

Two odometers in honeybees?

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SUMMARY

Although several studies have examined how honeybees gauge and report the distance and direction of a food source to their nestmates, relatively little is known about how this information is combined to obtain a representation of the position of the food source. In this study we manipulate the amount of celestial compass information available to the bee during flight, and analyse the encoding of spatial information in the waggle dance as well as in the navigation of the foraging bee. We find that the waggle dance encodes information about the total distance flown to the food source, even when celestial compass cues are available only for a part of the journey. This stands in contrast to how a bee gauges distance flown when it navigates back to a food source that it already knows. When bees were trained to find a feeder placed at a fixed distance in a tunnel in which celestial cues were partially occluded and then tested in a tunnel that was fully open to the sky, they searched for the feeder at a distance that corresponds closely to the distance that was flown under the open sky during the training. Thus, when navigating back to a food source, information about distance travelled is disregarded when there is no concurrent input from the celestial compass. We suggest that bees may possess two different odometers – a ‘community’ odometer that is used to provide information to nestmates *via* the dance, and a ‘personal’ odometer that is used by an experienced individual to return to a previously visited source.

Key words: odometer, celestial compass, path integration, honeybee, *Apis mellifera*.

INTRODUCTION

When foraging honeybees search for new food sources, they typically perform meandering journeys over large distances. Yet, when they have found a food source they fly a direct route back to their home (von Frisch, 1967; Chittka and Kunze, 1995). After returning to the hive, these bees communicate to their nest mates the distance and direction in which to fly to reach this food source. The information is encoded in the waggle dance (von Frisch, 1967), which consists of a series of alternating clockwise and anti-clockwise loops, interspersed by a phase in which the bee waggles her abdomen from side to side. The length of this waggle run signals the distance flown and the orientation of the waggle axis relative to gravity signals the azimuthal direction of the food source, relative to the direction of the sun (von Frisch, 1967). Thus the waggle dance not only enables the forager to convey important information about the location of an attractive food site to her nestmates, but also allows the experimenter to probe the bee’s internal representation of space.

After the waggle dance, the foraging bee will set out again for the very same food source, only a few minutes later. The ability to navigate back and forth between the food source and the hive is partly based on the knowledge of familiar terrain (De Marco and Menzel, 2005), but also partly on a path integrator, which performs an approximate form of dead reckoning (Collett and Collett, 2000; Wehner and Labhart, 2006; Wehner and Srinivasan, 2003; Wehner and Wehner, 1990). To perform path integration, an animal would need two types of information: (1) directional information with reference to an external compass cue and (2) information about the distance travelled in a particular direction (Müller and Wehner, 1988; Wehner, 1994). It is well established that bees estimate the distance flown by measuring the optic flow perceived during flight (Dacke

and Srinivasan, 2007; Esch and Burns, 1995; Esch and Burns, 1996; Si et al., 2003; Srinivasan et al., 1996; Srinivasan et al., 1997; Srinivasan et al., 2000; Esch et al., 2001). The cues involved for the assessment of travel direction are however less clear, but celestial cues are likely to play a major role. When given a view of the sky – or a beam of artificially polarized light – a dancing bee will momentarily orient its dance to the orientation of this compass cue (Rossel and Wehner, 1982; Rossel and Wehner, 1984; Rossel and Wehner, 1986; von Frisch, 1949; von Frisch, 1967; Wehner and Strasser, 1985). Morphological and electrophysiological studies of the bee retina further show that an extensive part of the dorsal eye is structurally and functionally similar to the dorsal rim area that is known to be used for polarized light navigation in other insects, such as desert ants, crickets and dung beetles (Dacke et al., 2003; Labhart, 1980; Menzel and Snyder, 1974; Wehner, 1982; Wehner and Labhart, 2006).

In honeybees, very little is known about how the information on the distance and direction of flight is combined to determine where the food source is located in relation to the nest. Here we address the question by asking how information about travel distance is used in the absence of directional (celestial compass) information. Individually marked bees were trained to find a reward of sugar solution that was placed at a fixed distance inside a tunnel. The length of the tunnel that was visible to the sky (or occluded from it) was under experimental control – part of the open top was closed by means of opaque panels. In one set of experiments, we filmed the waggle dances of the trained bees when they returned to the hive. In another series we recorded the behaviour of the trained bees, one by one, when they searched for the food in a fresh, identical tunnel that carried no reward.

