J Comp Physiol A (2014) 200:563–573
DOI 10.1007/s00359-014-0902-6

REVIEW

Going with the flow: a brief history of the study of the honeybee's navigational 'odometer'

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Received: 3 January 2014 / Revised: 16 March 2014 / Accepted: 19 March 2014 / Published online: 17 April 2014

Abstract Honeybees navigate to a food source using a sky-based compass to determine their travel direction, and an odometer to register how far they have travelled. The past 20 years have seen a renewed interest in understanding the nature of the odometer. Early work, pioneered by von Frisch and colleagues, hypothesized that travel distance is measured in terms of the energy that is consumed during the journey. More recent studies suggest that visual cues play a role as well. Specifically, bees appear to gauge travel distance by sensing the extent to which the image of the environment moves in the eye during the journey from the hive to the food source. Most of the evidence indicates that travel distance is measured during the outbound journey. Accumulation of odometric errors is restricted by resetting the odometer every time a prominent landmark is passed. When making detours around large obstacles, the odometer registers the total distance of the path that is flown to the destination, and not the "bee-line" distance. Finally, recent studies are revealing that bees can perform odometry in three dimensions.

Keywords Honeybee · Navigation · Vision · Optic flow · Odometry

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Introduction

Honeybees are expert long-distance navigators, flying distances of up to 10 km (von Frisch 1993) in search of food, often through unfamiliar territory, and returning home rapidly and unerringly. How do they achieve this feat?

If an insect is to navigate successfully to a food source and back, it needs to know (1) the direction in which it is travelling, and (2) how far it has travelled, i.e., it needs an 'odometer', with a function analogous to that found in the dashboard of a car. Research over the past 70 or so years––pioneered by Karl von Frisch and his colleagues, and followed up by many other studies—has established that honeybees use the position of the sun, and/or the pattern of polarised light that it creates in the sky, as a 'celestial compass' to determine the direction in which they are heading (revs Wehner 1992; von Frisch 1993). In this review, I shall not describe the work on the celestial compass, but focus instead on the second important aspect of navigation, namely, establishing how far the bee has travelled. In other words, what is the nature of the honeybee's odometer?

In principle, there are a number of ways in which a flying insect could keep track of how far it has progressed during its journey. For example, it could (a) monitor the duration of flight, (b) count wing beats, (c) measure energy consumption, (d) sense and integrate airspeed, (e) measure the apparent motion of the environment in the eye, or (f) use some form of inertial navigation involving sensing and integrating the animal's accelerations.

Odometry in flying insects has been studied most intensely in the honeybee. The reason for this probably arises from the famous "waggle" dance, which bees perform after returning home from an attractive food source to advertise to their nest mates the distance and direction of the goal (von Frisch 1993). The dance is performed on the vertical surface of the honeycomb. The bee moves in a series of double loops, each shaped roughly like a figure of eight. Towards the end of each loop, the bee waggles her abdomen from side to side. The duration of the waggle is proportional to the distance of the food source from the hive, and the angle between the axis of the waggle and the vertical direction is equal to the azimuthal angle between the sun and the direction in which a bee should fly to find the goal. The information in the dance is decoded and used by the nest mates to locate the food source, and to harvest it efficiently. But the waggle dance is also useful for the researcher, who wishes to unravel the mysteries of the honeybee's odometer, because it provides a window into the bee's perception of how far she 'thinks' she has travelled.

Early studies of the waggle dance suggested that distance travelled is measured in terms of the total energy expended during flight (rev Heran and Wanke 1952; Heran 1956; von Frisch 1993). The evidence for this was twofold. First, if a foraging bee was made to carry an extra load, by attaching a small steel ball to her thorax, she signalled a greater travel distance in her dances. Second, bees signalled larger distances when they flew to food sites located uphill from the hive, than when they flew to food sites positioned downhill at the same distance.

Recent advances in the study of honeybee odomtery

More recent investigations, conducted over the past 30 years, have questioned the above hypothesis and suggest that other, or additional cues may be involved (Neese 1988; Goller and Esch 1990; Esch et al. 1994). An important odometric cue appears to be the extent to which the image of the environment moves in the eye as the bee travels to the target (Esch and Burns 1995, 1996; Schöne 1996; Srinivasan et al. 1996, 1997, 2000; Esch et al. 2001). In other words, the odometer is driven by a visual, rather than an energy-based signal. Here we shall describe some of the new work that led to this insight.

Learning optic flow cues to know where to find food

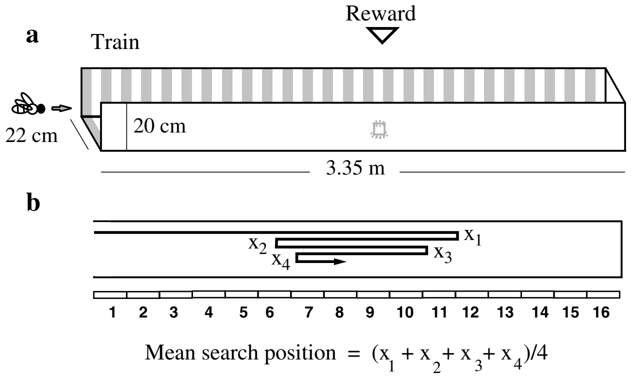

Fig. 1 Experimental setup for investigating odometry in flying honeybees. **a** Bees are trained to forage at a feeder placed at a fixed position inside a tunnel. The walls and floor are lined with vertical, *black-and-white* stripes, and the tunnel is covered with a sheet of transparent perspex. **b** The trained bees are tested individually by allowing them to enter a fresh, identical tunnel, with no reward, and monitoring their searching behaviour. The tunnel is subdivided into numbered sections, for the purpose of analysis. The mean searching location in the tests is given by the mean of the positions of the first four U-turns, and a searching distribution is computed by evaluating the number of times the bee enters each of the sections. Adapted from Srinivasan et al. (1997)

