

SMALL-SCALE NAVIGATION IN THE HONEYBEE: ACTIVE ACQUISITION OF VISUAL INFORMATION ABOUT THE GOAL

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Summary

In a series of behavioural studies we found that bees use depth information extracted from self-induced image motion in several visual tasks involving pin-pointing the goal. Some of the results are reviewed here in an attempt to emphasise the active nature of this performance. They show that bees acquire depth information during free flight by employing two different strategies. One is to adapt flight behaviour, upon arrival at the food source, to the requirements of the task, a performance that is based on a

learning process. The other is based on a stereotyped, innate flight pattern performed upon departure from the food source. The latter has probably evolved specifically for the acquisition of depth information.

Key words: honeybee, behaviour, small-scale navigation, active vision, image motion, depth perception, colour blindness, range estimation, object-ground discrimination, edge detection, scanning, turn-back-and-look behaviour.

Introduction

The excellent learning capacity associated with the bee's foraging task has been exploited for many decades in training experiments for investigating large-scale navigation based on celestial and terrestrial visual cues (reviewed by von Frisch, 1965; Wehner, 1981), as well as small-scale orientation based on the odour, colour and shape of the target (reviewed by von Frisch, 1965; Menzel, 1985, 1990) and on the goal's position relative to nearby landmarks (e.g. Cartwright and Collett, 1979, 1983). More recently, we have employed training experiments to investigate another aspect of small-scale navigation in the bee, namely the use of cues derived from *image motion* for localising the goal. In previous work, the only motion-induced behaviour investigated in the bee has been the optomotor response to rotational motion (reviewed by Kaiser, 1975), which is an innate behaviour common to all insects that serves for maintaining the desired course of locomotion (reviewed by Wehner, 1981), rather than for pin-pointing the goal.

A major problem of visual systems is that, although the world is three-dimensional, its image on the retina is only two-dimensional. Whereas vertebrates have evolved several mechanisms for depth perception (reviewed by Collett and Harkness, 1982), such as stereoscopic vision, convergence of the eyes or accommodation of the lens, most insects lack all of these mechanisms. Thus, the bee has only two ways to estimate the distance to an object. One way is to exploit the object's apparent size (e.g. Cartwright and Collett, 1979): an object of a given size subtends a larger angle at the eye when it is near than when it is farther away. The other way is to use the speed at which the object's image moves on the eye during translational locomotion: the image of a near object moves faster than does

that of a more distant one, irrespective of the object's size. In several studies we have demonstrated that bees use the speed of image motion in a variety of tasks involving small-scale navigation. The results reviewed here show that bees acquire depth information by actively producing appropriate image motion and that they do so in two different ways.

Experiments and results

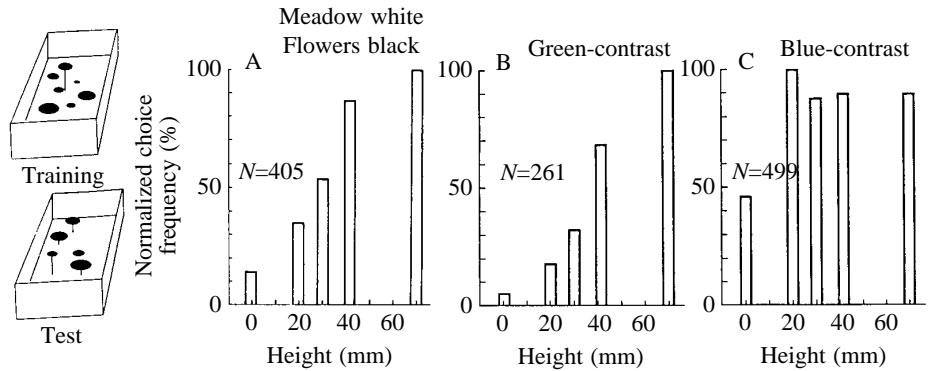
Active acquisition of depth information on arrival at the food source

Bees keep returning to a profitable food source, thus optimising their foraging strategy. Upon arrival, they recognise the food source by its odour, colour and shape. But these cues are not sufficient for safely landing on it. Pin-pointing the goal requires that its distance be known.

The use of self-induced image motion for distance estimation

To investigate the bee's use of motion cues for estimating the distance of an object (Lehrer *et al.* 1988), we had to prevent the bees from learning the object's size, because otherwise they would infer distance from the visual angle subtended by the object at the eye (see Introduction). We trained bees to collect food on a white meadow surrounded by a white wall. Six black discs of different sizes, each carrying a drop of tapwater, were placed flat on the ground, while one disc, placed on a thin stalk 70 mm above the ground, offered a reward of sugar water (Fig. 1, upper left-hand panel). The positions of all seven discs were varied after every rewarded visit, and at the same time the size of the rewarded disc was varied. Thus, the only cue

Fig. 1. The use of size-independent cues for range discrimination. Insets to the left show the training and test situations. During training, the rewarded disc was placed 70 mm above the ground. Sizes and positions of all discs were varied between rewarded visits. In the tests, no reward was offered. Proportions of landings recorded during tests (ordinate, normalised to highest response) are shown as a function of the height of the test disc (abscissa). (A) Black discs on a white ground, containing contrast visible to all three spectral photoreceptor types. (B) As in A, but blue discs on a yellow ground. Contrast was detectable exclusively by the green-sensitive receptors. (C) As in B, but contrast visible to the green-sensitive receptors was absent. N = total number of landings. The results show that bees discriminate range irrespective of disc size and that this performance is colour blind, being mediated exclusively by the green-sensitive receptors. After Lehrer *et al.* (1988).



which could be used by the bees for identifying the rewarded disc was its height above the ground, which was the only parameter that was kept constant.