MATERIALS AND METHODS

The experiments were performed in Canberra, Australia. Bees (*Apis mellifera* L.) from an observation hive were trained to forage within a linear tunnel placed outdoors, 10 m from the hive. The tunnel was 11 cm wide, 20 cm high and 7 m long. The walls and floor of the tunnel were lined with a black-and-white checkerboard pattern of 3 cm×3 cm squares. A strip of black insect screen formed the roof of the tunnel, allowing the bees a full view of the sky. Opaque panels, made out of thick cardboard, could be fitted on top of the tunnel to prevent the bees from receiving skylight input in selected segments of the tunnel. The panels were 12 cm wide and 33.3 cm or 66.6 cm long.

For each experiment, up to 30 individually marked bees were trained to forage from a feeder containing sugar solution placed 4 or 6 m into the tunnel. The bees were allowed to fly back and forth between the nest and the feeder for at least 1 day, in order to get accustomed to the tunnel. The far end of the tunnel was closed, and bees could only enter or leave the tunnel through the end nearest to the hive. Dances performed by marked bees returning from the hive were filmed using a digital video camera and later analysed.

Analysis of waggle dance

In the first series of experiments, a group of bees was trained to visit a feeder placed in an open tunnel. The feeder was placed at a distance of 4 m or 6 m along the tunnel (Fig. 1A). Dances of bees returning from the tunnel were then recorded for both distances. A second group of bees was trained to fly 6 m into a straight tunnel covered with three opaque panels, each 66.6 cm long. The panels were placed 0.66, 2.0 and 3.33 m down the tunnel (Fig. 1B). This formed a set-up in which celestial compass cues for orientation were unavailable in 2 m of the first 6 m of the tunnel. The dances of bees returning from the partly covered tunnel were also recorded.

The walls of the observation hive were transparent, thus enabling the viewing and filming of bee dances. A dance performed by a bee returning from the tunnel typically consisted of a number of loops. Most of these loops included a waggle component, whereas a few did not. The duration of the waggle component was measured for 30 dances under each experimental condition. The Student's *t*-test and single factor ANOVA were used to test for statistically significant differences between the mean waggle durations under different flight conditions.

Analysis of food searching behaviour

As described above, 20 honeybees were trained to fly within a 7 m tunnel covered with 3 opaque panels, each with a length of 66.6 cm (with a total length of 2 m), to find a reward of sugar solution placed

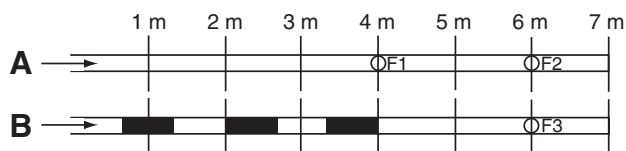


Fig. 1. Schematic representation of the tunnels used for training foraging honeybees. (A) Bees were trained to forage in an open tunnel, with the feeder (F1) placed first 4 m and then 6 m (F2) down the tunnel. (B) A second group of bees was trained to fly to a feeder (F3) placed 6 m down the tunnel fitted with three opaque panels, each 66.6 cm long. The panels were placed 0.66, 2.0 and 3.33 m into the tunnel. The black areas represent the covered sections. By placing the panels on top of the tunnel, the use of celestial cues for compass orientation was made impossible in 2 m of the first 6 m of the tunnel.

6 m into the tunnel (Fig. 2A). After training, the bees were individually tested in an 8 m long tunnel that contained no food reward. Different tunnel lengths for training and testing the bees ensured that the distance to the end of the tunnel could not be used as an indication of the position of the reward. Three kinds of tests were performed. In the first kind of test, the panels used to occlude skylight were identical in position and size to those used during training (Fig. 2B). In the second kind of test, the total occlusion of the tunnel was decreased to 1 m. A panel of length 66.6 cm was placed 0.66 m from the tunnel entrance, and a second panel of length 33.3 cm was placed 3.66 m from the entrance. (Fig. 2C). In the third kind of test, all panels were removed and the bees flew with a full view of the sky along the entire length of the tunnel (Fig. 2D).

For the purpose of analysis the test tunnel was subdivided into 80 sections, each 10 cm long. In their search for food, the bees typically flew back and forth along the test tunnel, making a number of U-turns as they searched for the missing reward. This searching behaviour was quantified by recording visually the position in the tunnel at which the bee made the first four U-turns. By measuring the number of times the bee entered each unit during these turns, we could estimate the spatial distribution of its search (Fig. 2E). For each test, the mean and standard deviation (s.d.) of the search positions of the four U-turns measured for each bee were calculated. Student's *t*-tests were used to test for the statistical significance of any difference between the search positions in the three experiments, as well as the difference between the expected and the experimentally measured positions.