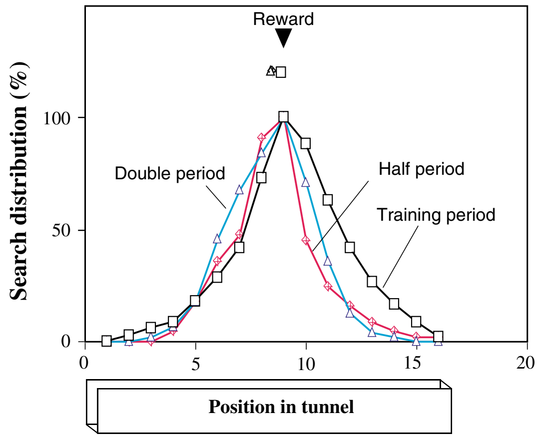

Fig. 2 Searching distributions of bees in tests, after they had been trained to forage from a feeder positioned in section 9. The peak and mean value of the searching distribution are very close to the position of the feeder during the training. This is true regardless of whether the walls and floor of the test tunnel are lined with striped patterns of the same period as in the training (*black curve*), half the period (*red curve*) or double the period (*blue curve*). Further details in Srinivasan et al. (1996, 1997). Adapted from Srinivasan et al. (1997)

Some 28 years ago, researchers in Canberra trained bees to find a food reward placed in a tunnel, and then explored the cues by which they inferred how far they had flown to get to the food. The walls and floor of the tunnel were lined with black-and-white stripes, usually perpendicular to the tunnel's axis (Fig. 1a). The reward consisted of sugar solution offered by a feeder placed in the tunnel at a fixed distance from the entrance. During training, the position and orientation of the tunnel were changed frequently to prevent the bees from using any external landmarks to gauge their position relative to the tunnel entrance. 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 training and test tunnels were covered by a transparent sheet of perspex, and subdivided into numbered sections for the purposes of analysis. In the tests, the bees' behaviour whilst searching for the reward was recorded by noting the locations of the first four U-turns (Fig. 1b). From this data it was possible to estimate the mean searching location, and the extent to which the search was distributed about this mean (details are given in the figure legend and in Srinivasan et al. 1996, 1997).

Bees trained in this way showed a clear ability to search for the reward at the correct distance, indicated by Fig. 2 (black curve). How were the bees gauging the distance flown? A number of hypotheses were examined, as described below.

Were the bees learning the position of the feeder by counting the stripes en route to the goal? To examine this possibility, bees were trained in a tunnel lined with stripes of a particular spatial period and tested in a tunnel lined with stripes of a different period. The test bees searched at the correct distance from the tunnel entrance, regardless of stripe period (Fig. 2, red and blue curves). Therefore, distance is not gauged by counting the number of stripes or other features passed whilst flying through the tunnel (Srinivasan et al. 1996, 1997).

Were the bees measuring distance travelled in terms of the time required to reach the goal? To examine this possibility, bees were trained as above and tested in a tunnel that presented a headwind or a tailwind, generated by a fan at the far end of the tunnel. In a headwind, bees flew slower and took longer to reach the estimated location of the reward. The opposite was true in a tailwind (Srinivasan et al. 1997). Therefore, distance is not estimated in terms of time of flight, or other correlated parameters such as the number of wing beats. In a headwind, bees overshot the location of the reward; in a tailwind, they undershot it. Therefore, distance flown is not measured in terms of energy consumption.

Were the bees measuring distance travelled by gauging the extent of motion of the image of the surrounding panorama as they flew to the goal? To investigate this possibility, bees were trained in a tunnel of a given width and then tested in a tunnel that was narrower or wider. In the narrower tunnel, the bees searched at a shorter distance from the entrance; in the wider tunnel, they searched farther into the tunnel (Srinivasan et al. 1996, 1997). These results suggest that distance flown is gauged by measuring the total overall motion of the images of the walls and floor on the eyes during the flight through the tunnel.

To test this image motion hypothesis critically, bees were trained and tested in conditions where image motion was eliminated or reduced. This was achieved by using tunnels that carried axially oriented stripes on the walls and floor. Such tunnels provided no information on image motion, because the bee's flights in them were parallel to the direction of the stripes. In the experiments using axial-striped tunnels, the bees' behaviour was strikingly different: they showed no ability to gauge distance travelled. The bees searched uniformly over the entire length of the tunnel, showing no tendency to stop or turn at the former location of the reward (dashed curve, Fig. 3). Evidently, when bees are deprived of image motion cues, they are unable to gauge how far they have flown. This finding provides direct and rather compelling evidence that the honeybee's odometer is driven by image motion (Srinivasan et al. 1996, 1997).

