

VISUALLY MEDIATED ODOMETRY IN HONEYBEES

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Summary

The ability of honeybees to gauge the distances of short flights was investigated under controlled laboratory conditions where a variety of potential odometric cues such as flight duration, energy consumption, image motion, airspeed, inertial navigation and landmarks were manipulated. Our findings indicate that honeybees can indeed measure short distances travelled and that they do so solely by analysis of image motion. Visual odometry seems to rely primarily on the motion that is sensed by the lateral regions of the visual field. Computation of distance

flown is re-commenced whenever a prominent landmark is encountered *en route*. ‘Re-setting’ the odometer (or starting a new one) at each landmark facilitates accurate long-range navigation by preventing excessive accumulation of odometric errors. Distance appears to be learnt on the way to the food source and not on the way back.

Key words: honeybee, visual odometry, navigation, flight distance, image motion, landmark.

Introduction

It is well known that honeybees can navigate accurately and repeatedly to a food source, as well as communicate to their nestmates the distance and direction in which to fly to reach it (for a review, see von Frisch, 1993). It is also well established that honeybees infer the direction of their flight by making use of the celestial compass (for reviews, see von Frisch, 1993; Wehner, 1992). However, the cues by which they gauge the distance flown to the goal have been a subject of controversy. Early studies suggested that this distance is measured in terms of the total energy expended during flight (von Frisch, 1993; Heran and Wanke, 1952; Heran, 1956). But recent findings question this hypothesis (Neese, 1988; Goller and Esch, 1990; Esch *et al.* 1994) and suggest that an important cue is the amount of image motion experienced by the honeybee’s visual system on the way to the target (Esch and Burns, 1995, 1996; Schöne, 1996; Srinivasan *et al.* 1996).

In principle, there are a number of ways in which a flying insect could keep track of how far it has travelled. These include monitoring the duration of flight, counting wingbeats, measuring energy consumption, sensing and integrating airspeed, integrating the image motion experienced by the eye, using some form of inertial navigation involving sensing and integrating the accelerations of the animal, and using reference landmarks along the way. Here, we investigate the ability of honeybees to gauge short distances flown under strictly controlled laboratory conditions where a variety of potential,

distance-signalling cues are manipulated. A preliminary account of this work is given in Srinivasan *et al.* (1996).

Materials and methods

In each experiment (unless otherwise specified), 10–15 honeybees (*Apis mellifera*) were trained in a large indoor flight room to fly into a tunnel 3.2 m long, 22 cm wide and 20 cm high to find a reward of sugar water placed at a fixed location (Fig. 1A). The walls and floor of the tunnel were lined with black-and-white stripes of period 4 cm, oriented perpendicular to the axis of the tunnel. In some experiments, the period of the stripes was changed, the stripes were oriented axially, or the tunnel was lined with a randomly textured, black-and-white Julesz pattern of pixel size 1 cm. The tunnel was covered by a transparent ceiling of Perspex. During training, the position and orientation of the tunnel were changed frequently to prevent the honeybees from using external landmarks to gauge their position in the tunnel.

The honeybees were subsequently tested individually in an identical, fresh tunnel which carried no reward. Typically, the honeybees flew back and forth along the tunnel, making a number of U-turns as they searched for the reward (Fig. 1B). For the purposes of analysis, the tunnels were subdivided into 16 units, each 20 cm long (Fig. 1B). In the tests, the searching behaviour of the bee was quantified by recording visually the unit numbers x_1 , x_2 , x_3 and x_4 in which she made the first,

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second, third and fourth U-turns respectively (Fig. 1B). The average of the four values provided an estimate of the mean search position (\square). The spatial distribution of the search (depicted by the histogram in Fig. 1C and by the curves in subsequent figures) was estimated by measuring the number of times the bee entered each unit during the period over which the first four U-turns were made.

For each test, the mean and the standard deviation (S.D.) of the search position were calculated as the mean and S.D. of x_1 , x_2 , x_3 and x_4 measured for a number of flights (N). Student's t -tests were used to test for the statistical significance of the difference between the expected and the experimentally measured search positions, as well as the difference between search positions measured in different experiments. The F -test was used to test for differences in S.D. between different experiments.

Results

Honeybees were trained to fly to a fixed reward in a striped tunnel, as described in Materials and methods and illustrated in Fig. 1. The walls and floor of the tunnel were lined with a pattern of black-and-white stripes. The bees were then tested by recording their searching behaviour in a fresh tunnel, which carried no reward and was devoid of any scent cues. The searching behaviour of the trained honeybees was analysed as described in Materials and methods. The trained bees showed a clear ability to search for the reward at the correct distance from the tunnel entrance (Fig. 2A, squares). The mean search position was not significantly different from the position of the reward (unit 9) during training ($P > 0.30$). The search distribution under these conditions typically exhibited a half-width of 4 units (80 cm), but this is likely to be an overestimate of the bees' error in distance judgment because the distribution reflects the boundaries of the region that is searched by the bee when the reward is absent. Supplementary experiments, in which training and testing were carried out with the entire tunnel situated inside a long, white featureless tent, yielded very similar results.

How were the honeybees gauging the distance flown into the tunnel? A number of experiments were carried out to unravel the cues that they were using.

Cues based on the appearance of salient landmarks

Were the bees gauging their position in the tunnel by using the visual angle subtended by the entrance or the end wall? As a bee moves further into the tunnel, the entrance subtends a progressively smaller angle, and the end wall a progressively larger one. To investigate this possibility, we trained bees as in Fig. 1A and tested them in situations in which the entrance aperture to the tunnel was made smaller or where the length of the tunnel was extended. We found that the trained bees searched at the correct distance from the tunnel entrance, regardless of these manipulations (Fig. 2B). These results eliminate the possibility that the bees were gauging their position in the tunnel by using the visual appearance of salient