In subsequent tests, five discs of five different sizes, none rewarded, were offered at five different heights (Fig. 1, bottom left-hand panel). In these tests, the distribution of the bees' landings among the five discs was strictly correlated with the discs' heights (Fig. 1A). Consequently, bees can infer distance even in the absence of size cues, showing that the speed of image motion is sufficient to cope with this task. Frame-by-frame analyses of flight trajectories video-recorded during some of the tests revealed that the trained bees approach perpendicular to the discs' boundaries (see Fig. 3 in Srinivasan *et al.* 1989), thus maximising the amount of translational image motion.

Repeating the experiment using blue discs on a yellow ground that offered contrast detectable exclusively by the green receptors (Fig. 1B), we obtained similar results. However, in the absence of green contrast, range discrimination broke down (Fig. 1C). (For details of calculations of receptor-specific contrasts, see Srinivasan and Lehrer, 1988.) This finding corroborates the conclusion that image motion is involved, because, like the optomotor response (Kaiser and Liske, 1974), all of the motion-dependent behaviours investigated by us in the bee (reviewed by Lehrer, 1993a) are colour blind, being mediated exclusively by the green-sensitive photoreceptor (see also Concluding remarks).

Using a modified set-up we were able to train bees not only to the highest disc, but also to the lowest one or to one placed at an intermediate height (Srinivasan *et al.* 1989). Thus, the preference for the highest disc manifested in Fig. 1 is not simply a consequence of a spontaneous preference for fast-moving objects (Erber, 1982; Lehrer and Srinivasan, 1992), but rather of the bee's ability to distinguish among various speeds of image motion.

The use of self-induced image motion for object-ground discrimination

The results described above inspired us to investigate the bee's use of image motion in another task that is relevant to

pin-pointing the goal, namely object-ground discrimination (Srinivasan *et al.* 1990). We trained bees to collect sugar water from a randomly patterned figure placed 5 cm above a

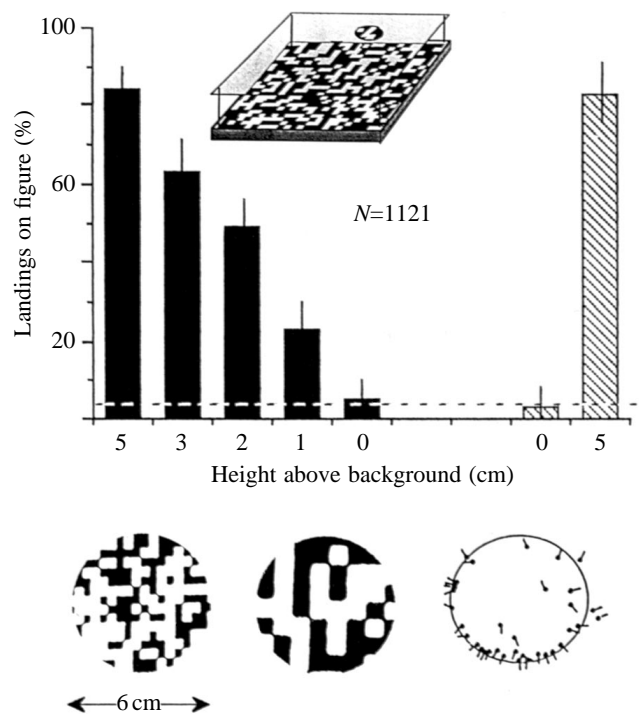


Fig. 2. Figure-ground discrimination. Top panel shows training and test situations. The bar histogram shows the proportion of landings on the figure (ordinate) as a function of its height above the ground (abscissa). Black bars denote a situation in which the figure (inset bottom left) carried the same pattern as the ground. Hatched bars denote a situation in which the figure carried a much coarser pattern (inset bottom middle). The dashed line depicts random-choice level. N = total number of landings. Error bars are standard deviations of the mean values calculated from the results of all tests. Inset at bottom right is an example showing that landings occur perpendicularly to the disc's boundaries. (Dots denote the bee's head position, dashes the orientation of her longitudinal axis.) The results show that bees use motion parallax cues in this task. After Srinivasan *et al.* (1990).

similarly patterned ground (Fig. 2) and found that the trained bees cannot detect the figure when it is placed flat on the ground (0 cm in Fig. 2), whether or not the pattern on the figure differs from that on the ground. However, when the figure is raised above the ground, it is detected better the higher it is placed (Fig. 2). Consequently, bees use motion parallax information in this task. Analyses of video recordings made during several tests revealed that the bees land on the figure in directions perpendicular to its boundaries (Fig. 2, right-hand inset at bottom), thus, again, maximising translational image motion.

