins. Reproduced from Collett 1971b.

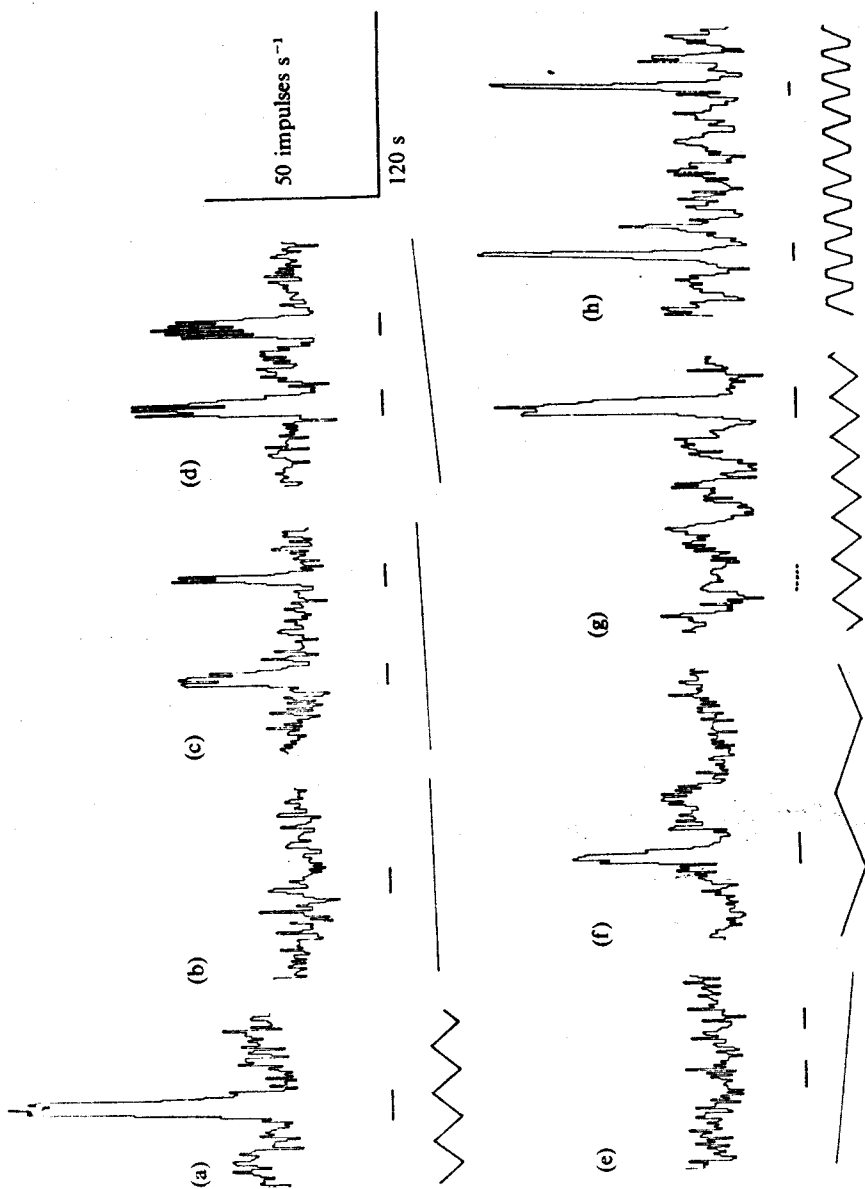


FIG. 20.17. The effect of grating of  $30^\circ$  period moving at  $16^\circ \text{ s}^{-1}$  across the left eye on the response of AOT unit to a bar moving through  $25^\circ$  at different speeds. The solid line beneath the print-out indicates when the grating moved forwards, the dashed line back wards. The vertical position of these lines indicates the zero level of the print-out. Traces are arranged in the order in which different bar speeds were tested. Speeds were: (a) 1.7; (b) 0.04; (c) 0.08; (d) 0.2; (e) 0.5; (f) 2.2; (g) 6.2  $^\circ \text{ s}^{-1}$ . In all traces except *e* the grating moved while the bar travelled in the preferred direction. Firing rate averaged over 1 s bins. Reproduced from Collett, 1971b.

when the insect follows closely behind the target, they must be sensitive to low velocities, but for the initial detection and acquisition of the target only neurons capable of responding to higher velocities are required.

