SHORT COMMUNICATIONS

HOW HONEY-BEES KNOW THEIR DISTANCE FROM A NEAR-BY VISUAL LANDMARK

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Insects generally have eyes that are close together and lenses with a very short focal length. In consequence neither stereoscopic nor focus cues can be used to measure the distance of objects that are further than a very few centimetres. To do this insects must rely on information provided by retinal image size or by motion parallax. If an insect knows how large an object appears to be at one distance, it can use image size to compute any other object distance. This method is probably used by some male hoverflies when tracking conspecifics (Collett & Land, 1975). Bulldog ants snap at an image of constant retinal size, and so open their jaws when an appropriately sized prey object comes within range (Via, 1977). The distance of an object can also be specified by the way in which its image travels across the retina or changes size when an insect moves a known distance or at a known speed. To date only stationary locusts have been shown to exploit motion parallax, which they do by performing a specialized side-to-side head and body movement (Wallace, 1959; Collett, 1978). Very little, however, is known about the ways in which freely flying insects measure their distance from stationary objects. We were interested in studying this question in honey-bees because they clearly have a good appreciation of the arrangement of stationary features in their environment, which they will demonstrate all day long as they fly between a food source and their hive. Bees can learn to locate a source of food using near-by landmarks and to do this they must know their distance from such landmarks (Lauer & Lindauer, 1971; Anderson, 1977). In this paper we show that honey-bees use both motion parallax and image size or change in image size in determining how far they are from a single landmark.

We have used two slightly different methods. The first is an adaptation of Anderson's technique for studying landmark learning in the laboratory. A single marked bee from a hive a few metres away was trained to feed from a 1 cm diameter sucrose reservoir placed on a white painted table, 250 × 250 cm, covered with light-green scribbles to provide a stabilizing background. Exept for a narrow gap through which the bee entered, the table was surrounded by white curtains reaching to the ceiling. The bee was trained to associate the reservoir with a single cylindrical landmark placed at a constant distance on one side of the food. During training, landmark and food source were frequently shifted together across the surface of the table to persuade the bee to associate the two and to ignore other cues. After half a day
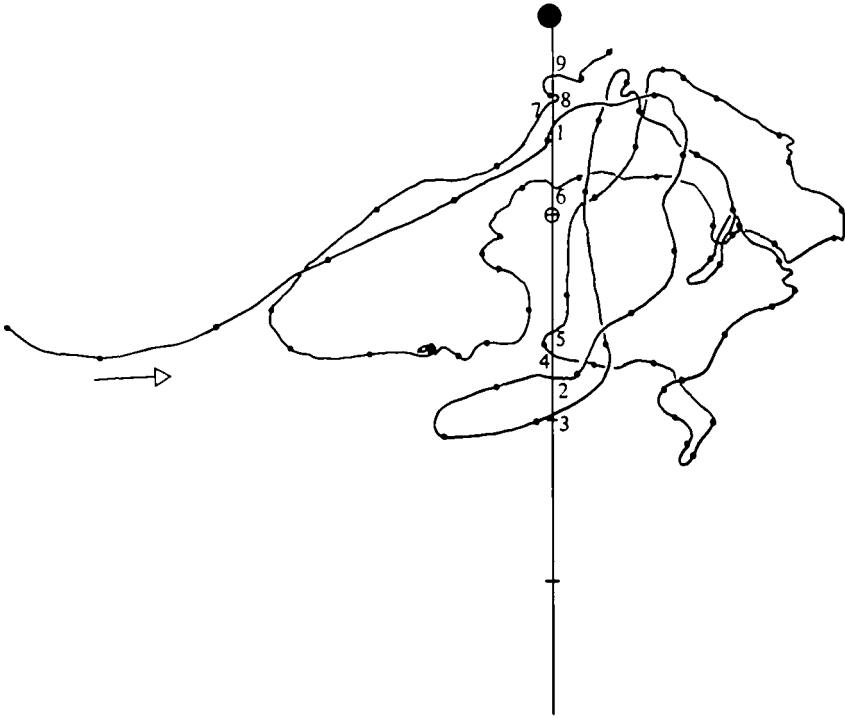
Fig. 1. Flight path of a trained bee during one test trial. Bee trained to food source placed 35 cm from landmark. The position of the bee is marked by a dot every 400 ms and numbered where it crosses the imaginary line. The open circle marks the position of the food source relative to the landmark during training and the filled circle the landmark. Horizontal lines are drawn every 35 cm. A single test lasts for ten crossings or 30 s, whichever is the shorter.