The use of self-induced image motion for edge detection

In a more recent study (Lehrer and Srinivasan, 1993), we trained bees to collect sugar water at an edge between two randomly patterned surfaces, one raised above the other (Fig. 3). All of the tests were video-recorded from above. Evaluation of the video tapes showed that 88% of all landings on the edge occurred facing the raised surface (Fig. 3). In addition, the majority of bees flying towards the raised surface landed, whereas bees flying in the opposite direction mostly crossed the edge without landing on it (see landings/crossings

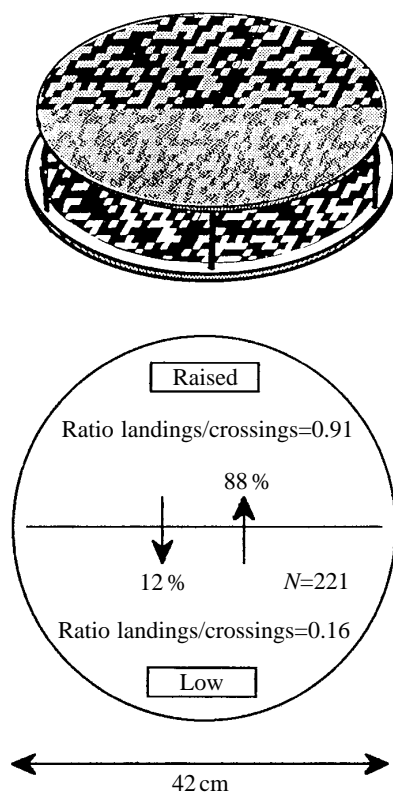


Fig. 3. Detection of an edge between a low and a raised randomly textured surface. The experimental set-up is shown in the top panel. The bottom panel shows the proportion of landings that occur during crossings of the edge from the low to the raised side and from the raised to the low side (arrows; N = total number of landings). The ratio of landings to crossings for the two flight directions is shown as well. Landing on the edge is triggered by a change from slow to faster image motion. After Lehrer and Srinivasan (1993).

ratios in Fig. 3). Because with the randomly patterned surfaces, the speed of motion perceived from the raised side of the edge (that is nearer to the bee) is higher than that perceived from the low side, we concluded that the edge elicits landing when the bee perceives a change from slow to faster image motion, but not when the change is from fast to slower motion. The conclusion that motion cues are involved in this task is corroborated by the results of an earlier study which showed that edge detection is green-sensitive and colour blind (Lehrer *et al.* 1990).

In the next experiment, we used linear gratings rather than random patterns (Fig. 4A,B). With this set-up, unlike the previous one, the speed of image motion depends on the bee's flight direction, because flight *parallel* to the contours will produce no image motion, in which case the bee would be unable to tell which side of the edge is nearer. Even in this experiment (Lehrer and Srinivasan, 1993), the majority of the landings occurred facing the raised surface (Fig. 4C), from which we concluded that flight was *not* parallel to the stripes.

Indeed, frame-by-frame analysis of the bees' flight directions in several hundred video-recorded flight trajectories

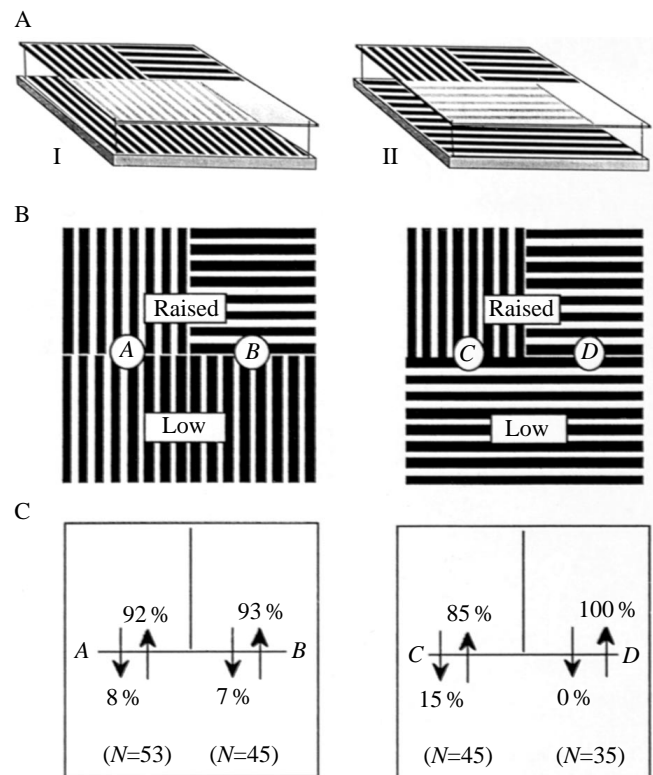


Fig. 4. Detection of an edge between a low and a raised surface carrying linear gratings. (A) View of the experimental set-up. During training as well as tests, bees were presented alternatively with two situations, I and II. (B) Definition of types of edge. (C) Percentages of landings on each type of edge in either direction (arrows), as revealed by evaluation of video recordings. N = total number of landings. The results show that image motion is used even in this case, suggesting that bees avoid flight parallel to the contours of the stripes. After Lehrer and Srinivasan (1993).