RESULTS

We began by training bees to fly first 4 m, and then 6 m down a linear tunnel with a full view of the sky (Fig. 1A). As has previously been reported, the mean waggle durations of these dances were substantially greater than for similar distances flown outdoors. Furthermore, and as previously reported (Si et al., 2003), the duration of these dances increased with distance flown in the tunnel. The mean waggle duration was 141 ms at a distance of 4 m ($N=30$, 275 loops) and 260 ms ($N=30$, 252 loops) at 6 m (Fig. 3). This is consistent with earlier conclusions that honeybees gauge the distance flown from the extent of the image motion that is experienced by the eye en route to the food source (Dacke and Srinivasan, 2007; Esch and Burns, 1995; Esch and Burns, 1996; Si et al., 2003; Srinivasan et al., 1996; Srinivasan et al., 1997; Srinivasan et al., 2000; Esch et al., 2001).

In this study we address the question of whether information about travel distance is used in the absence of directional information. The above results from flights in an open tunnel provide a baseline against which to compare data from flights inside a partly covered tunnel.

Distance estimation encoded in the waggle dance after a foraging flight with an interrupted view of the sky

A fresh group of bees was trained to fly to a feeder 6 m into an 8 m long tunnel fitted with three opaque panels on top, each panel was 66.6 cm long (Fig. 1C). This set-up prevented the bees from obtaining any celestial cues for 2 m of the first 6 m of the tunnel. In other words, the bee had access to celestial compass information for 4 m of the 6 m long flight to the feeder. If the bees ignore information on travel distance when there is no concurrent input from the celestial compass, we would expect the mean waggle duration of the dance performed after a flight down this partly covered tunnel to be similar to that obtained after a 4 m flight down a fully open tunnel.

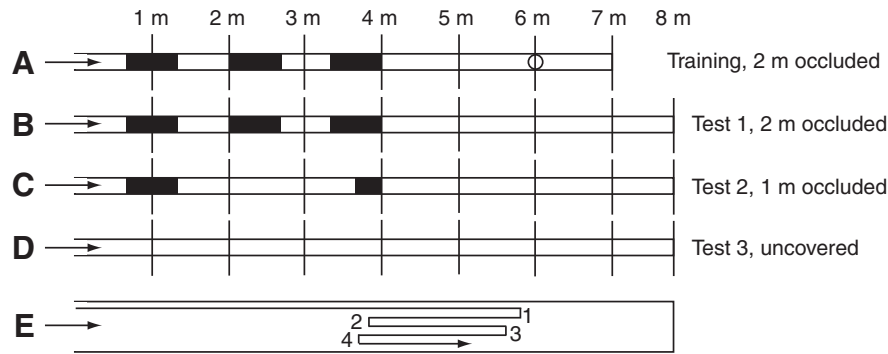


Fig. 2. Schematic representation of the tunnels used for training and testing foraging honeybees. (A) Training tunnel. Bees were trained to forage from a feeder (F) placed 6 m down a tunnel fitted with three opaque panels, each 66.6 cm long. The panels were placed 0.66 m, 2.0 m and 3.33 m into the tunnel. The black areas represent the covered sections. The opaque panels prevented the use of celestial cues for orientation in 2 m of the first 6 m of the tunnel. (B–D) Test tunnels. In the first test (B), the opaque panels were identical in position and size to the ones used during training. In the second test (C), the total covering of the tunnel was decreased to 1 m. A panel with a length of 66.6 cm was placed 0.66 m down the tunnel, and a second panel, 33.3 cm long, were placed 3.66 m down the tunnel. In the last test (D), the bees flew with a full view of the sky along the entire length of the tunnel. (E) In their search for food, the bees typically flew back and forth along the test tunnel, making a number of U-turns as they searched for the missing reward. This searching behaviour was quantified by observation and recording of the position in the tunnel at which the bee makes the first four U-turns (1–4).

The analysis of the dances of marked bees returning from this partly covered tunnel reveals that this is not the case (Fig. 3). The mean waggle duration of 286 ms ($N=30$, 335 loops) is significantly different from that measured for a 4 m flight ($P<0.001$), but is not significantly different from that obtained after a 6 m flight in a fully open tunnel ($P=0.27$). These results indicate that the waggle dance encodes the total distance flown, irrespective of celestial input.