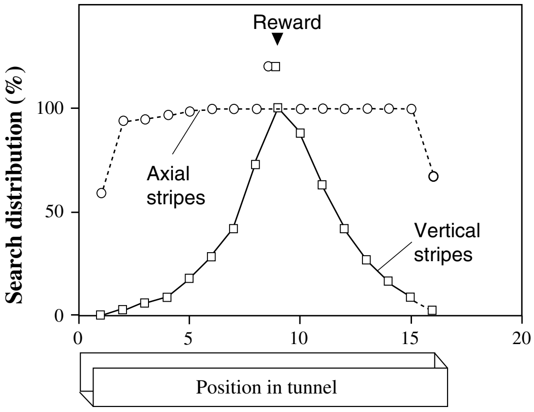

Fig. 3 Comparison of searching distribution of bees that have been trained and tested in tunnels lined with vertical stripes (*solid curve*), as in Fig. 2, with searching distribution of bees that have been trained and tested in tunnels lined with axial stripes (*dashed curve*). This result indicates that eliminating image motion cues, by using axial stripes, completely disrupts the bees' ability to learn the position of the feeder. Further details in Srinivasan et al. (1996, 1997). Adapted from Srinivasan et al. (1997)

Further experiments, in which honeybees were trained to find a feeder in a stationary tunnel, and then tested inside a moving tunnel, ruled out the possibilities that distance flown is gauged by (a) measuring and integrating airspeed or (b) measuring and double-integrating acceleration. Details of these experiments can be found in Srinivasan et al. (1997).

A similar set of studies, conducted subsequently on stingless bees (*Melipona seminigra*), has revealed that that these creatures, too, rely on optic flow cues for gauging foraging distance (Hrncir et al. 2003). Furthermore, these bees also use optic flow information to locate food sources in the vertical plane—which is important, given that they live and forage in forest environments in which the nest and the food source can be separated in three dimensions (Eckles et al. 2012).

The waggle dance as a window into the bees' perception of travel distance

Esch and Burns (1995, 1996) investigated distance measurement by honeybees through a different experimental approach; namely, that of filming the bees' dances in the hive when they returned from an artificial feeder, placed

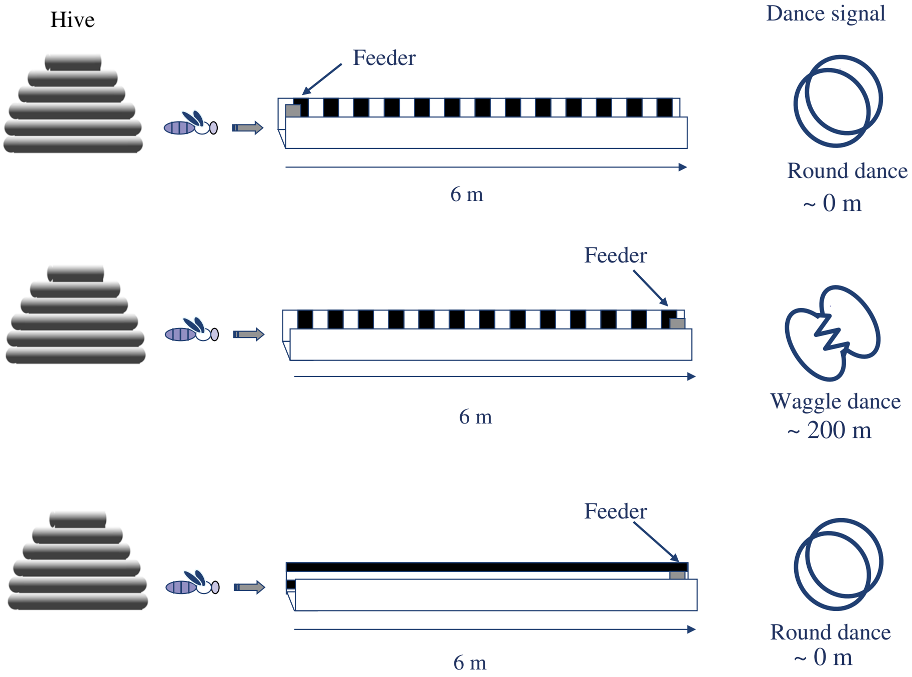

Fig. 4 A test of the hypothesis that bees measure the distance travelled to a food source in terms of the optic flow experienced en route. Bees were trained to forage in a narrow tunnel, 6 m long, placed very close to the hive. When foraging at a feeder placed at the tunnel entrance, they performed a round dance (*upper panel*). However, when the feeder was moved to the end of the tunnel, the bees performed a waggle dance indicating a distance of 200 m, hugely overestimating the distance that they had actually flown (*middle panel*). When the feeder was kept at the same position but the transverse stripes lining the tunnel were replaced by axially oriented stripes (which induced little or no optic flow) the bees performed a round dance, signalling that they had now flown a negligible distance (*lower panel*). This experiment (Srinivasan et al. 2000) confirms the hypothesis that the honeybee's odometer is driven by optic flow

outdoors in an open meadow. They investigated how these dances changed when the height of the feeder above the ground was varied systematically, by attaching it to a weather balloon. When the feeder was on the ground, 70 m away from the hive, the bees correctly indicated a distance of 70 m. However, when the altitude of the feeder was increased, the bees did something quite surprising. Instead of signalling a larger distance—as one might expect, since they were now flying a longer route to the feeder, and expending more energy to get to it—they signalled a *shorter* distance. When the feeder was 90 m above the ground, and at a horizontal distance of 70 m from the hive, the bees indicated a distance of as little as 25 m! From this observation, Esch and Burns inferred that distance flown is gauged in terms of the motion of the image of the ground. The higher the bee flies, the slower the ground beneath her appears to move. This conclusion is completely consistent with the results of the tunnel experiments. Evidently, then, visual odometry is not only used in short-range navigation––as in the tunnel experiments—but also in situations that typify longer, outdoor flights.