It is worth remarking on a possible advantage of making the neurons insensitive to low velocities unless there is appropriate movement through the surround. The main problem in making a simple velocity servo perform as well as the primate smooth pursuit system is that of stability. As the eye begins to follow a target, the slip speed of the target across the retina drops, so reducing the velocity error signal. This in turn lessens the signal to the effectors, whereupon the eye again lags behind the target and the velocity error signal rises. Oscillations generated in this way would occur if a high open-loop gain were coupled with appreciable delays round the feedback loop. Instability could, however, be avoided if some quantity related to eye speed provided a positive feedback signal to the system. In this case the fall in the velocity error signal when the eye catches up with the target would be balanced by an increase in the signal related to eye speed (Robinson 1971). The speed at which the background apparently travels across the eye is one measure of eye speed. Therefore, it is possible that the facilitation of low velocity responses by background movement helps increase the stability of a velocity error servo.

#### 20.7. Centrifugal neurons to the optic lobe which monitor an insect's own movements

The hypothesis of the previous section suggested that a signal related to eye speed could be used to modify the responsiveness of movement detectors and so enhance the efficiency of a tracking system. Information of this kind relayed back to the optic lobe would also help the visual system distinguish target motion from background motion. In principle such a signal could be derived either from motor commands to the effectors, or from the visual or mechanical consequences of the movement. Both sources of information have their difficulties and inaccuracies. If signals obtained from motor commands are to be employed, they must be related accurately to the intended movement, rather than to the muscular forces needed to perform it. Too little has been discovered about the higher organization of motor behaviour in insects to know whether the appropriate signals are available at all. Visual feedback should provide information about the movement that actually occurred and should not be disturbed by any imprecision in the execution of a motor command. However, in practice, as we have already seen, the quantitative information provided by movement detectors is somewhat ambiguous. It is possibly because of these uncertainties that the behaviour of the anterior optic tract neurons is not a graded function of the speed of surround motion. The direction of surround movement determines

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whether the response is inhibited or facilitated but the amount of facilitation does not depend reliably on its speed.

Some of the many neurons which in arthropods project centrifugally to the optic lobe are directionally-selective movement detectors with large binocular or monocular receptive fields and response properties which make them suitable monitors of the visual consequences of the insect's movements (Collett 1970). Moreover, as befits neurons carrying such information, there is no sign that they receive anything but visual information: they do not respond to non-visual stimuli, and their response properties are not altered when the flight motor is active. Their behaviour in fact resembles rather