A dancing bee that shuttles back and forth between the hive and the feeder in the tunnel is believed to base its navigation between these two sites on path integration (Collett and Collett, 2000; Wehner and Labhart, 2006; Wehner and Srinivasan, 2003; Wehner and Wehner, 1990). We can estimate the performance of this path integrating process by examining how precisely a bee is able to pinpoint the location of the food reward to which it has been trained.

Integration of distance information when navigating to a food source

Bees were trained to fly to a feeder placed 6 m down a 7 m long tunnel. The tunnel was covered with three opaque panels, each 66.6 cm long (Fig. 2A), to prevent the bees from receiving any skylight input for a total of 2 m of the 6 m they had to fly to reach the feeder. The bees flew back to the hive along the same tunnel. After training, bees were subsequently tested by recording their searching behaviour in a fresh 8 m long tunnel that carried no food reward (see Materials and Methods). Three types of tests were performed. In the first type of test, the configurations of the panels on top of the tunnel remained identical to those used during training (Fig. 2B). In the second type of test, half of this covering was removed, and the bees could now receive directional information from celestial cues for 5 m out of the first 6 m (Fig. 2C). In the third type of test, all of the panels were removed and the searching behaviour was recorded for bees flying with an uninterrupted view of the sky (Fig. 2D).

The results are shown in Fig. 4. The mean searching position (at 5.9 ± 0.5 m) in the tunnel with panels placed identically to the set-up used during training, is not significantly different from the position of the reward (at 6.0 m) during training ($P=0.56$; Fig. 4A). When we remove the covering, and provide the bees with celestial compass information over a relatively longer proportion of the tunnel

than during training, the position of search can be affected in two possible ways. If the distance to the feeder is again processed independently of the availability of celestial cues, we would expect the bees to continue to search 6 m down the tunnel irrespective of the portion of the tunnel that is covered. If, on the other hand, the bees, do *not* register distance flown in the absence of skylight input, we would expect them to search progressively closer to the entrance, as more and more of the covering is removed. Finally, when the tunnel is fully open, we would expect them to search for the feeder after they have flown just 4 m into the tunnel.

In the second test, with an additional 1 m of the tunnel open to the sky, the mean searching position (at 5.1 ± 0.5 m) was now found to be approximately 1 m closer to the entrance than in the first test (Fig. 4B). Following the above reasoning this result indicates that the distance travelled when returning to a known food source is largely ignored when there is no simultaneous input from the sky-view-based compass. The observed mean searching position at 5.1 m is not significantly different from the searching position of 5 m expected on this basis ($P=0.53$). In the third test, in which the 2 m of the covering used during training was removed, the mean searching position, at 4.3 ± 0.6 m, was now 2 m closer to the entrance (Fig. 4C). This position of search is also significantly different from that observed in the first and the second tests ($P<0.001$). The search distribution is broader than in the test in which the panels were positioned in the same way as in the training set, but the mean position of search does not differ significantly from an expected search distance of 4 m ($P=0.67$). The broadening of the search pattern in this condition suggests that additional cues, apart from the optic flow and celestial compass information, are to some extent involved in the navigational process. These cues could involve the spatial arrangement of the panels.

DISCUSSION

The encoding of spatial information

Our findings indicate that the location where the bees search for the missing feeder depends critically on the extent to which the sky is occluded during their journey to it. When bees are trained in a tunnel that is partially occluded and then tested in a tunnel that is fully open, they search at a distance that corresponds only to the distance that was flown under the open sky during the training. Thus,

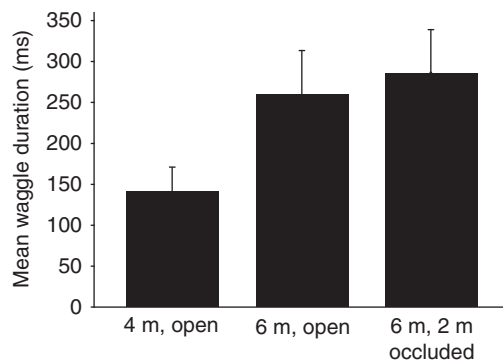


Fig. 3. The effect of varying the availability of celestial compass cues on the mean waggle duration of bees returning to the hive after feeding inside a tunnel. The bees returned from at a feeder that was positioned 4 m or 6 m into a straight tunnel that was fully open to the sky, and then from feeding 6 m down a tunnel where they were prevented from receiving any celestial input during 2 m of the first 4 m of the tunnel (for details of the set-up, see Fig. 1). Values are means \pm s.d. for each experimental condition. The mean waggle duration varies with the length of the tunnel, but not with the access to skylight cues.

in this case, information about travel distance is disregarded when there is no concurrent input from the celestial compass (Fig. 4).