The above findings may partly explain why the early studies erroneously concluded that the honeybee's odometer uses energy consumption as the primary cue. Burdening a bee with a steel ball would tend to make her fly closer to the ground, thereby increasing the image motion that she experiences from the ground and causing her to report a larger distance in her dance (Esch and Burns 1996). Similarly, when a bee flies in a headwind she may fly closer to the ground, either to maintain the same image velocity as she would in still air, or simply to 'duck the breeze'. This would, again, increase the image motion, and therefore the odometric reading. Although these explanations are presently only speculations that need to be checked, they illustrate, rather disturbingly, how easily one can be led to erroneous conclusions about mechanisms.

We have seen above that the balloon experiment caused bees to underestimate the distance they had flown, because they experienced an optic flow that was weaker than what they would normally experience during normal, level flight. What happens when bees encounter the opposite situation; namely, one in which image motion cues are artificially exaggerated?

Srinivasan et al. (2000) explored this question by training bees to fly directly from their hive into a short, narrow tunnel that was placed very close to the hive entrance (Fig. 4). The tunnel was 6 m long and 11 cm wide. A feeder was placed 6 m from the entrance. The walls and floor of the tunnel were lined with vertical stripes. The dances of bees returning from this feeder were video-filmed. Incredibly, these bees signalled a flight distance of ca. 200 m, despite the fact that they had flown only a small fraction of this distance. Evidently, the bees were overestimating the distance they had flown in the tunnel, because the proximity of the walls and floor of the tunnel greatly magnified the optic flow that they experienced, in comparison with what would normally occur when foraging outdoors. On the other hand, when the bees were flown in a tunnel of the same dimensions, but lined with axial stripes, the bees produced a ‘round dance’ (von Frisch 1993), signalling the experience of a very short journey (Fig. 4). Evidently, in this case, the absence of optic flow caused the odometer to barely tick over (Srinivasan et al. 2000). These experiments again drive home the point that image motion is the dominant cue that bees use to gauge how far they have travelled.

Do the hive mates pay attention to the ‘erroneous’ dances made by bees returning from the tunnel, and if so, how do they respond to these dances? It turns out that the dances indeed recruit other foragers (Esch et al. 2001). Furthermore, the foragers do not fly into the tunnel in search of the advertised food: they search at the distance indicated by the dance, i.e. almost 200 m away! This finding reveals that the dance does not signal an “absolute” distance to potential recruits: rather, it specifies the amount of image motion that they should experience en route to the food. The recruits simply fly outdoors, in the appropriate direction, until they have “played out” the prescribed amount of image motion.

The above experiment also addresses another controversy that has lingered in the literature for many years in relation to the significance of the honeybee’s waggle dance. An alternative hypothesis (Wenner and Wells 1990) proposes that—although the dance undoubtedly contains information about the distance and direction of the food source—this information is not used by the recruits to find the food. Rather, the recruits home in on the food source by following scent cues acquired from the nectar or pollen that she has brought back, or by following the dancer herself to the food, using visual or olfactory cues (Wenner et al. 1969). According to this view, the waggle dance that is orchestrated by a bee is simply a device to gather the attention of potential recruits, to convey food samples to them, and to induce them to follow her, or the scent of the food, to the destination. Although it is possible (and even likely) that the recruits use these alternative strategies to help find the destination, they cannot account for the entire phenomenon of recruitment. In the tunnel experiment described above, if the recruits were relying purely on olfactory or visual cues to lead them to the food, they should have all arrived at the feeder in the tunnel. In fact, none of the recruits arrived at this feeder—all of them searched for the food at the dummy feeders that were located outdoors, far away from the tunnel feeder. Therefore, these recruits must have indeed been interpreting the dance in the symbolic, geometric fashion that von Frisch had initially postulated. In summary, the recruits derive abstract information about the location of the food source from the dance and, where feasible, they take advantage of additional olfactory and visual cues to find the destination.

From all of the above findings, we see that the ‘true’ calibration of the honeybee’s odometer cannot be in terms of the absolute distance to a food source. Rather, it must be in terms of the image motion that the bee experiences en route. The tunnel-dance experiment provides us with a convenient means of obtaining the desired calibration, because the tunnel environment, as well as the trajectory of the bee in it, are very well defined. Taking into consideration the geometry of the tunnel and the bee’s flight path within it, one can calculate a calibration factor for the honeybee’s dance as ca. 18° of image motion per millisecond of waggle duration (Srinivasan et al. 2000). In other words, 1 ms of waggle represents an 18° movement of the image of the environment in the eye.

Subsequent studies by Si et al. (2003) indicate that the perception of distance travelled is relatively robust to variations in the contrast or the spatial frequency content of the patterns that are used in the experimental tunnel. Thus, the visual odometer is capable of measuring the true extent of image motion in the eye, largely independently of the visual properties of the environment through which the flight occurs. Furthermore, a strong odometric signal is generated even when it is only the walls or the floor of the tunnel that provide optic flow cues. It appears, therefore, that distance flown is measured by a mechanism that is quite robust to variations in the texture or the sparseness of the visual environment that the bee experiences. However, when this sparseness is pushed to the limit, such as during flight over a still lake, the odometric signal does become weaker (Tautz et al. 2004).