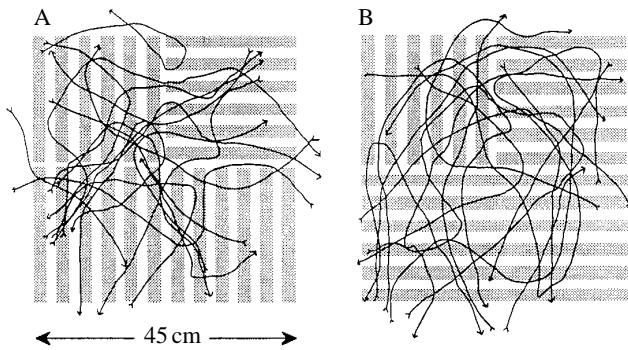


Fig. 5. (A,B) Examples of flight trajectories of bees video-recorded from above in situations I and II shown in Fig. 4A. Each trajectory is represented by a line connecting the bee's head positions in successive frames of the video tape. Shaded bars depict the orientation of the stripes (not to scale). A detailed quantification of the flight directions is given in Table 1 (late tests). The results show that bees avoid flight parallel to the stripes. From Lehrer and Srinivasan (1994).

(examples in Fig. 5) revealed that in only 12% of the frames did the bees fly parallel to the contours of the stripes.

The bees' scanning behaviour

The findings that bees avoid contour-following in the edge detection task and that they approach the target's boundaries in perpendicular directions in the distance estimation and the object-ground discrimination tasks are in strong contrast to earlier results obtained in a study concerning pattern discrimination. In that study (Lehrer *et al.* 1985), evaluation of video-recorded flight trajectories showed that bees follow the contours of the patterns in front of which they are flying (Fig. 6). This behaviour, which we termed 'scanning', is innate to the bee and is not subject to habituation, i.e. bees follow the contours contained in the pattern irrespective of whether they have previously been trained to it (Fig. 6B) or see it for the first time (Fig. 6C).

Why was the scanning behaviour absent in the edge detection task? One reason could be that in the latter the patterns were presented on a horizontal plane (see Fig. 4), whereas in the pattern discrimination experiments they were placed on a vertical plane (Fig. 6). Differences in visual performance among different eye regions were indeed found in several visual tasks, such as shape recognition (Wehner, 1972) and spatial localisation (Lehrer, 1990). Another