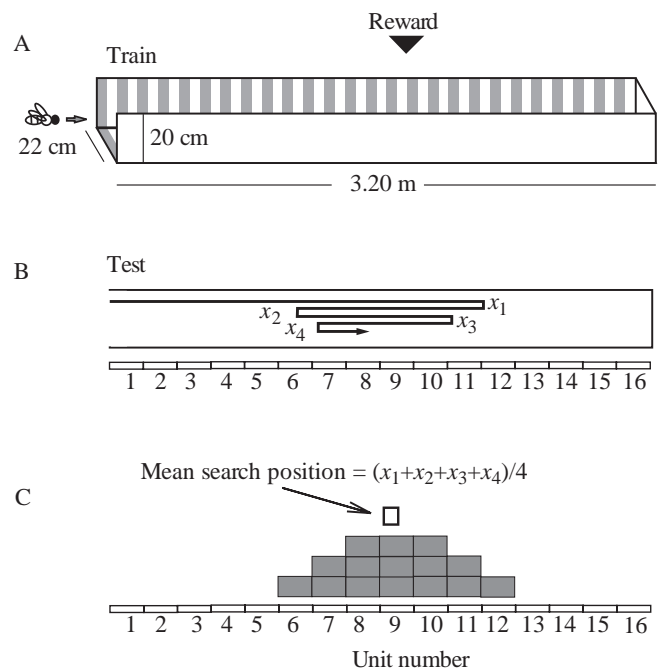


Fig. 1. Honeybees, trained to find a reward in unit 9 of a training tunnel (A), were subsequently tested in a variety of tunnels that carried no reward. The searching trajectories of the trained bees were quantified and analysed (B,C) as described in Materials and methods. In all subsequent figures, the filled arrowhead indicates the former position of the reward, the curve shows the spatial distribution of the search, and the symbol above the curve indicates the mean search position.

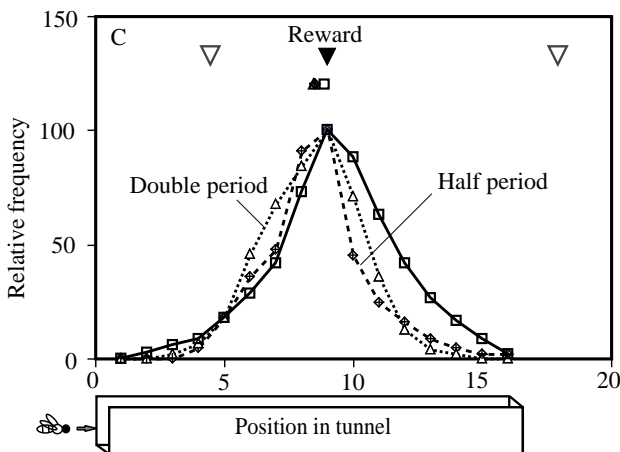
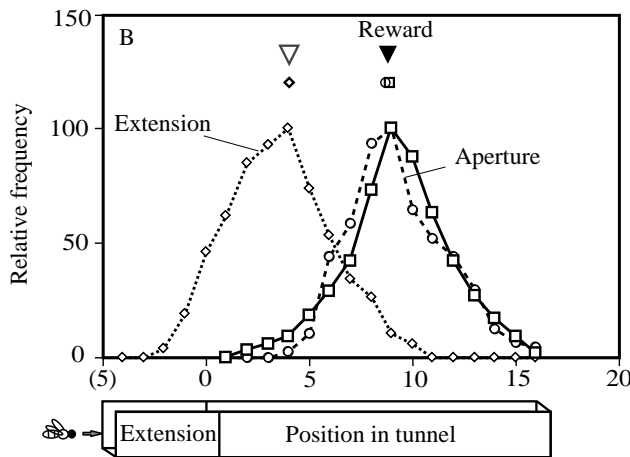
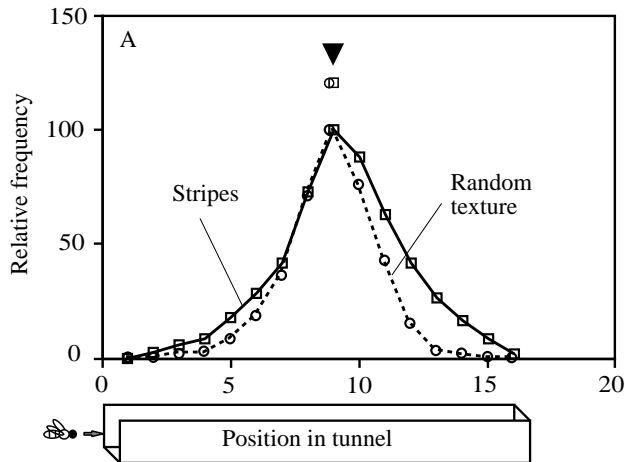
features within it. They do suggest, however, that the bees were using the tunnel entrance as a reference landmark from which to commence the measurement of distance.

Cues based on counting features en route

Were the bees gauging the location of the reward by counting the number of stripes or other features passed whilst flying through the tunnel? This is an intriguing possibility, especially in the light of recent evidence that honeybees exhibit a capacity for 'counting' objects *en route* to a target (Chittka and Geiger, 1995). We found, however, that bees trained as in Fig. 1A searched at the correct distance from the tunnel entrance even when the number of stripes lining the tunnel was altered in tests (Fig. 2C). This eliminates stripe-counting as a means of estimating distance flown in our experiments.

The above conclusion was confirmed by a different experiment in which we trained bees to find a feeder in a tunnel lined with a random (Julesz) pattern. Since such patterns are not periodic, they preclude the use of cues based on counting a succession of features. We found that the trained bees searched at the correct distance even in the randomly textured tunnel, displaying an accuracy comparable with that obtained with the striped patterns (Fig. 2A, circles). In this experiment, the test tunnel carried a different random pattern with the same statistical properties as the pattern in the

training tunnel. The test pattern was produced by using a different seed for the random number generator which created the random texture. Since the pattern in the test tunnel was different from that in the training tunnel, the bees could not have used the structure of the pattern in the vicinity of the reward during training as a cue to help them locate the former position of the reward.



Cues based on energy consumption or flight duration

Could the bees be gauging the location of the reward in the tunnel by measuring the energy consumed *en route*, the duration of flight or other related parameters? To investigate this, honeybees were trained as in Fig. 1A and tested in a tunnel that presented a headwind or a tailwind, created by a fan which blew or sucked air at the far end of the tunnel. In a headwind, bees flew slower and took longer to reach the estimated position of the reward. The opposite was true in a tailwind. The mean times elapsed between the entry into the tunnel and the first U-turn were 7.2 ± 2.6 s in still air, 10.1 ± 2.7 s in a headwind of 0.7 m s^{-1} and 5.9 ± 1.8 s in a tailwind of 0.65 m s^{-1} . Since these times were significantly different from each other ($P < 0.02$ in each case), we infer that distance travelled is not estimated in terms of time of flight or of other correlated parameters such as number of wingbeats. In a headwind, bees overshoot the position of the reward slightly, but significantly; in a tailwind, they undershot it (Fig. 3A). While the reasons for these misjudgments remain to be discovered, it is clear that distance flown is not measured in terms of energy consumption, because the errors made by the bees are in directions opposite to those expected on this basis.