There are three plausible explanations for this phenomenon. (1) The panels used to occlude the sky also serve as prominent landmarks, so that the position of the feeder is defined by the spatial distribution of these panels. (2) It is too dark underneath the opaque panels for optic-flow-based odometry to function correctly, so that flight distance is registered only in the open sections of the tunnel. (3) Odometric information is not processed when there is no directional information from the sky.

If the first explanation is correct then the positions of the individual panels, or the number of panels, served as landmarks to pinpoint the position of the feeder. Prominent landmarks in similar experimental set-ups are known to reset the odometer and help to define the distance to the feeder (Srinivasan et al., 1997), and the spatial distribution of landmarks can further help to pinpoint the position of the feeder (Collett and Collett, 2004; Collett and Zeil, 1996). It is clear from our test in the open tunnel, where all the panels had been removed, that the position of the search was not set by the positions of any of the panels. If the bees were pinpointing the position of the feeder on the basis of the position of the panels, they would not have commenced their search until they had encountered at least one of these panels. In the open tunnel the bees concentrated their search around the middle of the tunnel: a flight straight down to the end was never observed. By the same line of reasoning, we can also exclude the possibility that the feeder was pinpointed by counting the number of panels that preceded it (Chittka and Geiger, 1995; Dacke and Srinivasan, 2008).

Even if the prominent panels that covered parts of the tunnel did not serve as the primary cue in pinpointing the feeder, the searching distribution in the open tunnel was slightly wider than that recorded in the tunnel that was identical to the training configuration. This suggests that the spatial distribution of the panels may have played a small, but relatively insignificant role.

The second possible explanation of the change in search positions recorded in the differently covered tunnels, is that the bees could not reliably detect the optic flow cues that were provided by the textured walls and floor underneath the covered sections. This would be the case if the ambient light intensity in these occluded sections

