

## SHORT COMMUNICATION

# THE LANDING RESPONSE OF TETHERED FLYING *DROSOPHILA* IS INDUCED AT A CRITICAL OBJECT ANGLE

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An investigation was made to find which simple parameters of a visual stimulus are critical to induce a landing response in tethered flying *Drosophila melanogaster*.

The stimulus consisted of a circular black disk, against a white background, moving towards the fly. A glass plate was placed between fly and disk to ensure that only a visual stimulation was presented. The landing response involves an extension of the forelegs in front of and above the head. To monitor this movement, the shadow of the fly was projected by red light through a microscope onto a small screen (Erber & Schildberger, 1980) and the motion of the forelegs was recorded by two light gates at different positions with respect to the fly's shadow (Fig. 1 inset). The disk approached the fly at a given velocity and its movement was timed, from a marker at a fixed distance from the fly, up to the moment when the first light gate detected the start of the landing response. The expansion of the stimulus covered an object angle subtended on the fly's retina ( $\alpha$ ) of 10–95°. The diameter of the disk was 35 or 70 mm. The range of disk velocities was 5–40 cm s<sup>-1</sup>.

In a first experiment, short (20 ms) expansion stimuli were used which elicited a landing response with a latency of 50 ± 15 ms, similar to values obtained for *Musca domestica* (Wagner, 1982; Borst, 1986).

The object angle subtended on the fly's retina 50 ms before the onset of the landing response dropped from 80° at small retinal expansion velocities to a nearly constant value, about 50°, above retinal expansion velocities  $d\alpha/dt$  of 300° s<sup>-1</sup> (Fig. 1). This angle was independent of disk diameter. So the absolute disk angle on the fly's retina was the critical parameter and not the absolute distance between stimulus and fly. From measurements of landing activity an analogous result for larger flies was obtained when they were tested with variable disk diameters and a constant disk velocity (Goodman, 1960; Eckert & Hamdorf, 1980).

The angle subtended on the retina has also been found to be critical for male *Syrphid pipiens* to compute their distance from a female (Collet & Land, 1975). In contrast, the velocity of the landing object has been found to be critical for the

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landing response in *Lucilia sericata* (Goodman, 1960) and for the onset of final deceleration before landing of free-flying *Musca domestica* (Wagner, 1982).

Since larger flies fly faster and have a greater momentum to drag ratio, it might be necessary for them to shift the landing manoeuvre to greater distances at higher

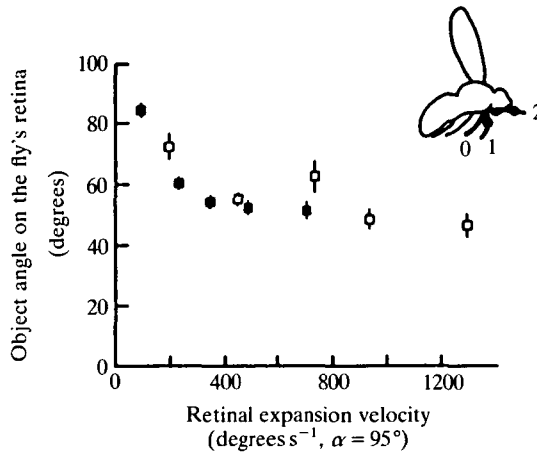


Fig. 1. Inset: schematic drawing of *Drosophila* (0 = forelegs in normal flight position). The beginning of the landing response (1) is monitored by a light gate (filled circle) near the forelegs in their normal flight position. The landing criterion is established by a light gate in front of the antennae (2). The angle of the landing object (disk) subtended on the fly's retina 50 ms before the beginning of the landing response plotted against the retinal expansion velocity of  $\alpha = 95^\circ$  (filled squares, diameter of disk = 70 mm; open squares, diameter of disk = 35 mm). Data are the mean values for 15 male flies (Berlin +). Error bars denote S.E.M. The position of the equator of the retina was fixed at  $0^\circ$  in the horizontal plane. The head and body of the flies were shielded against the projecting red light during the test.

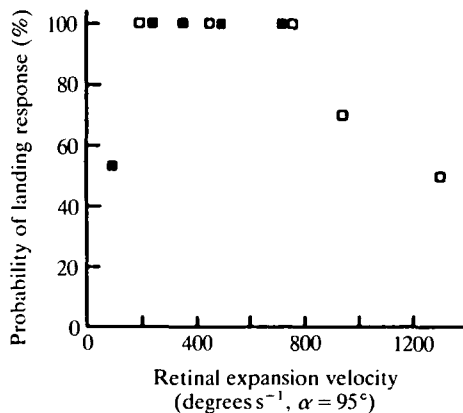


Fig. 2. The probability of obtaining a landing response plotted against the retinal expansion velocity of the flies in Fig. 1 (symbols as in Fig. 1). The expansion covers a range of  $10^\circ$ – $95^\circ$  for the angle subtended on the fly's retina. We could see no effects of habituation under the given stimulus conditions.

flying speed which would require a longer stopping distance. Since the landing response of *Drosophila* is elicited at a constant object angle, there will be insufficient time to exhibit the landing response at high disk velocities.

The performance time of the landing response was measured as the time taken for the flies to extend their forelegs from light gate 1 to light gate 2. The performance time was 35 ms and was independent of the disk velocity. Together with the latency of 50 ms this gives *Drosophila* 85 ms to land before the object expands to  $180^\circ$ . This indicates that at an expansion velocity above  $1600^\circ\text{s}^{-1}$  (at  $\alpha = 95^\circ$ ) it is impossible for *Drosophila* to land in time when the landing response is induced at an object angle of  $50^\circ$ . When the landing response was carried out, all the experimental flies landed in time, but at high expansion velocities, above  $800^\circ\text{s}^{-1}$ , the probability of landing decreased (Fig. 2). Thus the experiments were carried out over the whole range of expansion velocities in which the landing responses could be elicited with high probability. Furthermore, this shows that the landing mechanism of *Drosophila* is optimally triggered only when the landing response can be carried out in time.

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