Cues based on analysis of image motion

Were the bees measuring distance flown to the reward by integrating the motion of the image of the surrounding panorama *en route*? To examine this possibility, we trained honeybees in a tunnel of a given width and then tested them in a tunnel that was narrower or wider. For a given distance

Fig. 2. Honeybees, trained to find a reward in unit 9 of a training tunnel (see Fig. 1A), were subsequently tested in a variety of tunnels that carried no reward. (A) Squares: test in tunnel identical to training tunnel ($N=121$). The mean search position was not significantly different from that corresponding to the position of the reward (unit 9) during training ($P > 0.30$). Circles: results of a similar experiment in which the training and testing tunnels were lined with a random Julesz texture, as described in Materials and methods and Results ($N=42$). The mean search position was not significantly different from that corresponding to the position of the reward (unit 9) during training ($P > 0.70$). (B) Tests in tunnels that carried a $4 \text{ cm} \times 4 \text{ cm}$ aperture at the entrance ($N=35$) or a 1 m extension at the front end ($N=81$). In neither case was the distance of the mean search position from the tunnel entrance significantly different from that obtained in test A above ($P > 0.30$ in each case). The open arrowhead on the left depicts the search position expected with the extension if the bees were to search at a constant distance from the tunnel entrance. (C) Tests in tunnels that carried stripes of half (2 cm) or double (8 cm) the period of the stripes in the training tunnel ($N=24$ and $N=22$, respectively). In each case, the mean search position was not significantly different from that obtained in test A above ($P > 0.40$ in each case). The open arrowheads depict the positions at which the honeybees would be expected to search in the tests with the narrower (left-hand arrowhead) and wider (right-hand arrowhead) stripes if they were estimating the distance to the reward by counting stripes. The mean search positions measured in the tests were significantly different from either of these hypothetical positions ($P < 0.001$ in each case).

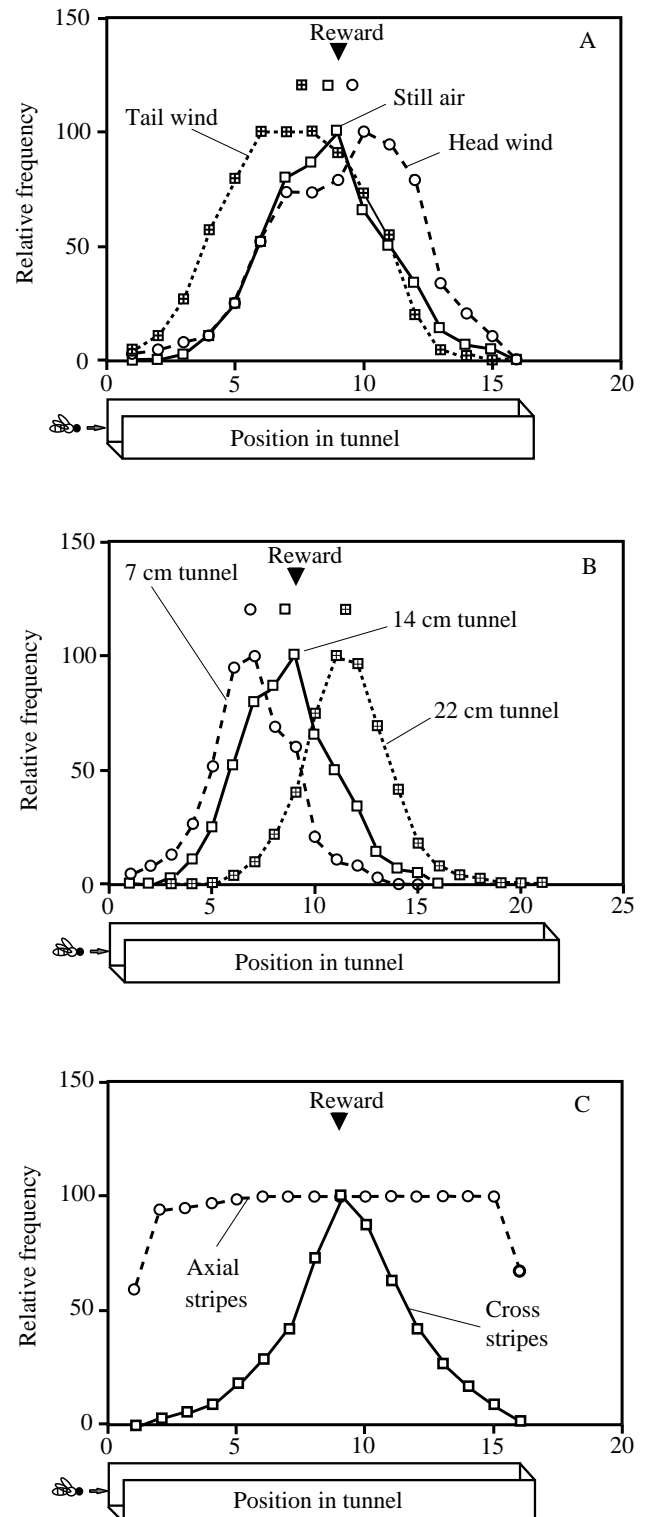
travelled by the bee, the narrower tunnel induces a larger image motion on the eye, and the wider tunnel a smaller image motion. Thus, if bees integrate image motion to estimate the distance travelled along the tunnel, they should search at a shorter distance from the entrance in the narrower tunnel and at a farther distance in the wider one. This is indeed what we found (Fig. 3B). These results suggest that one cue used by honeybees to gauge distance flown is the total amount of image motion experienced whilst flying through the tunnel.