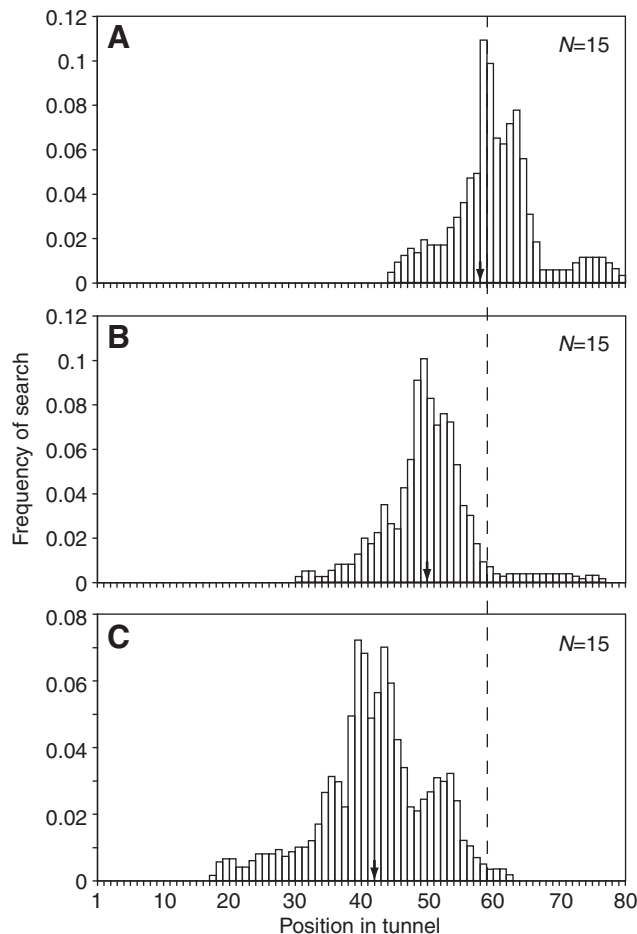


Fig. 4. The effect of celestial input on the position at which bees search for a previously visited feeder. Honeybees were trained to find a reward at a feeder placed 6 m into a tunnel (dotted line), with opaque panels placed on top of the tunnel to prevent the bees from receiving any skylight input in 2 m of the first 4 m of the tunnel (see Fig. 2A). The bees were subsequently tested in a fresh and slightly longer tunnel that carried no reward. When tested in a tunnel with a covering configuration identical to that used during training (A), the mean searching position at 5.9 m was not significantly different from the position of the feeder during the training. When tested in a tunnel in which the occlusion of the sky was decreased by 1 m compared to the training situation (B), the mean searching position changed to 5.1 m (the spatial layout of the panels is shown in Fig. 2C). When tested in a fully open tunnel (C), the mean searching position, at 4.3 m, was approximately 2 m closer to the entrance than in the training situation. The mean searching positions in the three experiments corresponded well to the availability of skylight cues along the flight in the tunnel and were not significantly different from the expected search positions of 6 m (A), 5 m (B) and 4 m (C), respectively. The arrows denote the mean searching positions and the bars show the search distributions recorded in each test. For details of the experimental set-up, see Fig. 2.

was below the critical level for enabling vision in the bee, and in particular, for driving its movement-detecting pathways. The visual odometer would then run only in the open sections of the tunnel where day light levels prevailed. This possibility can be ruled out by the observation that the waggle duration after a 6 m flight into the partly covered tunnel was not significantly different from the waggle duration after a 6 m flight into an open tunnel (Fig. 3).

We favour the third explanation, which proposes that the omission of skylight cues does not blind the visual system, but instead

suppresses the accumulation of odometric information when a bee navigates back to a previously visited food source. In all of the three tests that recorded searching behaviour, the bees concentrated their search approximately around the point that was reached after a total flight distance of 4 m in the *open* tunnel. This is the same distance that was left uncovered during training. It is of course possible that the bees could still get a view of the sky for some centimetres while flying in or out from underneath the covered sections of the tunnel. The distance flown with a full view of the sky during training will then effectively be slightly longer than 4 m, which may be one of the reasons for the slight shift of the mean search distribution away from 4 m in Fig. 4C.

It appears that odometric information is either completely omitted, or fed in with a reduced weight if there is no concurrent input from the celestial compass. This interpretation is in good agreement with similar studies of the interplay between these two pieces of information in desert ants (Sommer and Wehner, 2005; Ronacher et al., 2006). The study of the homing paths of these walking insects has led to the same conclusion, namely, that odometric information is not accumulated when celestial compass information is absent.

However, the honeybee's estimate of distance flown, as signalled by the duration of the waggle dance that she performs upon her return to the hive, does *not* seem to depend upon how much of the journey was flown under the open sky. The waggle-dance duration depends *only* upon the total distance that the bees have flown, regardless of the extent of sky occlusion. In the waggle dance, the bees always indicate the total distance flown to the food source, irrespective of the skylight input. Thus, distance conveyed in the waggle dance after a 6 m flight in a partly covered tunnel is not significantly different from that signalled after a flight of the same length in an open tunnel.

Two odometers in the honeybees?

We propose that the honeybee senses odometric information in two ways, depending upon the mode, or context in which this information is used. In one context (reporting distance flown to nestmates through the waggle dance), the odometer provides a measure of the *total distance travelled* by integrating optic flow information along the entire route, regardless of whether the sky is visible or not. In the other context (navigating back to a previously visited food source), the distanced estimate is *gated* by the presence (or absence) of information from the celestial compass. These two types of odometric information can serve different functions. The information that is provided by the waggle dance could serve to inform potential recruits about the entire flight distance to a food source, irrespective of partial occlusions by overhead canopies. Together with an appreciation of the quality of the food source, represented by the duration and liveliness of the dance (Seeley et al., 1991; Seeley et al., 2000), the scouts can – at least in theory – use this information to evaluate the most energy efficient food source to visit. This assessment would be difficult to make if the potential recruits were given sky-gated distances, rather than true distances. From the perspective of what information the dance-following bees need to find the food source, the total distance flown is also the most relevant measure. When these bees leave the hive in response to a dance, and set out to find the advertised food source, all they need to know is how far they should fly in the indicated direction. Presumably, these recruits will be performing path integration as they fly out to the food source, so that they can find their way back home.