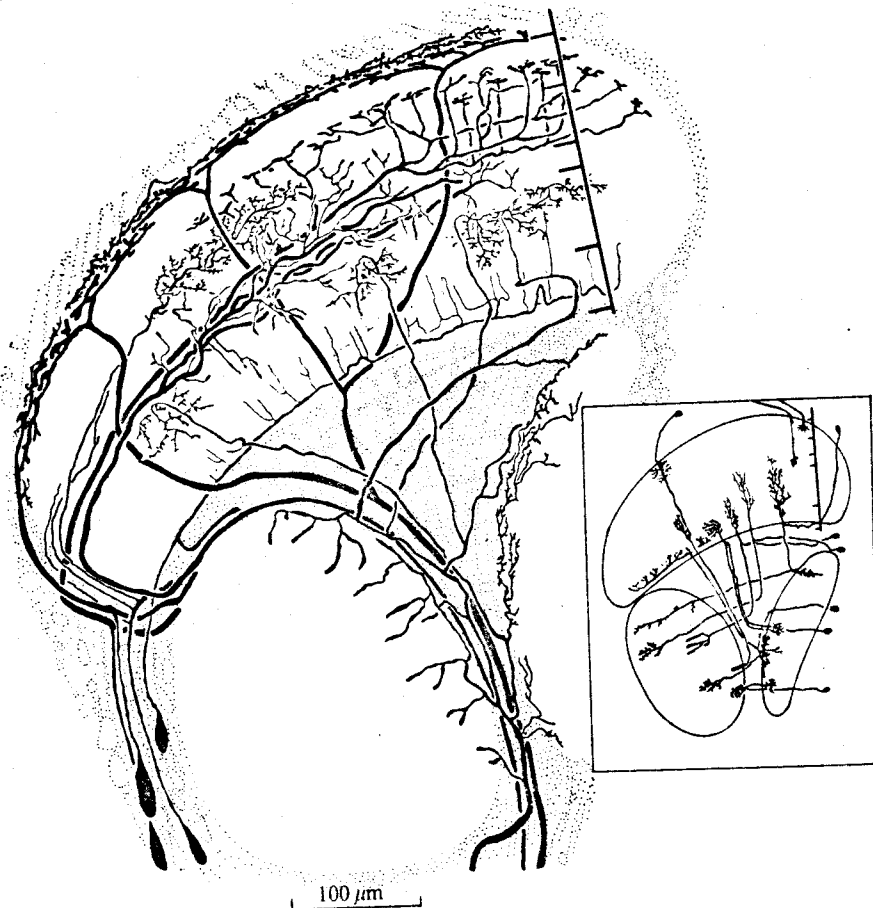


FIG. 20.18. Drawing of some tangential cells in the medulla of the privet hawk-moth shown in horizontal section. Reconstructions made from wholly or partially-impregnated cells stained using the Golgi-Colonnier method. Inset shows perpendicular cells carrying the mosaic projection from the retina. Figure prepared by N. J. Strausfeld. Reproduced from Collett, 1970.

closely that of neurons recorded in the ventral nerve cord, which are possibly involved in generating optomotor torque, and there is some evidence that they and the thoracic neurons in part receive a common input (Collett 1971*b*). Thus the same visual information may be routed to the motor system to control orientation and back to both optic lobes to tell the visual system what movements were performed.

Centrifugal neurons have been shown to project to the medulla (Collett 1970) and to the lobula complex (Collett 1970; McCann and Foster 1971). There is evidence from the privet hawk-moth (Collett 1970) that the binocular directionally-selective movement detectors projecting to the medulla can be identified with an anatomically defined class of cell—the tangential cell (Strausfeld and Blest 1970) which has terminal branches that cover much of the retinal projection to the medulla (Fig. 20.18). Therefore one might expect the information carried by these cells to be distributed widely over the medulla.

There are probably two of the binocular neurons detecting horizontal movement projecting to each medulla with opposite preferred directions across the two eyes. These neurons respond optimally during yaw. However, because of the asymmetrical distribution of their inhibitory inputs, they are probably also active during forward flight (Collett 1971*b*). Consider, for example, a neuron with backward-preferred direction across the right eye and forward-preferred direction across the left eye. Backward motion across the left eye (i.e. in the anti-preferred direction) does not suppress the response to backward motion across the right eye, although forward motion across the right eye will suppress the response to forward motion across the left eye. In other words these neurons receive direct or indirect inhibitory inputs from movement detectors excited by forward motion, but not from ones with backward-preferred direction. This feature may well be important because centrifugal neurons which would respond optimally during forward flight (i.e. sensitive to backward motion across both eyes) have not been found in the medulla. Some information about the forward motion of the insect can thus be obtained from the summed activity of the neurons with clockwise and anticlockwise preferred direction, whereas the differences between the activities of these neurons will signal that the insect is turning.

#### ACKNOWLEDGEMENT

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