The above results indicate that image motion is critical to odometry in bees, and suggest that distance travelled is measured by integrating the amount of image motion that is experienced over time. Ugolini (1987) transported wasps passively in transparent containers from their nests to various sites, then released them and observed their homing trajectories. He found that the wasps headed accurately toward their homes when they had been taken to the release site in a transparent container—and could thus observe their passage through the environment—but not when they were transported in an opaque container. These findings indicate that wasps, like bees, infer the direction and distance of their travel by observing the apparent orientation and motion of the visual panorama.

Advantages and limitations of visual odometry in honeybee navigation

What are the advantages and disadvantages of a visually based odometer? Unlike an energy-based odometer, for example, a visually driven odometer would not be largely affected by wind or by the load of nectar that the bee carries. It would also provide a reading that is independent of the speed at which the bees flies to the destination, because this reading would depend only upon the total amount of image motion that is registered by the eye, and not upon the speed at which the image has moved during the journey. However, as we have seen above, a visual odometer would work accurately only if the bee followed a fixed route each time it flew to its destination (or if a follower bee adhered 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. Indeed, the dances of bees from a given colony exhibit substantially different distance–calibration curves, when they are made to forage in different environments (Esch et al. 2001). The strong waggle dances of bees returning from a short, narrow tunnel illustrate this point even more dramatically. However, the unavoidable dependence of the dance on the environment may not be a problem in many natural situations, because bees flying repeatedly to an attractive food source tend to remain faithful to the route that they have discovered (e.g. Collett 1996). Since the dance indicates the direction of the food source as well as its distance, there is a reasonably good chance that the new recruits, which fly in the same direction as the scout that initially discovered the source, will experience the same environment, and therefore fly the same distance.

There is another complication, however. Even if all bees take the same route to a food source, they may not necessarily fly at the same height. And if they derive their odometric signal from the motion of the image of the ground, the signal will vary substantially, depending upon the height of flight. The question that then arises is: Which regions of the bee's visual field contribute to the odometric signal? To explore this question, Srinivasan et al. (1997) investigated the ability of bees to locate the position of a feeder placed in tunnels in which optic flow cues were selectively removed from the walls or the floor. These results suggested that odometric cues are derived primarily from the lateral fields of view, and not the ventral field. However, this is in contradiction to the findings of Si et al. (2003), described above, which suggest that both the ventral and the lateral fields of view contribute substantially to the odometric signal.

One advantage of ignoring the ventral field and using just the lateral fields of view when the environment contains lateral structures (e.g. tall trees), is that the odometric signal would be independent of the height at which the bee flies above the ground. The balloon experiment of Esch and Burns (1995), however, suggests that bees do pay attention to the apparent motion of the ground beneath them. However, these experiments were conducted in an open meadow where the only motion signals that were available were those generated by the ground. 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 may have estimated distance more accurately, had they had visual access to laterally located structures. Further work is needed to explore, in a more comprehensive way, which eye regions are used for visual odometry, and to examine whether these regions vary, depending upon the environment in which the bee forages. It is also necessary to investigate whether bees tend to (a) fly at a preferred height, or (b) have some way of estimating and accounting for the height at which they are flying when making their odometric calculations—although the findings of Esch and Burns seem to argue against this possibility.

Preventing the accumulation of errors in odometry

What are the consequences of measuring travel distance by integrating optic flow? One consequence would be 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, Srinivasan et al. (1997) examined the accuracy with which bees were able to localise a feeder when it was placed at various distances along a tunnel. The results (Fig. 5) show that the width of the search distribution indeed increases progressively 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, Srinivasan et al. (1997) examined the bees' performance when they were again trained to fly to a feeder placed at a large distance into a tunnel (Fig. 5), but now had to pass a prominent landmark (a baffle consisting of a pair of overlapping partitions) occurring en route to the feeder. If these bees reset their odometer at the landmark, they should display a smaller error because they would then only need to measure the distance between the landmark

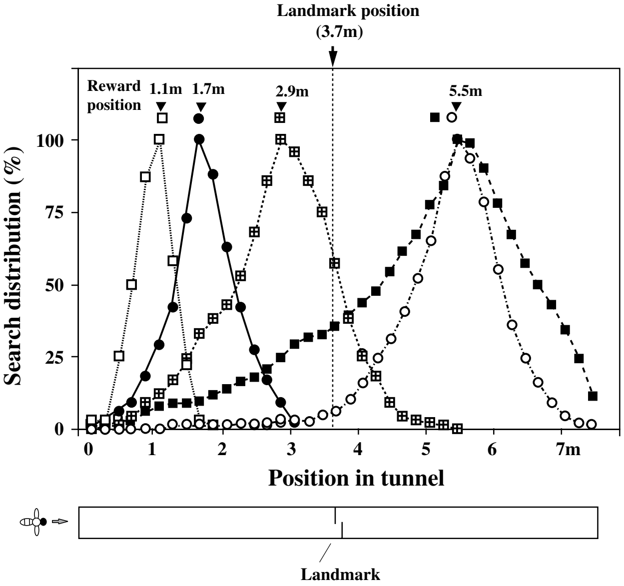

Fig. 5 Search distributions of bees that have previously been trained to forage at a feeder that has been positioned at a distance of 1.1 m (*open squares*), 1.7 m (*filled circles*), 2.9 m (*grid squares*) or 5.5 m (*filled squares*) from the entrance of a long tunnel. The search distribution becomes progressively wider as the training distance increases, indicating that the error in distance estimation increases with distance flown. However, if bees are trained to the long distance (5.5 m) with a prominent landmark, consisting of a baffle placed en route at 3.7 m, the resulting search distribution is substantially narrower (*open circles*). This indicates that bees reduce cumulative errors in the odometer by resetting the odometer at prominent landmarks. Further details in Srinivasan et al. (1997). Adapted from Srinivasan et al. (1997)

and the feeder. This is precisely what occurred: the search distribution was then significantly narrower (open circles, Fig. 5). Furthermore, when the trained bees were confronted with a test in which the landmark was positioned closer to the tunnel entrance, the bees' mean search position shifted toward the entrance by almost exactly the same distance (Srinivasan et al. 1997). These results confirm that bees re-commence computation of distance when they pass a prominent landmark, and that such landmarks are used to enhance the accuracy of the odometer.