However, the sky-gated distance information would be more useful to an experienced bee that is returning to a well-known food site. It is generally believed that large scale feeding excursions of honeybees

are partly achieved through the use of a path integrator (Collett and Collett, 2000; Wehner and Labhart, 2006; Wehner and Srinivasan, 2003; Wehner and Wehner, 1990). For such a path integrator to work, the animal needs to obtain information about distance travelled in a particular direction *together* with directional information of this leg of the trip (Müller and Wehner, 1988; Wehner, 1994). When only one of these two pieces of information is available, neither distance nor direction can be processed on its own in a meaningful way in order to produce a useful home vector. Under such circumstances it would be safest to temporarily suppress path integration, rather than to continue it by guessing a distance or direction. If we assume that the trained bees that return to the tunnel in search of the feeder are using a process of path integration to find the feeder, then the results are consistent with this interpretation, namely, that, during path integration, odometric distance is largely ignored if there is no concurrent input from the celestial compass. Thus, when an experienced bee flies under a canopy, it would instead have to resort to piloting using learned local landmarks (De Marco and Menzel, 2005; Chittka and Kunze, 1995).

Further evidence for the existence of two odometers comes from observations that suggest that the distance-measuring capacity of the honeybee appears to have different characteristics, depending upon how it is measured experimentally. On the one hand, when this capacity is measured using the waggle dance, the results indicate that the estimate of distance flown is rather insensitive to changes in the region or the extent of the visual field that experiences optic flow. Thus, the bee's estimate of the distance to a feeder placed inside a tunnel, as indicated by the waggle dance, remains largely unchanged even when optic flow cues are removed from the walls or the floor of the tunnel (Si et al., 2003). This indicates that a forager returning from a food source is likely to provide a robust indication of the distance that she has flown, even in conditions where the environment offers relatively sparse visual cues for the measurement of optic flow. On the other hand, when the honeybee's capacity to estimate distance flown is measured by using its searching behaviour (i.e. by training a bee to forage at a feeder and examining its ability to pinpoint the feeder's location when it is removed), then the bee's distance estimate depends rather critically on the region of the visual field that experiences optic flow. In such experiments the estimate of distance flown (as indicated by the position in the tunnel at which the bee searches for the missing feeder) is unaffected when optic flow cues are removed from the floor of the tunnel, but is severely compromised when these cues are removed from the walls (Srinivasan et al., 1997). This suggests that an experienced forager returning to find a previously visited food source relies largely on the optic flow that would be provided by laterally positioned structures in the environment (such as trees), and not by the ground beneath the bee. Thus, distance flown, as estimated by an experienced forager, would be largely independent of the height at which the bee flies to the food source.

In summary, bees may well possess two different odometers – a 'community' odometer that is used by a forager to convey information to its nestmates about the distance to a food source *via* the dance, and a 'personal' odometer that is used by an experienced individual to return to a previously visited food source. In the first case, the odometer provides a measure of the total distance travelled by integrating optic flow information along the entire route, regardless of whether the sky is visible or not. In the other case, the distanced estimate is gated by the presence (or absence) of information from the celestial compass.

In a recent study we have shown that bees flying along three-dimensional routes that include a vertical component, signal in their

dance the *total* distance flown irrespective of its three-dimensional configuration (Dacke and Srinivasan, 2007). The present account which, for the very first time presents us with the possibility of two odometers in the bee, begs the question of whether a flying bee can perform path integration in three dimensions to obtain an accurate 'personal' spatial representation of the position of the food source, for the purpose of re-visiting it.

Celestial input is necessary for directional information

Our result that the foraging bee does not process the distance information accumulated by the odometer when it is prevented from receiving celestial input also suggests that neither magnetic nor idiothetic information (which remained unmanipulated throughout this study) replace the directional information from the sky. Directional information could possibly be replaced by interpolating the directions flown before and after the covered sections, but our results also rule out this option. A number of morphological, electrophysiological and behavioural studies show that bees possess a dorsal rim area capable of analyzing the pattern of polarized light in the sky (Labhart, 1980; Menzel and Snyder, 1974; Rossel and Wehner, 1982; Rossel and Wehner, 1984; Rossel and Wehner, 1986; von Frisch, 1949; von Frisch, 1967; Wehner and Strasser, 1985; Wehner, 1992; Wehner and Labhart, 2006), but its involvement in the navigation of the bee remains largely unexplored. The results from this study suggest that celestial cues alone provide sufficient directional information for the distance estimation of the foraging bee, but further studies need to be done to determine the relative contributions of the sun, the polarized light pattern and spectral gradients to the celestial compass.

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