

## OPTOMOTOR CONTROL OF SPEED AND HEIGHT BY FREE-FLYING *DROSOPHILA*

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The optomotor reactions of *Drosophila* have been studied intensively, with the conclusion that in flight there are two main types of response. One of these controls the course of the animal by adjusting the relative amplitudes of the wingbeats on the two sides of the body. The other controls the total thrust produced by the wings (Götz, 1968). *Drosophila* do not change the direction of the thrust produced relative to the body axis (Götz, 1968; Vogel, 1966; David, 1978) but do change the distribution of their total power output between lift and thrust by changing the inclination of the body axis (David, 1978). This could not, however, be observed in tethered fliers on which previous work had been done. Nevertheless, it has been implied that free fliers alter only their lift, so that the control of power output is used only to control height (Götz, 1972; Buchner, Götz & Straub, 1978). Here I report some experiments on free-flying *Drosophila hydei* Sturtevant showing that speed (and hence thrust) as well as height (and hence lift) are controlled by optomotor reactions to features of the surroundings.

The flies were flown in the horizontal wind-tunnel built by the Agricultural Research Council Insect Physiology Group at Imperial College Field Station, Silwood Park, and described previously (David, 1978). They flew at about the same groundspeed when flying in still air and against winds of up to  $0.6 \text{ m s}^{-1}$ , thus compensating in large measure for the changes in wind speed. Flies flying downwind reduced their airspeed as the windspeed was increased, but not enough to compensate for the increase in groundspeed caused by the wind. The flies' groundspeed was shown to be controlled by visual reactions to the ground by moving the patterned floor of the tunnel beneath them. When it was accelerated downwind under flies progressing upwind they reduced their airspeed and could be held at one point in the tunnel or carried downwind whilst still facing upwind. When the floor was accelerated upwind the flies progressing upwind accelerated. The percentage of flies responding by floor-following speed changes increased as the speed to which the floor was accelerated increased: it was greater at any one rate of floor acceleration for floor movements in the direction of the flies' flight than for floor movements in the opposite direction (Fig. 1). Similar asymmetries in response have been reported from mosquitoes (Kennedy, 1940).

Changes in airspeed of flies following the movement of the floor were used as an assay in determining which parts of the eyes were responsible for perceiving the floor movement. Different parts of the tunnel floor pattern were hidden from the flies under black paper masks and the proportion of flies responding to floor accelerations of a

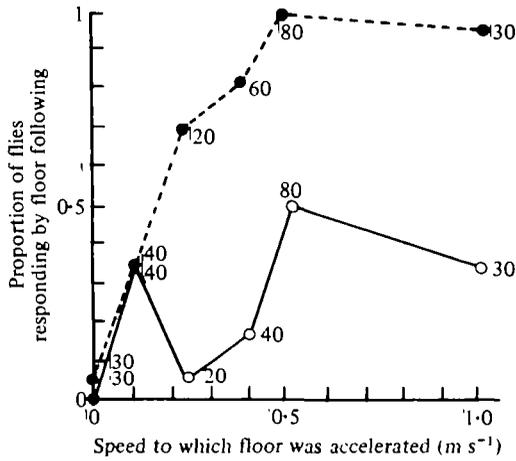


Fig. 1. The proportion of flies responding by floor-following speed changes when the floor was accelerated within 0.5 s to the speed shown. ●, Floor accelerated in the same direction as the flies' flight; ○, floor accelerated in opposite direction. Figures beside the points show the number of observations.

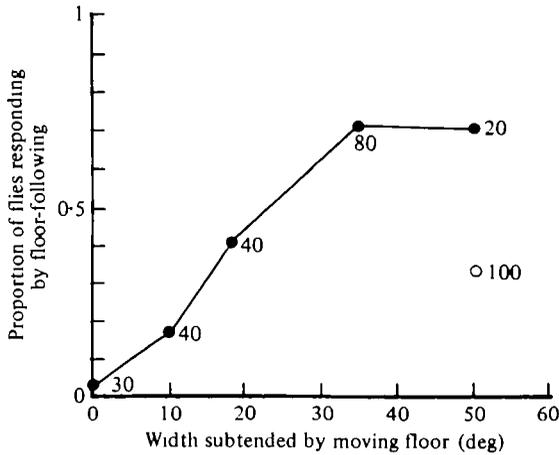


Fig. 2. The proportion of flies responding by floor-following speed changes when floors of different widths were accelerated. ○, Central strip of floor; ●, two equal lateral strips of floor. Figures beside the points show the number of observations.

particular rate was noted. Fig. 2 shows the result of an experiment in which flies that were 0.2 m above the floor in the centre of the tunnel in still air and flying along the length of the tunnel at about 0.2 m s<sup>-1</sup> were exposed to accelerations either of a central strip of floor pattern 0.7 m long and 0.2 m wide directly beneath them, or to two equal strips of floor pattern of varying widths, the outer edges of the strips being 0.5 m from the centre line of the tunnel. The central strip subtended a width of 52° at the position of the fly; the two lateral strips that produced the same proportion of floor-following responses subtended about 16° together. The lateral strips together subtending 52° had a significantly greater effect on the flies than did the central strip subtending that angle.