Further experiments are required to determine whether bees 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), and Collett and Collett (2002) and Chittka et al. (1995) indicates that foraging bees 'expect' to see a specific sequence of landmarks situated at particular distances on the way to the food source, and that they monitor their progress toward the destination by checking whether the expected landmarks show up at the appropriate distances. Considering their findings together with those described above, one may conjecture that bees 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 to thereby improve the accuracy of distance estimation. On the other hand, if a landmark appears much earlier than expected—or does not appear at all—the bee might resort to using the prevailing odometric signal to determine where to look for the target. Further investigation is needed, however, to fully understand the interplay between visual odometry and landmarks in navigation.

Can bees locate a food source by counting a small number prominent landmarks encountered en route?

In a pioneering investigation, Chittka and Geiger (1995) trained bees to forage at an outdoor feeder in a situation in which they had to pass three prominent landmarks (tents) that had been erected long the route. The trained bees were then tested for their ability to use a running count of landmarks to locate the position of the feeder. This test was carried out by varying the number of landmarks along the route, and determining the bees' preferred searching positions by comparing the frequencies with which they visited a series of empty feeders placed along the route. They found that, whilst the bees searched primarily at a location that corresponded to the correct odometric location (i.e. at the actual distance of the feeder from the hive during the training), there was a second, but weaker search effort that was concentrated at a location that corresponded to the correct landmark count. In other words, even when the separation between the landmarks was varied substantially, there was a small tendency to search for the feeder when the correct number of landmarks had been passed. This was the first demonstration that bees can count the landmarks that they encounter sequentially on the way to a food source. This ability was subsequently confirmed by Menzel et al. (2010), who also showed, however, that the dominant distance cue is odometry. Dacke and Srinivasan (2008) showed that bees could be trained to ignore their odometer, and rely almost exclusively on landmark counts, if the training paradigm is modified such that the distance of the feeder is varied frequently and randomly during the training, whilst the number of landmarks that are passed is held constant. This paradigm, in effect, teaches the bees that the relevant cue is not the distance travelled, but the landmark count. In other words, this paradigm attempts to train the bees to ignore the signal from their visual odometer. These experiments revealed that bees could indeed be trained to ignore their odometer and locate the feeder by counting landmarks sequentially—independently of distance that they had flown. Bees were able to count up to a maximum number of four landmarks (Dacke and Srinivasan 2008). Further experiments revealed that bees, trained to find food after passing a prescribed number of landmarks, were able to accomplish this task even a novel situation where the landmarks were of a different shape and size (Dacke and Srinivasan 2008). This revealed that the bees were counting the landmarks as individual entities, and not simply summing-up the total retinal area of landmarks encountered en route, to pinpoint the goal. In a natural situation, however, where bees learn to locate a food source at a fixed distance from the hive, the ability to count landmarks along the way is evidently not called upon.

Is flight distance measured on the way to the food source, or on the way back?

This question, which has a long history (von Frisch 1993), was examined more recently in an experiment in which the outbound and inbound distances were manipulated independently (Srinivasan et al. 1997). Bees were trained to fly into a tunnel to a feeder that was placed at a certain distance (X) from the entrance. After a bee had entered the tunnel and alighted at the feeder, the tunnel was quickly extended by placing an additional section (of length Y) at the entrance. Thus, when leaving, the bee had to fly a distance ($X + Y$) to leave the tunnel. This procedure was carried out for each bee that was trained. When a bee trained in this way was tested in a fresh tunnel that carried no reward, it searched for the reward at a distance X from the entrance, after entering the tunnel. When the same bee was tested by allowing it to feed at a reward placed at a distance X from the entrance, and then quickly adding a long tunnel section to the front of the tunnel before it departed, the departing bee searched for the exit of the tunnel at a distance X from the feeder, in the homeward direction (Srinivasan et al. 1997). These findings indicate that, at least in this kind of experiment, honeybees register only the outbound distance to the food source, and not the return distance. However, similar experiments conducted with stingless bees (*Melipona seminigra*) yield the opposite result, namely, that the learned distance is that corresponding to the return flight (Hrncir et al. 2003). It is unclear whether this discrepancy is due to species differences, or other, as yet unknown factors. The results with the honeybees are in agreement with most of the earlier field studies in which honeybees were trained to forage at distant feeders under various environmental conditions, and their dances were recorded. For example, bees exhibited longer waggles in their dances when flying uphill (or upwind) to a feeder, rather than downhill (or downwind) to it (Heran and Wanke 1952; Heran 1956; von Frisch 1993). These findings suggest that distance is inferred on the way to the food source rather on the way back, regardless of the mechanisms that might be involved in estimating the distance (see Srinivasan et al. 1997 for a detailed discussion). The results of these experiments are consistent with the hypothesis that bees gauge distance primarily on the outbound flight. Otto (1959) trained bees outdoors to fly one distance to a feeder on their outbound flight, and a different distance in the return flight by quickly moving the feeder, with the feeding bees, to a different location before allowing them to return home. He found that the bees signalled in their waggle dances a distance that was intermediate in value between the outbound and the return distances, suggesting that they were using an average of the two distances. Further investigation is required to understand why Otto's findings are at variance with most of the others.