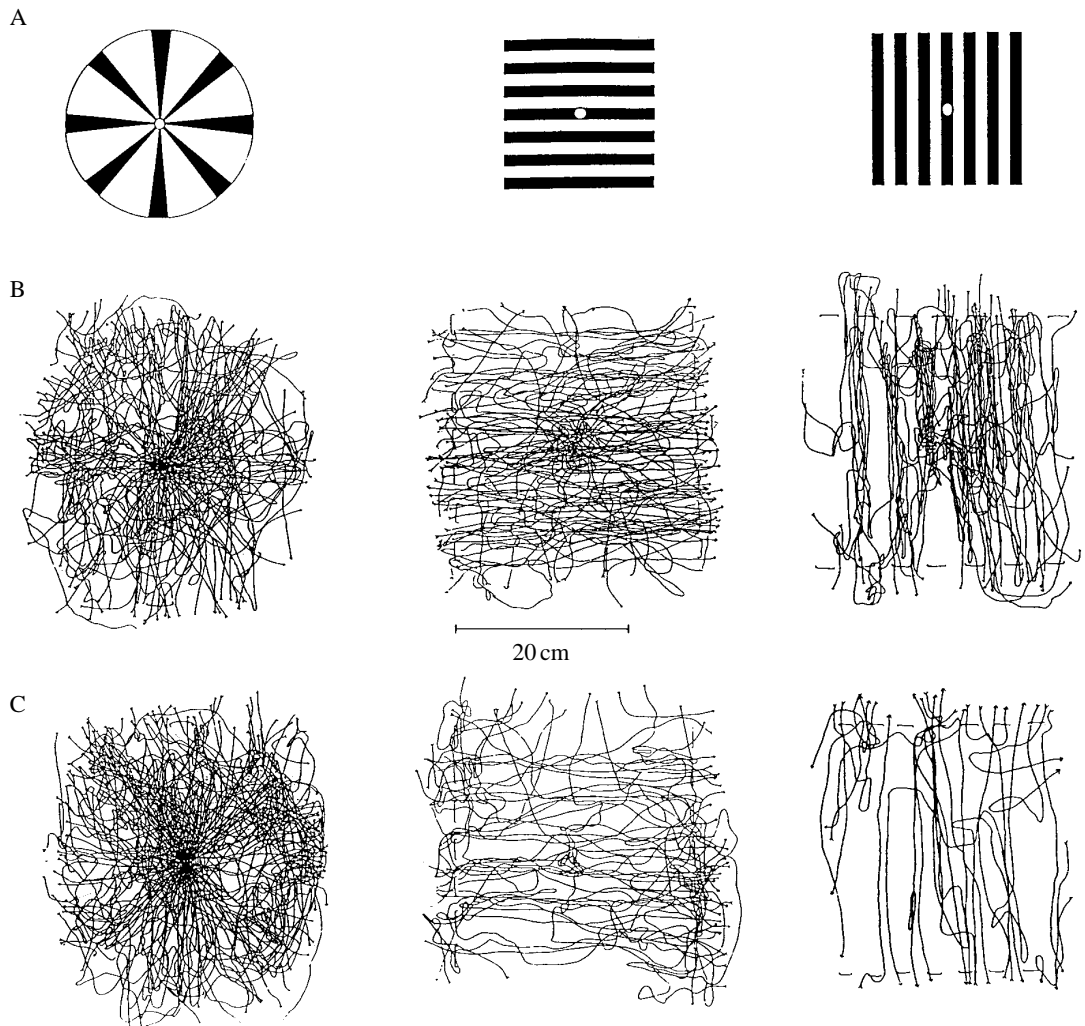


Fig. 6. The bees' scanning behaviour. (B,C) Evaluation of video recordings of bees flying in front of the black-and-white patterns (A) presented on a vertical plane. (B) Flight trajectories of bees video-recorded after they have collected 30–50 rewards from a tube penetrating the centre of the pattern. (C) Flight trajectories of bees presented with the same pattern for the first time. The results show that bees tend to follow the contours contained in the patterns and that this behaviour does not habituate as training proceeds. After Lehrer *et al.* (1985).

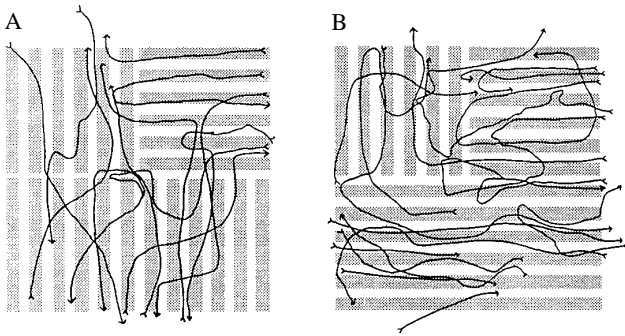


Fig. 7. As in Fig. 5, but bees were video-recorded on their first few visits to the experimental set-up. A detailed quantification of the flight directions is given in Table 1 (early tests). The results show that the scanning behaviour is not restricted to the frontal eye regions. From Lehrer and Srinivasan (1994).

Table 1. *Frame-by-frame evaluation of flight directions*

Flight direction	Early tests	Late tests
Oblique	16 %	74 %
Perpendicular	9 %	14 %
Parallel	75 %	12 %
Number of frames analysed	850	4000

Proportions of flight directions relative to the orientation of the stripes (see Fig. 4) are shown for the initial phase of training (early tests, Fig. 7) and for tests after approximately 30 rewarded visits (late tests, Fig. 5). It is evident that, during the course of the training, the bees learn to select a flight strategy that enables them to extract depth information from image motion. After Lehrer and Srinivasan (1994).

explanation would be that pattern discrimination does not require the use of image motion (Srinivasan *et al.* 1993), whereas the detection of camouflaged edges does.

Modification of flight behaviour based on a learning process

To decide between the two possibilities we repeated the experiment of Fig. 4, this time filming the bees during their *first* few visits to the experimental set-up, i.e. before they have had the chance to learn about the nature of the task (Lehrer and Srinivasan, 1994). Several examples are shown in Fig. 7. These bees followed the contours in 75 % of the frames, showing that scanning is not restricted to the frontal eye regions. A direct comparison between the bees' flight behaviour early in the training and later on (Table 1) shows that, as training continues, the bees learn to suppress the innate scanning behaviour and select, instead, a flight strategy that enables them to acquire depth information.

Active acquisition of depth information based on an innate flight behaviour

In the previous section, active acquisition of depth information required the suppression of an innate motor programme: the bee adapted her flight pattern such as to obtain