of training test trials were introduced every 30 min. The bee returned from the hive to find the landmark there but the food source absent. Its searching behaviour was recorded for 30 s using a moveable video-camera suspended on rails 2 m above the table. The reservoir was then replaced and training continued. On each trial the landmark was shifted to a new position.

During test trials the bee presumably searches an area in which it expects to find food. Since there are external cues (windows, etc.) to the direction of the food source relative to the landmark, we analysed the bee's search path by noting where it crossed an imaginary line running for 135 cm from the landmark through the point where the food source would be during training (Fig. 1). The data discussed here come from the distribution of passes across this imaginary line summed over many test trials. Fig. 2(a) shows that the distribution of passes varies with the training distance in a way that suggests that the bee can use its rather approximate knowledge of the distance between landmark and food source to guide its search.

Wehner & Flatt (1977) have shown that bees while hovering discriminate between different-sized visual patterns on the basis of retinal image and not physical size. If flying bees use this cue or change in image size to establish their distance from the landmark, then the distribution of passes will alter if the size of the landmark is changed. Reduction of landmark size will cause the distribution of passes to shift closer to the landmark and conversely a larger landmark will cause the distribution to be
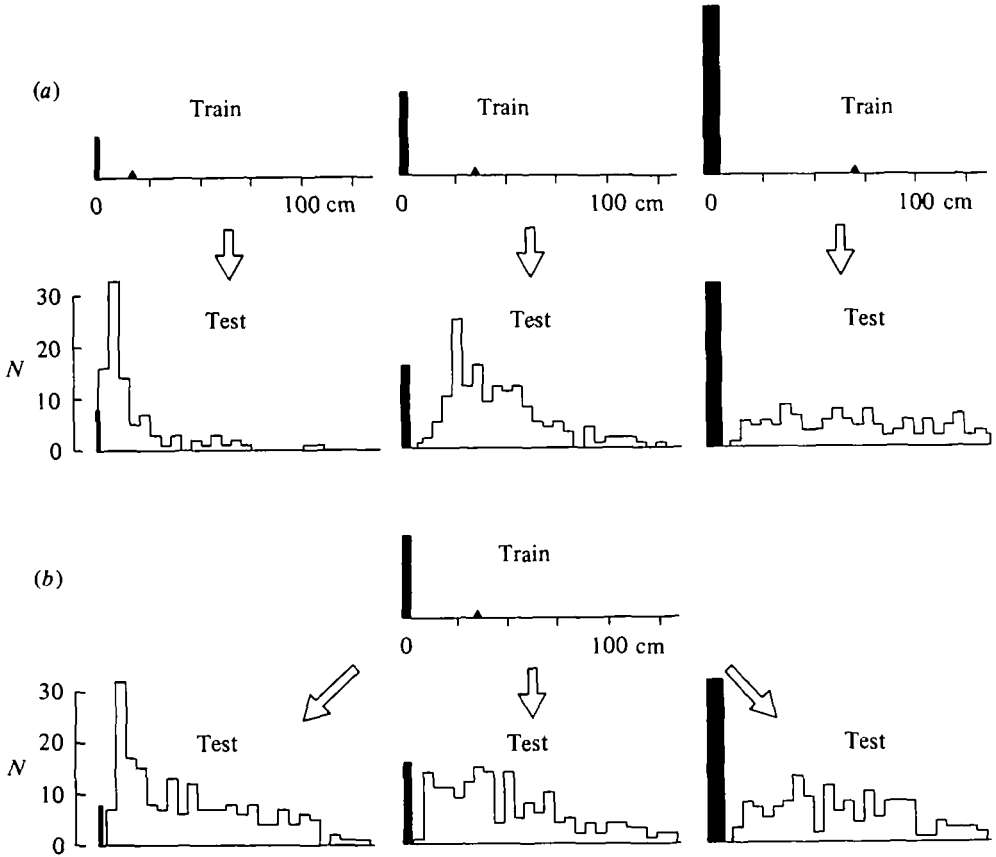
Fig. 2. Distributions of passes during test trials. (a) A bee is trained to a food source (▲) at a constant distance of 17, 35 or 70 cm from the landmark, as sketched above each distribution, and the bee is tested with the same landmark in the absence of the food source. The distributions of passes across the line are accumulated from a number of tests and are displayed as histograms. The histograms were obtained from three bees each trained to a different distance and are typical of those produced by a total of 10 bees. The forms of the distributions are a function of training distance and not landmark size. Bees have been trained to different-sized landmarks at these distances and the distributions were similar. (b) A single bee is trained to a food source 35 cm from a landmark 40 cm high and 4 cm diameter. Tests without food source employed three different landmarks sizes (20 × 2 cm; 40 × 4 cm; 80 × 8 cm). The larger the landmark, the more the distribution is pushed away from the landmark ($P < 0.01$, Jonckheere's ordered alternatives test) suggesting that this bee uses retinal image size to guide its search.

