

## Object Detection by Relative Motion in Freely Flying Flies

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The ability to detect objects and to distinguish them from the background (figure-ground discrimination) is essential if an animal is to navigate successfully in its environment. When an animal moves in the environment, the resulting motion of the retinal image carries powerful cues that can be used to extract information about the three-dimensional structure of the visual surround (e.g. [1]). Small animals that lack the interocular separation or visual acuity necessary for stereopsis [2] can still obtain depth information if they exploit the image motion cues generated by their own motion. As an example, consider the situation of an insect flying over a meadow with flowers raised above the grass. When the insect passes a flower, the image of the flower moves more rapidly across the retina than that of the ground, because the flower is closer to the animal's eye. Thus, relative image motion can be used to distinguish the flower from its immediate background, even if other cues such as differences in colour, brightness or texture are weak or absent.

The problem of figure-ground discrimination by relative motion has been studied intensively in the fly [3]. Experiments on tethered flying flies inside a rotating drum have revealed that flies are able to detect a stripe ("object") covered with the same texture as the interior of the drum ("background") when the stripe moves relative to the background, the only available cue to detect the stripe being the relative motion between stripe and drum [4]. Moreover, electrophysiological studies have led to the characterization of a neuronal circuitry which may underlie figure-ground discrimination by rela-

tive motion [5]. However, it has remained unclear so far whether flies use motion information for object detection in natural situations, that is, in free flight, where relative image motion is induced by the animal's own locomotion. Here it is shown that the relative motion between the images of a raised object and its background, induced by self-motion, can indeed provide an adequate cue for the fly to detect and land on such an object.

A wooden box ( $80 \times 60 \times 32 \text{ cm}^3$ ) was used as a flight arena (Fig. 1, inset). The floor and the walls of the box were covered with a random dot pattern with a standard pixel size of  $3 \times 3 \text{ mm}^2$ . Discs of diameter 5 cm could be positioned at different heights on thin stalks (diameter: 3 mm) of variable length at nine sites of the floor, organized rectangularly in three rows. In order to investigate object detection solely on the basis of relative motion cues, the discs and the stalks were covered with the same random dot pattern as the floor and the walls of the box. In this way other cues for detection of the discs such as differences in texture, luminance or colour were minimized. In the experiments seven discs were placed at different heights ranging from 0.2 cm to 6 cm, and a control disc was placed directly on the floor. Approximately 30 female flies of the species *Lucilia cuprina* were kept in the box. In 20 sessions, each of 45 min duration, the number of spontaneous landings on each of the discs was counted. The positions of the different discs were interchanged randomly after each session and the discs were cleaned with ethanol to remove traces of scent that could have been left by flies that had previously landed on the discs. The relative landing frequencies for each disc in each session were calculated, and the values for each disc height were averaged over the 20 sessions, yielding the

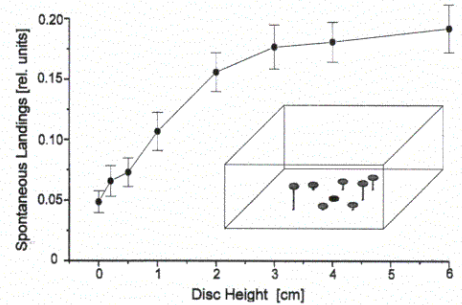


Fig. 1. Relative number of spontaneous landings on discs of different heights. Shown are the mean frequencies of landing obtained in 20 sessions and the corresponding standard error of the mean. A total of 700 landings was counted. Flies landed on the discs raised at least 1 cm above the floor significantly more often than on the reference disc ( $p < 0.01$ , Student's  $t$ -test). Inset, Schematic drawing of the free flight arena. The floor and the walls of the wooden box as well as the discs and the stalks (heights not drawn to scale) were covered with the same random dot pattern (not shown)

mean relative landing frequency (Fig. 1). Since the pattern on the discs did not differ from that on the background, the landing frequency on the reference disc at 0 cm can be assumed to correspond to the mean frequency of landings on any given patch on the ground with the same area.

Flies landed on the raised discs more often than on the reference disc. Obviously, they showed a spontaneous preference for elevated objects. The landing frequency increased continuously with increasing disc height, up to a height of 3 cm. This suggests that higher discs were detected more easily, possibly because higher discs provided a stronger relative motion cue than lower ones.