We examined the image-motion hypothesis further in an experiment where honeybees were trained and tested in tunnels in which this cue was eliminated. This was accomplished by using axially oriented stripes on the walls and floor. Honeybees flying along such a tunnel would experience very little image motion, since they fly in a direction parallel to the stripes. Strikingly, bees trained in the axial-striped tunnel displayed no ability to gauge distance travelled: they searched uniformly over the entire length of the tunnel (Fig. 3C). The behaviour of these bees was very different from that in the other experiments. Here, upon entering the tunnel, the bees flew directly to the other end – at a slightly higher speed, but no less stably – without turning, or even pausing, near the former location of the reward. After making a U-turn at the far end, they flew straight back to the entrance. Usually they then exited the tunnel and re-entered it to repeat this exercise over and over again. The search distribution exhibited by these bees is flat and very different in shape from the bell-shaped distribution produced by bees trained in a tunnel lined with the usual cross stripes (Fig. 2A, solid curve). Clearly, removal of image-motion cues completely disrupts the ability of the bees to localise the position of the reward. This finding confirms the hypothesis that image motion, integrated over time, is an important cue for estimating distance flown.

Fig. 3. (A) Honeybees, trained to find a reward in unit 9 of a training tunnel (see Fig. 1A), were subsequently tested in an identical tunnel in still air ($N=19$), in a headwind ($N=27$) or in a tailwind ($N=39$). Compared with the situation in still air, bees searched significantly farther into the tunnel in the presence of a headwind ($P<0.01$) and significantly undershot the former position of the reward in the presence of a tailwind ($P<0.01$). (B) Honeybees, trained to find a reward in unit 9 of a training tunnel of width 14 cm, were tested in tunnels whose widths were the same (14 cm; open squares; $N=35$), narrower (7 cm; open circles; $N=42$) or wider (22 cm; crossed squares; $N=56$). Bees tested in the narrower tunnel searched at a position that was significantly nearer to the entrance than those tested in the 14 cm tunnel ($P<0.01$), and bees tested in the wider tunnel searched at a position that was significantly farther away ($P<0.01$). (C) Honeybees, trained to find a reward in unit 9 of a training tunnel similar to that in Fig. 1A but lined with axial stripes of period 4 cm, and then tested in an identical tunnel, showed no ability to localise the former position of the feeder (circles, $N=30$). These bees exhibited a search distribution that was very much broader than that obtained when the tunnels were lined with cross stripes (squares, redrawn from Fig. 2A). The standard deviations of the search positions are significantly different in the two cases (s.d.=7.5 and 2.5 units, respectively; $P<0.01$, F -test for variance).

Visual fields for odometry

In a further set of experiments, we investigated which region(s) of the bee's visual field is used for the measurement and integration of image motion. This was done by training honeybees in tunnels where motion cues were selectively removed either on the floor or on the side walls by lining these surfaces with axial stripes. When bees were trained with axial



stripes on the floor (Fig. 4, squares), they performed nearly as well as under normal conditions (compare with Fig. 2A, squares). In contrast, when bees were trained with axial stripes on the side walls (Fig. 4, diamonds), their performance was substantially worse, and nearly as bad as when all of the surfaces of the tunnel were lined with axial stripes (compare with Fig. 3C, circles). These results suggest that visual odometry relies primarily on the lateral fields of view of the eyes.

Cues based on inertial navigation

Are there additional cues that honeybees use to measure their progress in the tunnel? For example, do they also use some form of inertial navigation? If honeybees possess an (as yet unknown) means of measuring translatory acceleration, they could, in principle, double-integrate this signal to estimate distance flown. To investigate this possibility, we trained honeybees as in the experiment of Fig. 1A and tested them in a tunnel that was moved continuously and smoothly along its long axis as the bee flew through it. The total displacement of the tunnel was 50% of its length, and the duration of this displacement was such that the movement was completed before the bee made its first U-turn. Bees tested in the moving tunnel searched at the previous location of the reward relative to the tunnel entrance, regardless of whether the tunnel moved with or against the bee (Fig. 5A). This means that, compared with the training situation, the bee flew a 50% greater absolute distance before making a U-turn when the tunnel moved with the bee, and a 50% smaller absolute distance when the tunnel moved against her. Thus, the bees were not measuring absolute distance flown, but the distance flown relative to the tunnel entrance. This finding rules out inertial navigation as a possible mechanism, but is consistent with a

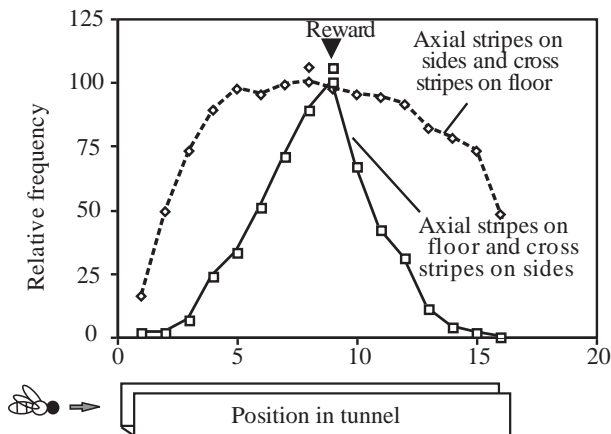


Fig. 4. Honeybees were trained to find a reward in unit 9 of a training tunnel similar to that in Fig. 1A but lined with axial stripes of period 4 cm either on the floor or on the side walls, and tested in identical tunnels. When the axial stripes were on the floor (squares, $N=20$), performance was nearly as good as in the test of Fig. 2A ($P>0.25$, F -test for variance). However, when the axial stripes were on the side walls (diamonds, $N=24$), the performance of the honeybees was substantially poorer, and only slightly better than in the test of Fig. 3C. The widths of these two distributions (s.d.=2.7 and 5.6 units, respectively) are significantly different ($P<0.05$, F -test for variance).

mechanism that commences to integrate image motion from the instant that the entrance is passed.