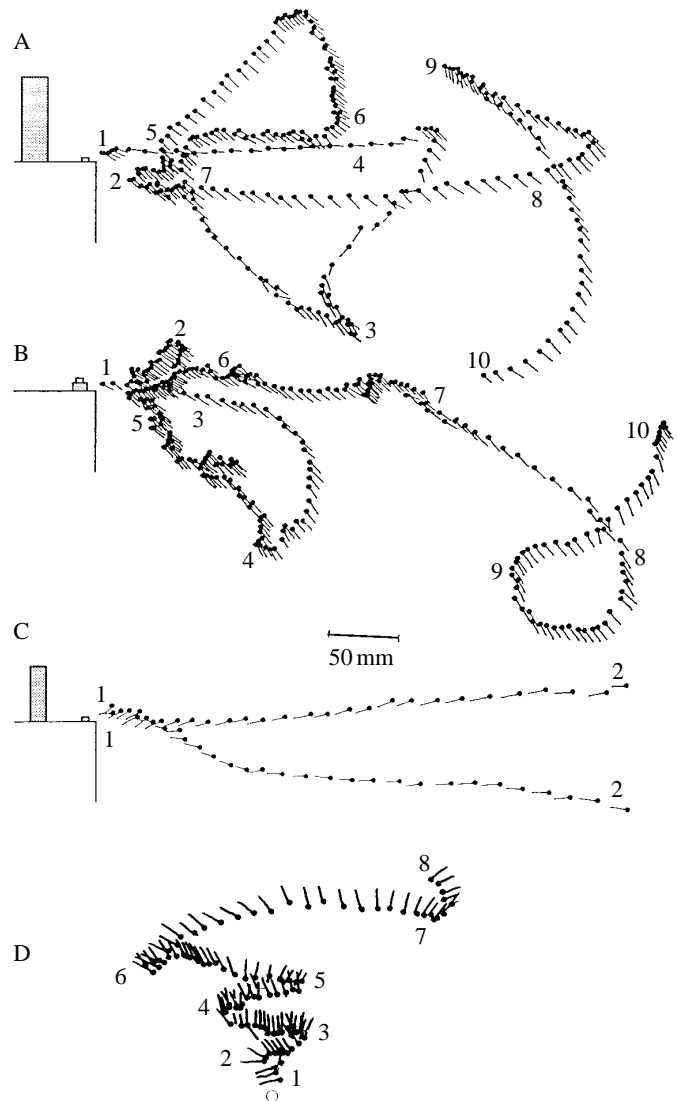


Fig. 8. The turn-back-and-look behaviour (TBL). Video-recordings of bees departing from a novel food source after feeding. Dots denote the bee's head position, dashes the orientation of her long axis in successive frames of the video tape. Numbers placed along the trajectories denote the direction of flight: low numbers at the start of flight and high numbers later in the flight. (A–C) Recordings from the side. The feeding dish, with a mark (shaded) associated with it, is placed near the edge of a table. In C, two bees leave the food source after the TBL phase (see text) has ended. In D, a bee leaving a food source (small circle) is filmed from above. A–C after Lehrer (1993b), D after Lehrer and Collett (1994).

the information that she needed. The present section is concerned with active acquisition of depth cues by means of an innate, specialised flight pattern.

The bees' turn-back-and-look behaviour

When bees depart from a newly discovered feeding place, they turn around to look at the food source prior to flying home (Fig. 8A,B,D), a behaviour we termed 'turn-back-and-look', abbreviated TBL (Lehrer, 1991). TBLs are performed on every

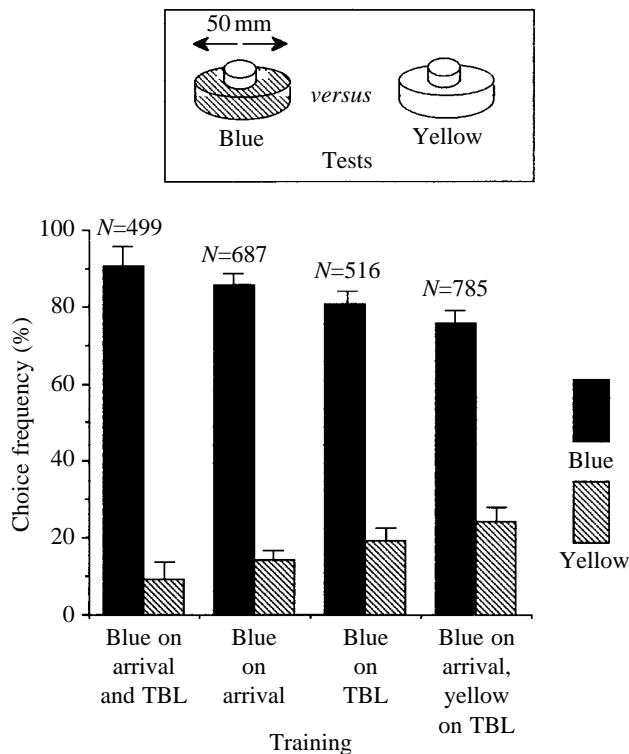


Fig. 9. The role of the TBL in a colour learning task. A small transparent feeding dish was placed on a blue model flower. Individual bees were trained in one of four different modes (abscissa). In one, the blue flower was present on both arrival and departure. In the second, the blue flower was present on arrival, but was removed from under the feeding dish while the bee was feeding. In the third, only the feeding dish was present when the bee arrived, but it was placed on the blue flower while she was feeding. In the final mode, the blue flower was viewed on arrival, but was replaced by a yellow flower while the bee was feeding. In the tests, conducted at the end of the TBL phase, each bee had to choose between the blue and the yellow flower (inset), irrespective of the training mode. The percentages of choices for the blue and the yellow flower are depicted by the black and shaded bars, respectively. Error bars are standard deviations of the mean values calculated from the results of the individual bees. N = total number of choices. The results show that bees learn the colour of a flower either exclusively on arrival or exclusively during the TBL, depending on the training mode. However, when learning on arrival is placed in competition with learning on departure, the former dominates over the latter. After Lehrer (1993b).

departure on 3–8 successive visits during the initial phase of training, termed the TBL phase. Once the TBL phase is over, the bee departs without looking back (Fig. 8C).

Why do bees turn back and look?