pushed away. Some bees behave in this way. Fig. 2(b) plots distributions from a bee trained to food source at a distance of 35 cm and tested with landmarks of three different sizes. There is a significant tendency for the distributions to move away from the landmark as its size is increased. Freely moving bees can thus use the retinal image size or change in image size of a landmark to guide their search.

The distributions of some bees were, however, virtually unaffected by landmark size, suggesting that these bees are guided by motion parallax, a cue which relies on image velocity (distance ∝ bee's velocity/image velocity). The best data that this is so come from experiments performed by one of us (B. A. C.) in Senegal (W. Africa) on *Apis mellifera adansonii*. In these tests bees were trained to forage for sucrose at a food source (an inverted bottle-cap, 2 cm diameter) 50 cm from a cylindrical landmark.
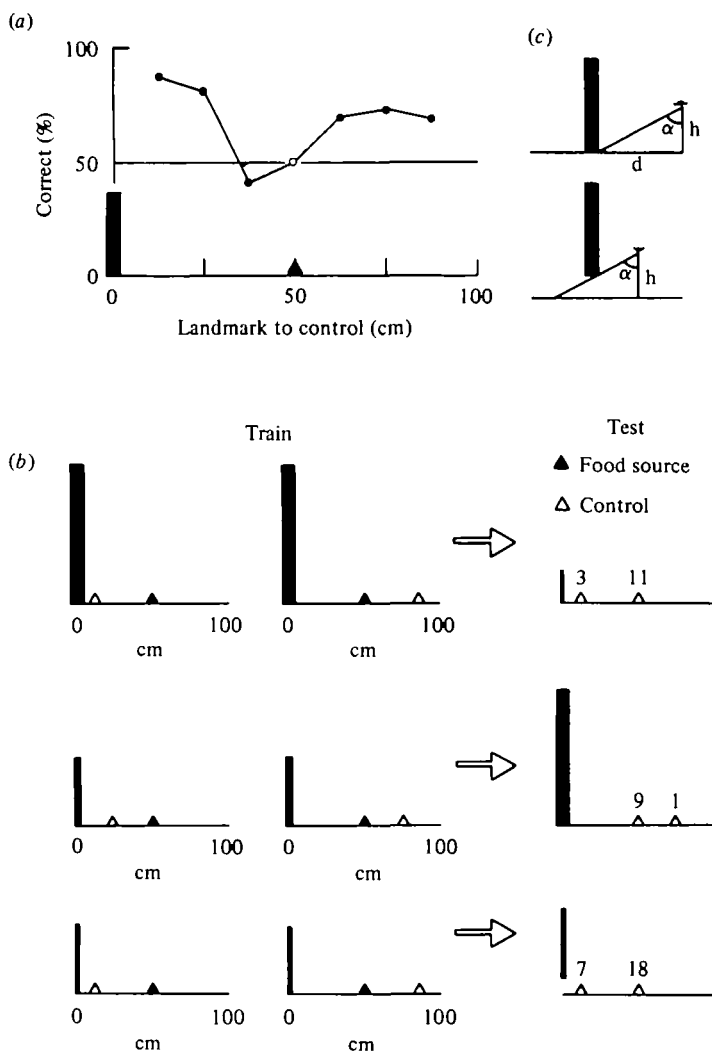
Fig. 3. Bees trained to discriminate between a food source positioned at a constant 50 cm from a cylindrical landmark and a similar control placed either nearer to or further from the landmark. (a) The percentage of correct choices is plotted against the distance between control and landmark. Each point is based on data from 100 to 200 trials. The bee becomes less accurate as control approaches reservoir. The open circle represents the distance at which the choice must be random since control and food source occupy the same position. (b) The bee is trained with the control placed at a constant distance from the 50 cm food source, nearer to the landmark on some trials and further on others in a pseudo-random sequence. Test trials are performed with two appropriately positioned controls. In the top row the bee is trained with a 90 × 12 cm landmark and tested with a 22 × 3 cm landmark. The control is 37 cm from the food source. In the middle row the bee is trained with a 45 × 6 cm landmark and tested with a 90 × 12 cm landmark. The control is 25 cm from the food source. In the bottom row the landmark is 22 × 3 cm and the distance between reservoir and control is 37 cm. Tests are with the same landmark raised 10 cm above the table. The number above each control bottle-cap shows how often the bee chose each on test trials. In all cases the bee prefers the control positioned 50 cm from the landmark (top $P < 0.05$; middle $P < 0.03$; bottom $P < 0.02$; 2-tail binomial tests), indicating that its choice is determined neither by retinal image size nor by base angle. (c) The effect of raising the landmark on the hypothesis that the bee measures distance (d) from the angle of elevation of the base of the landmark (α) and its own height (h).