Cues based on airspeed

Were the bees obtaining additional information on distance travelled by integrating airspeed? Most insects, including

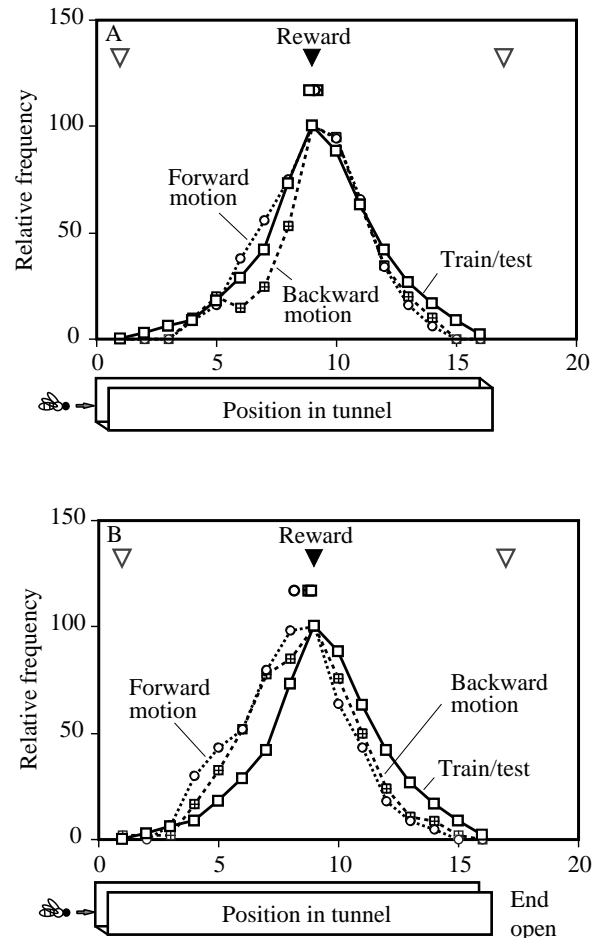


Fig. 5. (A) Honeybees, trained to find a reward in unit 9 of a training tunnel (see Fig. 1A), were subsequently tested in an identical tunnel that was stationary (Train/test), moved in the same direction as the bee's flight (Forward motion) or moved against it (Backward motion) at a mean rate of 0.36 m s^{-1} , for approximately 4.4 s. This was done with the far end of the tunnel closed (as in the other experiments) to test the inertial navigation hypothesis (A), and with the far end open to test the airspeed integration hypothesis (B). The open arrows indicate the search position relative to the tunnel as predicted by each hypothesis, when the tunnel was moved with the bee (left arrow) or against it (right arrow). In each case, there was no significant difference between the mean search position measured relative to the tunnel entrance when the tunnel was stationary and when it was moved in either direction ($P>0.30$). In the tests with the moving tunnels, the mean search positions were significantly different from the hypothetical locations indicated by the open arrows ($P<0.001$). The numbers of flights analysed to obtain these data were: (A) stationary tunnel, $N=121$; forward motion, $N=10$; backward motion, $N=10$; (B) stationary tunnel, $N=121$; forward motion, $N=18$; backward motion, $N=19$.

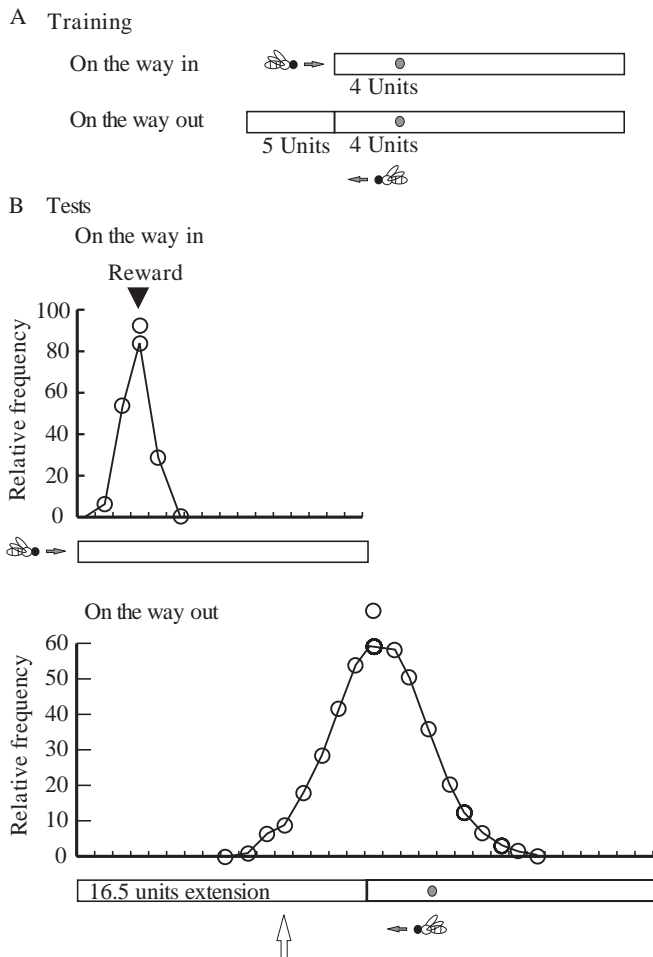


Fig. 6. Experiment investigating whether honeybees learn distance travelled on the way to the feeder or on the way back. (A) Training: honeybees were trained to fly 4 units into a tunnel to receive a reward at a feeder (filled circle) and to fly 9 units to exit the tunnel on the way back. (B) Tests: honeybees entering the tunnel, tested with the feeder removed, searched for the feeder at a distance of approximately 4 units from the entrance (upper section, $N=21$). When a long extension was added to the tunnel, bees departing from the tunnel after collecting a reward at the feeder searched for the exit at a mean distance of approximately 4 units from the feeder (lower section, $N=62$). The open vertical arrow depicts the mean searching position expected if the bees had learnt the exit distance of 9 units.

honeybees, possess wind-sensitive hairs on the head and eyes that could, in principle, be used to provide an indication of airspeed (Neese, 1965; Rowell, 1989). In the honeybee, Johnston's organ at the base of the antenna has also been implicated as a wind-sensing device that could play a role in navigation (Heran, 1959). If insects can measure airspeed and integrate it over time, they should be able to gauge the distance flown relative to the body of air in which they fly. (Such a mechanism, however, would indicate true distance flown only if the air were still.) To investigate this possibility, we tested honeybees in a moving tunnel as described above, but with the far end of the tunnel open. This ensured that the

body of air in the tunnel did not move with the tunnel but was stationary in space, as confirmed by an anemometer. Honeybees flying in the moving tunnel searched at the previous location of the reward relative to the tunnel entrance, irrespective of whether the tunnel moved with or against the bee (Fig. 5B). This meant that, compared with the training situation, the bee flew through a 50% longer column of air before making a U-turn when the tunnel moved with the bee, and a 50% shorter column of air when the tunnel moved against her. Thus, the bees were not measuring the distance flown relative to the air, but the distance flown relative to the tunnel entrance. This experiment rules out integration of airspeed as a possible mechanism, a conclusion that is also supported by the results of Fig. 3A,C.

Is distance learnt on the way to the food source or on the way back?