Investigating the possible function of TBL (Lehrer, 1991, 1993b), it was found that bees that can see the food source exclusively during TBLs learn its colour as reliably as bees that can see it exclusively on arrivals (Fig. 9). However, when bees are offered one colour on arrival and a different one on departure, they prefer, in subsequent tests, the colour learned

on arrival to that learned on departure (Fig. 9). Very similar results were obtained when learning involved the shape of the food source or the colour or shape of a landmark: the stimulus learned on arrival always dominated over the one learned during the TBL. From these findings, it was concluded that the TBL does not serve *primarily* for learning colour or shape (Lehrer, 1993b). Does it, perhaps, serve for acquiring depth information?

Acquisition of depth cues on departure from the food source

To examine this question, we trained individual bees to a cylinder of a fixed size placed at a fixed distance from the food source (Lehrer and Collett, 1994) (Fig. 10A, left-hand panel). Half of the bees could see the cylinder exclusively on departure (it was introduced *after* the bee had landed) and half could see it exclusively on arrival (it was removed *after* the bee had landed). At the end of the TBL phase, the bees were tested with two larger cylinders, one placed farther away, where it had the correct angular size, and the other at the correct distance, where it had the wrong size (Fig. 10A, middle panel). Bees trained on arrival preferred the cylinder of the correct size, whereas bees trained on departure preferred the one at the correct distance (Fig. 10A, right-hand panel). Very similar results were obtained from bees trained to a large cylinder and tested with two smaller ones (Fig. 10B). These and further results (Lehrer and Collett, 1994) show that, by performing TBL behaviour, bees acquire depth information.

Concluding remarks

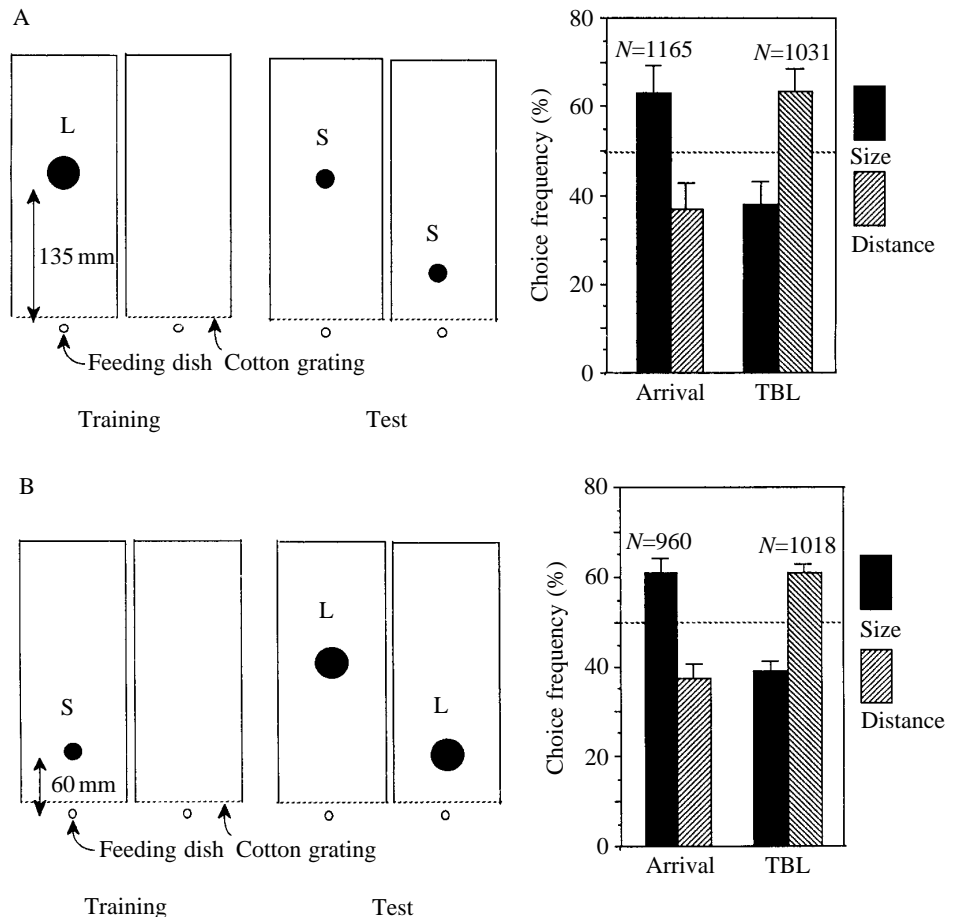
Despite the fact that every type of locomotion is bound to produce image motion at the eye, acquisition of depth information is not a trivial by-product of locomotion *per se*. Small-scale navigation, as opposed to large-scale navigation, does not bring the animal to new places, but rather serves for pin-pointing the goal once the animal has arrived at the relevant site.

Suppression of innate motor programmes

The results reviewed here show that, during small-scale navigation, bees *actively* produce the type of image motion that is needed for acquiring depth information, even when the task requires suppression of an otherwise innate flight pattern displayed in a different behavioural context. The bee's ability to select particular visual cues and to neglect others in the context of different visual tasks is discussed in more detail elsewhere (Lehrer, 1994).