nother control bottle-cap was placed at a variable distance from the landmark, either nearer or further than the food source. Bees tended to fly directly to one of the caps and soon learnt to choose correctly on significantly more than half the trials. To control for the possibility that bees were simply discriminating between baited and unbaited caps, both were frequently filled with sucrose and the bee prevented from feeding when it chose incorrectly. The adoption of this procedure did not change the distribution of choices. Fig. 3(*a*) shows how the percentage of correct choices varies with the distance between food source and control, and indicates that bees use their (surprisingly inaccurate) knowledge of the distance between landmark and food source in guiding their choice.

Every 30 min test trials were introduced in which a different-sized landmark and a pair of empty bottle-caps replaced the usual array. One cap was placed at the training distance and the other at a distance at which the landmark would appear to be the same (or nearly the same) retinal size as the one used in training. As Fig. 3(*b*) shows, the bee consistently selected the cap positioned at the training distance, indicating that image size cannot be determining their choice.

A further possibility which does not involve motion parallax is for a bee to learn the angular position of the base of the landmark when it flies at its normal cruising height (roughly 10 cm) directly above the food source (Fig. 3*c*). In this case, when the landmark is raised above the table, bees would tend to choose a cap that is considerably closer to the landmark than usual. Fig. 3(*b*) shows that this does not happen and leaves us with the conclusion that some bees must use motion parallax information to specify their distance from the landmark.

In these experiments a flying bee will be able to find its food provided that it can learn either the size of the image of a landmark or the way the image shifts across its retina, and we have found that bees are able to use either cue. However, some problems can only be solved by correlating image size with image motion. For instance, a bee can only compute the physical size of a landmark if it is able to interpret the size of its retinal image in terms of its distance from the landmark. We have been consistently unsuccessful in training bees to distinguish between landmarks on the basis of their physical size. They would not, for example, learn to fly towards the larger of two cylindrical landmarks to find an associated food source, unless the distances of the two cylindrical landmarks to find an associated food source, unless the distances of the two sistent retinal size difference. Bees may thus be unable to make the appropriate correlation between image size and image motion.

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