Do honeybees learn distance flown on the way into the tunnel, or on the way out, or on both routes? This question was investigated by manipulating the inward-bound and outward-bound distances during training. Bees entering the tunnel had to fly a distance of 4 units to reach the feeder, as shown in the upper section of Fig. 6A. However, bees departing after collecting the reward had to fly a distance of 9 units before exiting the tunnel. This was arranged by placing an additional tunnel, 5 units long, at the entrance to the original tunnel after the arriving bee had alighted on the feeder and commenced to collect the reward (lower section, Fig. 6A). A relatively small number of bees (three) was trained in this experiment, to ensure that only one bee was in the tunnel at any given time. This enabled the training procedure to be carried out properly without any difficulties caused by the simultaneous presence of arriving and departing bees in the tunnel. The tunnels were lined with a randomly textured (Julesz) pattern, as described in Materials and methods. When the trained bees were allowed to enter a test tunnel similar to the original tunnel but with the feeder removed, they searched at a location corresponding to the former position of the feeder (Fig. 6B, upper section). Thus, the bees were clearly learning the distance to the feeder on the way into the tunnel. Were they also learning the distance on the way out? To investigate this, the behaviour of the same bees was examined when the reward was retained in the tunnel and an additional, similarly textured tunnel of length 16.5 units was placed at the entrance to the original training tunnel. Bees departing the reward displayed a search distribution that was centred at a distance of 4 units from the feeder, rather than 9 units (Fig. 6B, lower section). Clearly, the departing bees 'expected' the tunnel exit to be 4 units away from the feeder, and not 9 units away. These results indicate that the bees were learning the distance to the feeder on the way into the tunnel and not on the way out. Furthermore, they used distance information learnt on the way in to navigate on the way out. That is, bees attend to, and rely upon, landmarks on the way in as well as on the way out, but they appear to learn distances primarily on the way in.