However, relative motion might not be the only source of information available for disc detection under the given circumstances. Since the pixels of the closer discs have a retinal size larger than the pixels on the floor, the flies might detect the elevated discs by means of these differences. This possibility was tested in a control experiment, in which an additional disc with pixels larger than the standard size ( $6 \times 6 \text{ mm}^2$ ) was placed on the floor. The frequencies of landings on the disc with increased pixel size and the reference disc were nearly the same: 3.68% of the landings (disc with bigger pixels) vs. 3.64% (reference disc). This

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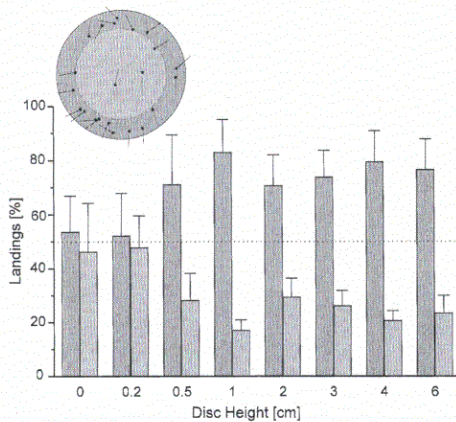


Fig. 2. Distribution of the landings in the outer (dark bars) and in the inner (light bars) regions of the discs. Error bars denote standard error of the mean. The same 20 sessions were evaluated as in Fig. 1. For analysis, the discs were divided into an inner and an outer region of the same area. For each disc height, the landings within each of the two regions were counted separately. These counts were averaged over the 20 sessions and the sum of the means of each pair was scaled to 100%. The standard errors of the mean were scaled accordingly. Significant deviations from a homogeneous distribution of landing sites can be observed on discs raised to a height of at least 0.5 cm ( $p < 0.001$ ,  $\chi^2$  test). Inset, an example of a protocol of the landings on a disc at a height of 4 cm. The position of the fly's head and the orientation of the longitudinal body axis at the instant of the landing are symbolized by a dot and a line, respectively. It should be noted that the subdivision into inner (light) and outer (dark) regions was done only after the experimental sessions

suggests that without relative motion cues, differences in pixel size on their own – at least within certain limits – do not provide the relevant cue for the detection of the discs.

In addition to the number of landings, we also recorded where the flies landed on the discs. This was performed by marking the position of the head at the instant of landing as well as the orientation of the longitudinal body axis on a protocol sheet (inset of Fig. 2). For data

analysis, the discs on the protocol sheets were partitioned into two concentric regions of the same area. The landing site was assigned according to the position of the head. If the head was on the border between the two regions the location of the body was taken as the criterion. The protocolling was carried out manually by the experimenter. Since most of the landing sites were located clearly either in the outer or in the inner sector, this method is regarded to be adequate.

On the reference disc and on the disc at a height of 0.2 cm, the flies landed about equally often in the inner and in the outer regions (Fig. 2). In contrast, at discs 0.5 cm above the ground or higher, the flies tended to land close to the edge, suggesting that these higher discs can be detected by the fly. Interestingly, and in contrast to the landing frequencies, the ratio of landings in the outer vs. in the inner region did not increase continuously with increasing disc height. Instead, it remained about the same for all heights above 0.5 cm, indicating a categorization into either "disc could be detected" or "disc could not be detected". The higher frequencies of landing in the outer region might be a consequence of the fact that the edges are visually detected on the basis of the motion discontinuities that they create in the retinal image of the moving fly.

Similar experiments on hawkmoths (*Macroglossum stellatarum*) [6] and on bees [7] have previously shown that these species use relative motion to infer depth information. The visiting frequency of hawkmoths on dummy flowers depends on the distance between flower and background in much the same way as it is the case for the fly. Bees, trained to land on randomly patterned, elevated discs are able to detect these discs if they are elevated to a height of at least 1 cm [8]. This obvious similarity in the performance of bees and flies might be surprising if one con-

siders the different strategies that bees and flies use in approaching a landing site. Whereas bees often scan the edge of a disc in slow flight before landing, flies fly around in the arena seemingly aimlessly and at high speed, before landing abruptly.

Irrespective of the differences in flight behaviour between flies and bees, it is clear that under conditions of natural, free flight both species detect camouflaged objects by sensing the apparent motion of the objects relative to the background.

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