When a scout bee first discovers a new food source, its initial outbound trajectory is likely to be tortuous, because it would not have known the location of the food. However, the return flight is likely to be closer to the proverbial 'beeline', if the bee's path integration system has functioned properly. From this standpoint, it would be more sensible for the scout bee to signal the direct, return distance to the recruits in her dance, rather than the tortuous distance measured during the outbound flight. Furthermore, since the recruited bees are meant to follow the direct route to the feeder, it would make sense to convey the distance as inferred by the optic flow signals that are experienced along the direct route. On the other hand, it should be noted that bees rarely dance upon their first return from a newly discovered food source. Typically, they begin to advertise the source only after they have visited it at least 4–5 times (von Frisch 1993; Tautz 2008). Presumably, this delay ensures that (a) the food supply is steady and reliable and (b) the direct route to the food source has been learned accurately, and flown repeatedly. Once this has occurred, it should not matter whether the distance is reckoned from the outbound or the inbound route, because the two routes coincide. Nevertheless, two further requirements need to be met. First, the series of images captured by the eyes during the outbound flight should be exactly that same as that captured on the return flight, only reversed in sequence. However, this will be strictly true only if the eyes capture a fully panoramic snapshot of the scene at each step along the route. If, on the other hand, flight distance is reckoned primarily from the flow experienced by the frontal and lateral fields of view (and not the rear field), then the outbound view from any point along the journey will, in general, be different from the homeward view at the same point. This is likely to be the case, because of the blind zone in the rear of the bee's visual field. Hence, the sequence of images experienced during the return flight would not simply be the reverse of the sequence experienced in the forward flight. Consequently, there is no guarantee that the integrated readings of optic flow will be the same in the two directions—unless the landscape and the illumination satisfy rather stringent symmetry requirements. Given this, it would be preferable to use visual information derived from the outbound flight to compute and signal the flight distance to a potential recruit, whose first journey will obviously be along the outbound route. Second, a bee will most likely fly with an empty crop to the food source, and return fully laden with her weight nearly doubled. If she uses energy consumption even only as a partial cue to obtain an estimate of the distance flown, this estimate will be considerably lower on the way to the food source, than on the way back (von Frisch 1993). Even if the distance estimate is based solely on optic flow information and not on energy consumption at all, it is likely that a fully laden bee returning home will fly closer to the ground and therefore experience a greater optic flow from it, than a lighter individual that flies from the hive to a food source (Esch and Burns 1996). Since recruits leave the hive with a nearly empty crop, it would make sense for a dancing bee to signal the distance as estimated from its outbound journey, so as to match the conditions that would be experienced by the new recruit.

Odometry in more than one dimension

When a bee flies a straight route to a food source and returns to the hive, she signals the distance to the food source in terms of the duration of the waggle phase in her dance, and the direction of the food source with reference to the celestial compass, as described briefly at the beginning of this article. What happens, though, when a bee has to circumvent a large obstacle—such as a hill or a building—to get to her destination? A number of classic ‘detour’ experiments carried out by von Frisch (1993) and colleagues have revealed that bees returning from such a journey signal the *bee-line direction* to the food source (i.e. the direction of the home-based vector that points to the food source). Interestingly, however, the distance that these bees signal in their dances is not the length of the resultant (short-cut) vector, but the *total length of the circuitous path* that they are forced to take as a result of the detour—a much larger distance. Thus, when bees are trained to fly around a hill to find a feeder on the other side, by moving the feeder steep by step around the perimeter of the hill—thus making a large detour on the way to the food—they signal in their waggle dances the *vector direction* of the food source from the nest, but the perimeter length of the circuitous journey, rather than the vector distance (von Frisch 1993, pp. 174–180). However, the bees that are recruited by the dance never take the detour—they heed the dancer’s instructions and take the short-cut over the hill, rather than fly around it (Gould and Gould 1988, pp. 178–80; von Frisch 1993, p. 64).

When bees are forced to make detours, why do they signal the total path length to the target rather than the direct vector distance, given that the recruits take the short-cut? One reason may be that even the short-cut route over the hill is likely to be longer than the direct distance between the hive and the nest in the horizontal plane, because the short-cut actually involves flying up and down the hill. In one such detour experiment conducted by von Frisch and Lindauer in 1950, the route around the hill was 133 m, the length of the short-cut vector in the horizontal plane was 80 m, and the length of the actual flight along the short-cut route that the recruits took (up and down the hill) was 150 m (von Frisch 1993, p. 177). Another reason for signalling the actual length of the route, rather than the vector distance, may be that the former value provides a more accurate estimate of the distance that must be flown if the obstacle is so tall that it cannot be flown over. The perimeter length would then give the potential recruits a realistic estimate of the distance that they would need to fly to get to the food, and thus enable them to compare the ‘attractiveness’ of that source with other sources that are being advertised by other dancers (but see later below).