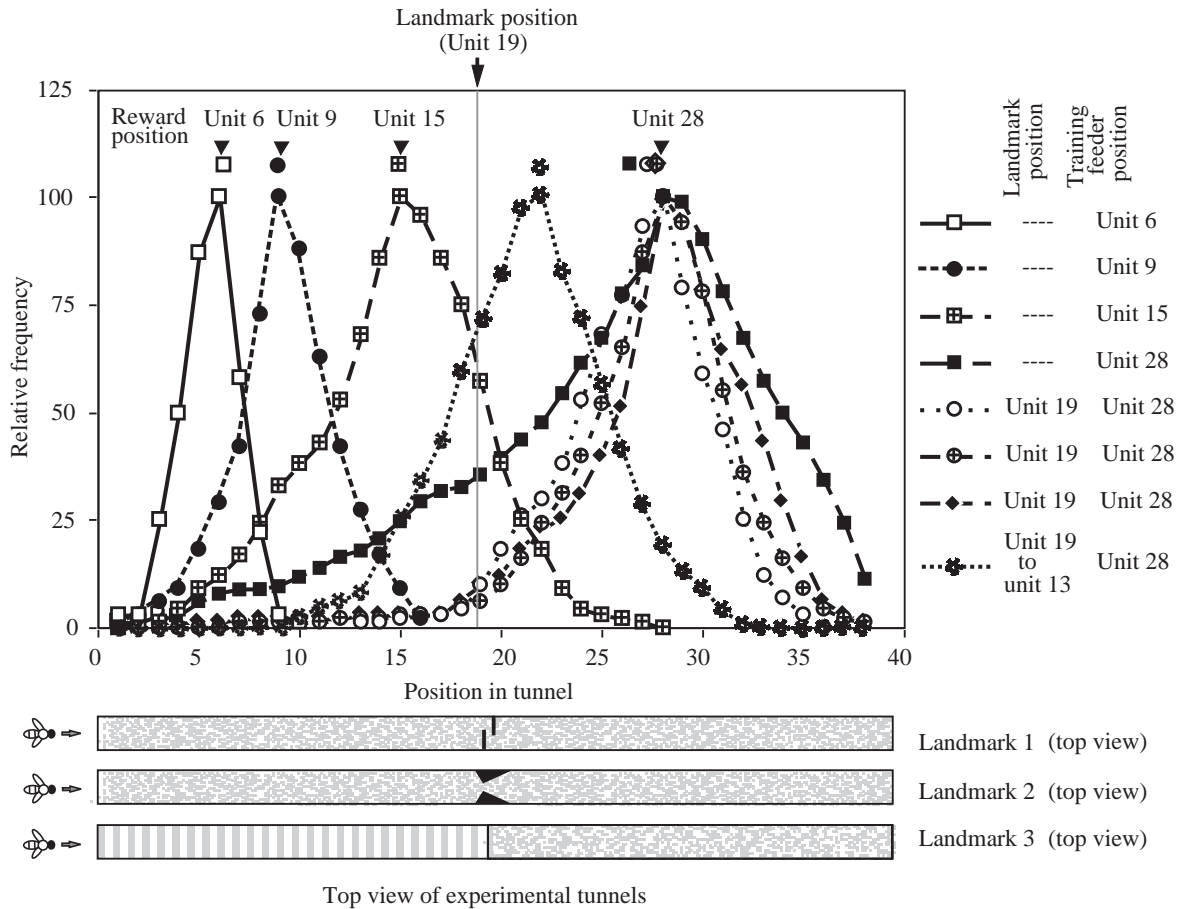


Fig. 7. Experiments investigating the ability of honeybees to locate a feeder placed at various distances along a long tunnel. The tunnel was 7.6 m long, 22 cm wide and 20 cm high. The walls and floor were lined with a random Julesz texture. The curves depict the search distributions of bees trained in separate experiments to feeders positioned at units 6, 9, 15 and 28, as indicated by the filled arrowheads. These data represent means of $N=65$, 71, 60 and 61 flights, respectively. In each experiment, the mean search position (symbol above each search distribution) was very close to that expected (filled arrowhead). The standard deviations (s.d.) of the search distributions in the four experiments were 1.84, 2.52, 4.14 and 7.30 units, respectively. The s.d. for the feeder at position 28 was significantly larger than those for the feeder at positions 6, 9 and 15 ($P<0.01$ in each case, F -test). The widths of the search distributions, measured at half maximum height, were 3.4, 4.0, 7.8 and 12.0 units, respectively, for the four experiments. Also shown are the results of three further experiments in which honeybees were trained to a feeder positioned at unit 28, and with a prominent landmark situated *en route* at unit 19. In one experiment, this landmark was a baffle consisting of a pair of partitions (Landmark 1); in another, it was a constriction in the tunnel (Landmark 2); and in a third, it was defined by the position in the tunnel where the pattern lining the walls and floor changed from black-and-white stripes to a random Julesz texture (Landmark 3). In each case, the mean search position was not significantly different from that expected (unit 28; $P>0.10$). However, the s.d. obtained in each of these three experiments (3.25, 4.24 and 4.90 units, respectively) was significantly smaller than that obtained with the feeder at the same position, but with no Landmark ($P<0.01$, F -test). The reduction in s.d. is also reflected in the changes of the widths of the search distributions. In the presence of Landmarks 1, 2 and 3, these widths were 6.5, 6.3 and 6.8 units respectively, all of which are substantially smaller than that obtained in the experiment with the feeder at the same position but with no landmark (12.0 units, see above). The data obtained in the presence of Landmarks 1, 2 and 3 represent means of $N=54$, 65 and 61 flights, respectively. Observations of the flights of the honeybees past the landmarks during training assured us that the narrowing of the search distributions was not due to the landmarks acting as a barrier hindering free flight past them. For example, during training with Landmark 1, bees turned back just prior to the Landmark in only 1 out of 63 flights on the way to the reward, and in only 3 out of 61 flights on the way back. In a final experiment, honeybees were trained as above with the feeder at unit 28 and Landmark 3 at unit 19. They were then tested with the landmark repositioned 6 units closer to the tunnel entrance, at unit 13. The mean searching position of the bees in this test was 6.45 units ahead of the position of the feeder during training ($N=67$ flights; dotted curve, circled stars). This indicates that the bees were locating the feeder by re-commencing their computation of distance at the landmark and flying approximately 6 units beyond it.

Examining the consequences of visual odometry

The experiments described in Figs 2–5 indicate that honeybees gauge distance travelled by integrating image

motion. The integrative nature of such a mechanism implies that errors in the measurement and integration of image speed accumulate with distance, so that larger distances would be

estimated with greater error. To test this prediction, we examined the accuracy with which honeybees were able to localise a feeder when it was placed at various distances along a long (7.6 m) tunnel. The results are shown in Fig. 7, for separate training experiments with the feeder positioned at units 6, 9, 15 and 28, respectively. It is clear that the width of the search distribution increases systematically with the distance of the feeder from the tunnel entrance. Thus, the error in estimating distance increases with distance flown, as would be expected of an integrative mechanism.

An integrative mechanism for measuring distance travelled would be feasible only if the cumulative errors are somehow prevented from exceeding tolerable levels. One strategy, which could be employed when traversing familiar routes, would be to re-commence the integration of image motion whenever a prominent, known landmark is passed. Do bees adopt such a tactic?

To investigate this, we examined the honeybees' performance when they were again trained to fly to a feeder placed at the largest distance (unit 28), but now had to pass a prominent landmark occurring *en route* at unit 19. If these bees reset their odometer at the landmark, they should display a smaller error because they would then only need to measure the nine additional units of distance between the landmark and the feeder. We experimented with three different groups of bees, each trained using a different kind of landmark (Fig. 7). It was clear that, in all three cases, the introduction of the landmark improved the accuracy of distance estimation substantially: the search distribution was then significantly narrower (Fig. 7). Furthermore, when the trained bees were confronted with a test in which Landmark 3 was positioned 6 units closer to the tunnel entrance (i.e. at unit 13), the mean search position of the bees shifted towards the entrance by almost exactly the same distance (6.45 units; Fig. 7). These results confirm that bees indeed re-commence computation of distance when they pass a prominent landmark.

Discussion

Our findings reveal that honeybees possess a visually driven 'odometer' that estimates distance flown by integrating the image motion that is experienced on the way to the goal. The tests with stripes of different periods suggest that this mechanism measures the speed of the image largely independently of its structure. This movement-detecting mechanism seems to be different from the one mediating the well-studied optomotor response, which is sensitive to the structure of the moving image and does not provide an unambiguous indication of its speed (for a review, see Reichardt, 1969). Our results also argue against the hypotheses that short distances flown are measured in terms of (a) time of flight, (b) energy consumption, (c) number of wingbeats, (d) integrated airspeed or (e) inertial navigation. The observation that honeybees are unable to locate the feeder when image-motion cues are removed provides further evidence against participation of the other cues in our experiments.

Our conclusion that the honeybee's odometer relies primarily on image motion is in general agreement with those of a recent study by Esch and Burns (1995), who investigated distance measurement by honeybees through a different experimental approach. They examined how dancing honeybees signalled the distance to a food source that was a constant horizontal distance away (70 m), but at a systematically varied elevation. They found that the bees signalled a shorter distance as the food was moved higher. From this, they inferred that distance flown is gauged in terms of the motion of the image of the ground below and not through energy consumption. Evidently, visual odometry is used not only in short-range navigation (as in our experiments), but also in situations that typify foraging flights of moderate length. Our conclusions are also consistent with those of Ugolini (1987), who transported wasps (*Polistes gallicus*) passively in transparent containers to demonstrate that they infer the direction and distance of travel by observing the apparent motion of the visual panorama. Recent studies on walking honeybees (Schöne, 1996) indicate that their perception of distance walked can be influenced by moving the surrounding environment. Movement of the surround against the walking direction causes the bees to overestimate the distance walked; movement in the same direction has the opposite effect. This finding demonstrates that image motion provides an odometric signal even for walking bees, although the participation of additional cues (such as kinesthetic signals from leg movements) remains to be investigated. Desert ants (*Cataglyphis fortis*) foraging in a featureless landscape use the motion of the image of the ground as one cue to estimate distance travelled, although idiothetic information may also play a significant role (Ronacher and Wehner, 1995). Interestingly, the ant's odometer is not affected by the burden that the ant carries, suggesting that there, too, energy consumption may not be the dominant distance-indicating cue (Schäfer and Wehner, 1993).