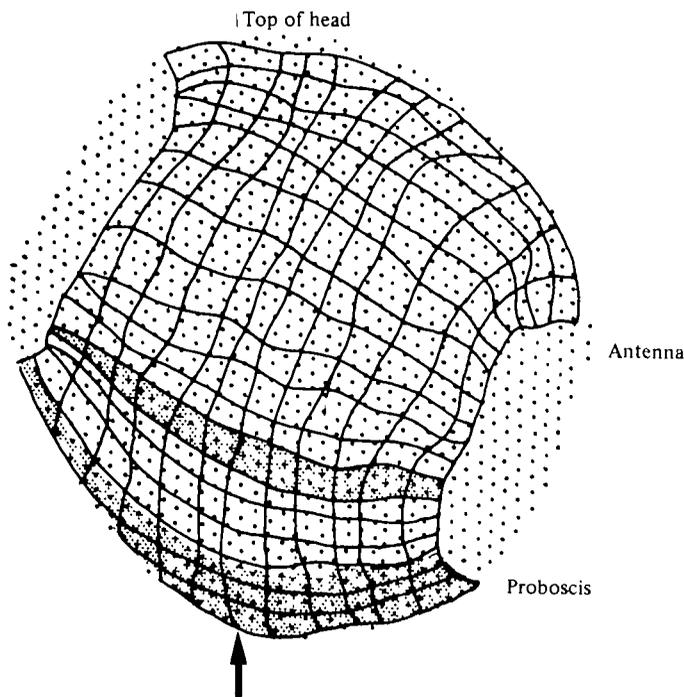


Figure 3. A map of the right eye of a fly, each dot showing the position of an ommatidium. The arrow indicates that ommatidium whose visual axis was straight down when the angle of the body axis to the horizontal was  $55^\circ$ , the angle taken up at an airspeed of  $0.2 \text{ m s}^{-1}$ . The grid lines show the position of the centre of the deep pseudopupil (Franceschini & Kirschfeld, 1971) at intervals of  $10^\circ$ . From these the visual axis of any ommatidium included in the grid can be determined. Thus the ommatidium at the bottom right-hand of the grid near the proboscis has a visual axis aligned along the dorsal-ventral mid line  $60^\circ$  up and to the front of the straight down direction. The visual field of this eye covered the whole hemisphere around the eye, with some overlap into the visual field of the other eye, except for a small region on the left of the figure, at the back of the head. The fine dots show those ommatidia whose visual fields included the lateral strips and the central strip of the wind-tunnel floor, which both produced equal optomotor effects.

The ommatidia that were looking at those two regions having equal optomotor effects are shown in Fig. 3. The flies' eyes were more regular than those of *D. melanogaster* Meigen and had none of the stretching of the hexagonal array seen in *Musca* (Braitenberg, 1967). There were between 1000 and 1350 ommatidia in each eye; that shown in Fig. 3 has 1312. In this eye the central strip of the floor pattern was looked at by 130 ommatidia, the lateral strip by 70. There is an inhomogeneous distribution of interommatidial angles in the flies' eyes, the angle being less near the equator than in downward-looking regions of the eye. However, this difference is not enough to explain the difference between the optomotor effects of the  $8^\circ$  wide strip  $22^\circ$  down from the equator of the eye, and that of the  $26^\circ$  wide strip looking down. There was a greater optomotor effect per ommatidium in the strip near the equator.

The flies did not change height in response to vertical movements of the floor pattern beneath them, but they were very responsive to vertical movements at their sides. About 70% of the flies followed the up and down movement of black horizon

screens at the sides of the tunnel in still air and when they were flying against winds of up to  $0.6 \text{ m s}^{-1}$ .

The optomotor reactions of *Drosophila* controlling lift and thrust must be at least as complicated as in other insects, even though *Drosophila* have a simpler flight control system. Since the body angle changes at different airspeeds the direction of image movement over the eyes, to which the fly must respond by appropriate changes of lift and thrust, also varies. So far no responses have been recorded from tethered flies that would provide a suitable negative feedback for controlling flight speed. However, walking flies do change speed with the movement of patterns past them (Götz & Wenking, 1973). The receptors for the course control response of *Drosophila* are homogeneous over most of the eye (Götz, 1964), whereas those governing the power output are reported to vary only in the upper frontal region of the eye (Buchner *et al.* 1978). The region looking down at a body angle of  $55^\circ$  has not been examined. The distribution of receptors for the course control and power output control systems is thus no help in deciding whether the movement detectors responsible for speed control are part of one of these two systems, or form a third one.

Optomotor-controlled flight speeds are found in other insects (Heran, 1955; Kennedy & Marsh, 1974; Kennedy & Thomas, 1974). A reason for *Drosophila* controlling its groundspeed may be to stop the insect from overshooting a target.

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