In a more recent study, bees were flown along a straight tunnel that simulated flight through an L-shaped tunnel, by rotating the artificial overhead compass cues by 90°, halfway down the tunnel (Evangelista et al. 2014). This was accomplished by providing the tunnel with polarized overhead illumination that was oriented perpendicular to the tunnel axis in the first half of the tunnel, and parallel to the tunnel axis in the second half. Bees returning from a feeder placed at the end of this tunnel signalled a direction of 45° for the food source in their dances, corresponding to its true vector direction. However, they did not indicate the apparent vector distance to the destination. Rather, they signalled a distance that corresponded to the full length of the straight tunnel (or the perimeter length of the virtual L-shaped tunnel). In a sense, this finding can be viewed as a small scale, laboratory-based confirmation of von Frisch’s hill-detour experiment, described above.

Signalling of the perimeter distance in dances is also observed when bees fly journeys in the vertical plane. For example, in another study, bees were trained to fly through an L-shaped tunnel in the vertical plane, which required them to fly initially through a vertical section—during which their eyes experienced vertically directed optic flow––and then through a horizontal section—during which the eyes experienced horizontally directed optic flow (Dacke and Srinivasan 2007). The distance that the bees then signalled in their waggle dances corresponded to the optic flow that was experienced over the total distance flown in the tunnel, rather than the distance corresponding to the hypotenuse (Dacke and Srinivasan 2007).

Is odometric information taken into consideration when signalling the profitability of a food source?

One would conjecture that the attractiveness or 'profitability' of a food source depends not only upon the quality of the nectar or pollen that it offers, but also upon the distance (and/or the time and the energy expenditure) that would be required to fly to it. Studies of the waggle dance have revealed that the attractiveness of a food source is signalled in terms of (a) the number of loops executed during a dance bout (the larger the number loops, the greater the attractiveness) and (b) the time interval between successive loops (the shorter the time interval, the greater the attractiveness) (Seeley 1995). Do honeybees take the apparent distance of a food source (as signalled by their odometer) into account in estimating its attractiveness? To examine this question, Shafir and Barron (2009) conducted an elegant series of experiments in which they compared the choices (and waggle dances) of bees in a setup that offered a choice of two tunnels, each of which had a feeder at the far end offering sugar solution of the same concentration. The walls and floor of both tunnels were lined with a visual texture that provided optic flow cues. One tunnel was short (but narrow), and was expected to generate a greater odometric signal than the other tunnel, which was 2.5 times long, but 4 times as wide. This was confirmed by comparing the waggle durations of bees returning from the two tunnels. However, the analysis of the dances revealed that the bees found the shorter tunnel to be more attractive, despite the fact that it generated a greater odometric signal. A comparison of the flight durations in the two tunnels revealed that bees required a significantly greater time to reach the reward in the long tunnel. This finding reveals that factors such as time of flight, and possibly energy consumption, play an important part in determining the attractiveness of a food source, although one cannot completely discount a role for the odometric signal as well.

Neural mechanisms that might underlie visual odometry

What are the neural mechanisms by which the distance signal is computed? Where, in the insect's brain, is the odometer located? At present we are completely in the dark with respect to the answers to these questions. It is well known that the visual systems of flying insects, in particular, flies (e.g. Egelhaaf et al. 2005; Borst 2009) and bees (e.g. Kaiser and Bishop 1970; Paulk et al. 2009), contain neurons that respond strongly to image motion. Ibbotson (1991, 2001) has reported the existence of spiking visual interneurons in the bee that respond to the movement of patterns in the front-to-back direction in each eye. The spike frequencies of these neurons increase approximately linearly with pattern velocity. The output of such a neuron, integrated over the time of flight, would provide a signal that indicates how far the bee has flown, independently of the speed at which the bee flies to the destination. In other words, the total number of spikes fired by the neuron would be a representation of the distance covered. Such a mechanism, however, would require a means of counting spikes over the rather long time that is characteristic of a bee's outdoor flights––typically, at least a minute.

Another possibility is that the distance flown is represented in terms of the activity of "place neurons", analogous to those that exist in the vertebrate hippocampus. It has been suggested that the so-called mushroom bodies of the insect brain are structures that are analogous in function to the hippocampus of rodents and primates (O'Keefe and Nadel 1978; Ekstrom et al. 2003). Indeed, there is some evidence for the existence of neurons in the mushroom bodies that display responses similar to the place neurons in the vertebrate hippocampus (Mizumani et al. 1998a, b). If this were the case, the bee's flight toward its destination would induce transient activity in a succession of place neurons, which register the passage through successive locations along the journey. The place neuron that is active at the end of the journey would represent the location of the food source, as well as the distance of the food source from the hive. In this scheme, there would be no need to accumulate spike counts over the entire journey—it would only be necessary to shift the activity from one place neuron to the next, every time the image motion, accumulated since the activating the most recent place neuron, has reached a prescribed threshold magnitude.

Although the honeybee possesses excellent trichromatic colour vision—comprising UV, blue, and green-sensitive photoreceptors—the evidence so far suggests that all of the movement-dependent behaviours in this animal are "colorbind", and are driven exclusively by the green-sensitive receptors (Srinivasan 2011). This is also true for visual odometry (Chittka and Tautz 2003). Thus, the movement-sensitive neurons that drive the visual odometer are also likely to be green-sensitive, and this characteristic spectral signature could be used to aid the search for the odometer in the honeybee's visual pathway.

Just how odometry works at the neural level remains a fascinating and enigmatic question that is yet to be explored.

Acknowledgments We thank the anonymous reviewers for their valuable suggestions for improvement of the manuscript. This work was supported by Australian Research Council (ARC) Centre of Excellence in Vision Science Grant CE0561903, ARC Discovery Grant DP0559306, and by a Queensland Government Premier's Fellowship.

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