Our findings suggest that visual odometry relies primarily on motion signals obtained from the lateral fields of view, and not the ventral field. This result differs somewhat from the observations of Esch and Burns (1996). Although they did not specifically investigate this question, most of their experiments were conducted in an open meadow where motion signals were available only in the ventral field. It is possible that bees 'prefer' to use signals from the lateral eye regions, and resort to using the ventral field only when no information is available laterally. We cannot rule out the possibility that the bees in Esch and Burns' experiments might have estimated distance more accurately if they had had visual access to laterally located structures. One advantage of ignoring the ventral field and using the lateral field of view when the environment contains lateral structures (such as tall trees) is that the odometric signal would then be independent of the height at which the bee flies above the ground. A ventrally driven odometric signal, in contrast, would be unreliable unless it were somehow corrected for the altitude of the bee.

The experiments described in Fig. 7 reveal that bees enhance

the accuracy with which they measure progress towards the goal by re-commencing the computation of distance when they pass a prominent landmark. This finding is supported by the recent work of Collett *et al.* (1996), who showed that a landmark encountered *en route* can trigger memories of the length and direction of the next leg of the journey. How often do bees reset their odometer (or start a fresh one)? We suggest that they do it at every opportunity. In our experiments, for example, a given honeybee did not always follow the same route from the hive to the tunnel entrance. There were two reasons for this. First, during training, the position and orientation of the tunnel were frequently changed to prevent the bees from using landmarks external to the tunnel, as described in Materials and methods. Second, the most direct route to the tunnel was often blocked by the presence of an experimenter or a displaced object. Therefore, the distance that a bee travelled *before* entering the tunnel could vary considerably from one visit to the next. Since the bees were able to locate the position of the feeder in the tunnel reliably in spite of these variations, it is very likely that they were treating the tunnel entrance as a reference landmark and re-commencing the integration of image motion when they flew past it on the way in. Further experiments are required to determine whether honeybees use a single odometer – resetting it to zero each time a landmark is passed – or start a new odometer at each landmark, leaving some or all of the earlier ones running. In conditions where landmarks are poorly visible or not stable, it may be advantageous to combine odometric readings referenced to a number of different landmarks encountered *en route* to obtain a reliable estimate of the distance flown.

The work of Collett (1993, review) and Chittka *et al.* (1995) indicates that foraging honeybees ‘expect’ to see a specific sequence of landmarks situated at specific distances on the way to the food source and that they monitor their progress towards the destination by checking whether the expected landmarks show up at the appropriate distances. Considering their findings together with ours, we conjecture that honeybees improve the robustness of goal-finding by combining and cross-checking information on landmark sequences and distances. If a landmark appears roughly at the expected distance, it is used to re-commence integration of image motion and thereby to improve the accuracy of distance estimation. However, if a landmark appears much earlier than expected – or does not appear at all – the bee resorts to using the prevailing odometric signal to determine where to look for the target. Further investigation is needed, however, to understand fully the interplay between odometric and landmark-based information in navigation.

Our findings do not imply that vision is the sole mechanism by which bees estimate how far they have travelled. The roles of other cues, such as energy expenditure, remain controversial (Neese, 1988; Goller and Esch, 1990; Esch *et al.* 1994; Kirchner and Braun, 1994). Although it is unlikely that energy consumption could serve as a reliable measure of distances as short as those prevailing in most of our experiments, it might,

conceivably, be used to provide a coarse indication whilst foraging over large distances.

Unlike energy-based cues, visual cues have the advantage that they are not affected by wind or by the weight of nectar that the bee carries. However, a visual odometer, as described here, would work accurately only if the bee were to follow a fixed route each time it flew to its destination (or if a follower bee were to adhere to the same route as a dancing scout bee). This is because the total amount of image motion that is experienced during the trip would depend upon the distances to the various objects that are passed *en route*. This is unlikely to be a problem in most circumstances, since honeybees flying repeatedly to an attractive food source tend to remain faithful to the route that they have discovered (e.g. Collett, 1996).

The results of the experiment described in Fig. 6 suggest that foraging honeybees learn the distance to a food source on the way to it, and not on the way back. This conclusion is at variance with that of Otto (1959), who trained bees to a feeder which he moved farther away from the hive after they had alighted on it, thereby causing the return flight to be longer than the outbound flight. By observing the dances of these bees, Otto concluded that foraging bees learn the distance flown in both directions, and use the average of the two measurements. Our finding is in agreement, however, with the conclusions of von Frisch (1993, review), Heran and Wanke (1952) and Heran (1956). von Frisch (1993), found that bees flying to a feeder located upwind from the hive signalled a greater distance in their dances than bees flying to a feeder placed at the same distance, but in the downwind direction. Heran and Wanke (1952) and Heran (1956) trained bees on a hill slope to two sites that were equally distant from the hive, one uphill and the other downhill. They found that bees flying to the uphill feeder signalled a greater distance than bees flying to the downhill feeder. These authors inferred, as we do here, that foraging bees learn distance on the way to the food source. However, their conclusion was based on the assumption that the odometric signal is derived from energy consumption. This assumption must be re-evaluated in the light of recent data that suggest an important role for vision in odometry (Esch and Burns, 1996, and present results). As suggested by Esch and Burns (1996), bees flying uphill probably signal a greater distance not because they consume more energy, but because they tend to fly closer to the ground and therefore experience larger image motion. Again, bees flying upwind probably tend to fly closer to the ground to minimize the headwind and, consequently, experience greater image motion.

What, if any, is the advantage of learning the distance to a food source on the way to it, rather than on the way back? A naive forager would create a meandering path to the food source that she eventually finds. To then make a ‘bee line’ back to the hive – which she does – her nervous system would have to sum the various segments of her outbound flight, vectorially, in order to determine how far and in which direction she has to fly to return to the hive. Clearly, this requires measurement of the distances flown along the various segments of the outward flight (for a review, see Wehner, 1992). Thus,

odometry would seem to be an indispensable element of the outbound flight, at least in the case of a naive forager. However, the return flight can also provide useful information on the distance to the food source. In fact, the return flight is likely to yield a more accurate estimate of this distance, because the bee would now fly an approximately straight line along the correct course to the hive, thus minimising errors that could arise from the process of vector summation (Müller and Wehner, 1988). Thus, it would seem useful to measure distances on the way to the food source as well as on the way back from it. Our experimental findings, however, suggest that honeybees measure distance only on the outbound route (Fig. 6). While this result remains enigmatic, it is congruent with the facts that (a) foraging honeybees receive a reinforcing food reward at the end of the outward journey, and not at the end of the return flight; and (b) the honeybee dance, by its very nature, signals the way to the food source, and not the way back from it (for a review, see von Frisch, 1993).

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