The suppression of the innate scanning behaviour is only one example of the flexibility of the bee's motor programmes. In earlier studies, we found that bees also suppress the optomotor response once they have learned that it interferes with their ability to fly on a straight course to their goal (Srinivasan *et al.* 1991) or to land at their target (Lehrer and Srinivasan, 1992). Even the fly *Drosophila melanogaster*, whose learning capacity is rather poor compared with that of the honeybee, has been shown to suppress the optomotor

Fig. 10. The use of either absolute distance or apparent size of a landmark in the task of pin-pointing the target. During training, bees could see the mark either exclusively on arrival or exclusively on departure (abscissa). Tests were conducted at the end of the TBL phase. (A) Bees trained with a large cylinder (L; left-hand panel) and tested with two smaller ones (S; middle panel). The proportions of the bees' choices between the correct angular size (black bars) and the correct absolute distance (shaded bars) are shown in the right-hand panel. Dashed line depicts random-choice level. N = number of choices. (B) Same as in A, but bees were trained with the small cylinder and tested with two large ones. The results show that the TBL serves for acquiring size-independent cues to distance. After Lehrer and Collett (1994). Error bars are standard deviations of the mean values calculated from the results of the individual bees.



response when required to fixate a visual stimulus in a particular eye region (Heisenberg and Wolf, 1992). In all of these examples, however, the suppression of the optomotor response had nothing to do with the acquisition of depth information.

Colour blindness of motion-dependent responses

The colour blindness of the optomotor response (Kaiser and Liske, 1974), as well as of the motion-dependent responses investigated by us (reviewed by Lehrer, 1993a), does not imply that every green-sensitive, colour-blind behaviour is motion-dependent. The conclusion that distance estimation, object-ground discrimination and edge detection are based on cues extracted from image motion is derived from the fact that no alternative cue could be used by the bees in these experiments. The finding that all of these behaviours are green-sensitive does not exclude the possibility that the green receptor might play an important role even in motion-independent tasks (Srinivasan and Lehrer, 1988; see also Srinivasan *et al.* 1996). However, an *exclusive* role of the green receptor in tasks that do not involve motion perception has not been demonstrated so far. Thus, the colour blindness of behaviours in which motion stimuli are involved can serve to corroborate the conclusion that these behaviours are, indeed, motion-dependent.

Active acquisition of depth information

A comparison between the bees' performance in the tasks of range discrimination (Fig. 1), figure-ground discrimination (Fig. 2) and edge detection (Fig. 3), on the one hand, and their performance in the turn-back-and-look behaviour (Fig. 10), on the other hand, shows that, for actively acquiring depth information, the bee has evolved two distinct strategies that differ from each other with respect to three properties. (i) *The role of learning.* Whereas modification of flight behaviour requires previous experience with the task at hand, the turn-back-and-look behaviour does not. (ii) *The timing of acquisition.* In the case of TBL, depth information is acquired on departure, whereas in the other tasks described here it is acquired during the arrival and landing phase. The latter conclusion is derived from the finding that, in the initial phase of training (which coincides with the TBL phase), the bees have not yet learned about the nature of the task. (iii) *The use of the information.* In range discrimination, figure-ground discrimination and edge detection, depth information is needed on every visit to the feeding site, because otherwise the bee would find neither the goal nor the food. Distance information acquired during the TBL, however, is used only in the initial phase of visiting the novel feeding site. Experienced bees arriving at a familiar food source use the size of the landmark as a cue to distance (Cartwright and Collett, 1979; Lehrer and

Collett, 1994). Lehrer and Collett (1994) propose that cues to distance are particularly important in the initial phase of learning, because near landmarks are more useful for pin-pointing the goal than are more distant ones. Thus, the insect must first of all determine which marks are near and should, therefore, be memorised.

A look at other insect species

As far as acquisition of depth information in insects is concerned, modification of motor patterns based on a learning process has only been reported for the honeybee. As opposed to this learned behaviour, *innate* behaviours that might serve specifically for acquiring depth information have been reported for several other insect species. For example, wasps (*Vespa vulgaris*) which keep returning to an artificial food source perform, on their initial 3–5 departures, TBLs similar to those performed by our honeybees (Collett and Lehrer, 1993). Locusts perform a peering behaviour, swaying from side to side prior to jumping to their goal (Wallace, 1959; Collett, 1978; Sobel, 1990), and so do mantids prior to walking (Horridge, 1988). Both of these motor patterns have been shown to serve for distance estimation. Several hymenopteran species, such as the digger wasp *Bembix rostrata* (van Jersel and van Assem, 1964), the sphecid wasp *Cerceris rybyensis* (Zeil, 1993a,b) and two species of ground-nesting bees, *Lasioglossum malachurum* and *Dasyglossa hirtipes* (Brünnert *et al.* 1994), have been reported to perform so-called orientation flights at the nest entrance prior to leaving for a foraging trip. These stereotyped flight patterns have been shown to mediate the acquisition of size-independent cues to the distance of nearby landmarks (Zeil, 1993b; Brünnert *et al.* 1994; see also Zeil *et al.* 1996). Little is known, however, about the behaviour of these insects at the foraging site. It is conceivable that the bee's capacity to modify flight patterns according to the requirements of the task is not unique. Other insects might have evolved, in addition to the stereotyped orientation flight reported so often, a second mechanism for actively acquiring depth information, one that requires previous experience with the food source and is thus based on a learning process.

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