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Interactions of visual odometry and landmark guidance during food search in honeybees

Tony Vladusich[1,]*, Jan M. Hemmi[2], Mandyam V. Srinivasan[2] and Jochen Zeil[2]

[1]*Laboratory of Experimental Ophthalmology and NeuroImaging Centre, School of Behavioural and Cognitive Neurosciences, University Medical Centre Groningen, Groningen, The Netherlands* and [2]*Centre for Visual Science, Research School of Biological Sciences, Australian National University, Canberra, ACT 2600, Australia*

*Author for correspondence (e-mail: t.vladusich@med.umcg.nl)

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Summary

How do honeybees use visual odometry and goal-defining landmarks to guide food search? In one experiment, bees were trained to forage in an optic-flow-rich tunnel with a landmark positioned directly above the feeder. Subsequent food-search tests indicated that bees searched much more accurately when both odometric and landmark cues were available than when only odometry was available. When the two cue sources were set in conflict, by shifting the position of the landmark in the tunnel during test, bees overwhelmingly used landmark cues rather than odometry. In another experiment, odometric cues were removed by training and testing in axially striped tunnels. The data show that bees did not weight landmarks as highly as when odometric cues were available, tending to search in the vicinity of the landmark for shorter periods. A third experiment, in which bees were trained with odometry but without a landmark, showed that a novel landmark placed anywhere in the tunnel during testing prevented bees from searching beyond the landmark location. Two further experiments, involving training bees to relatively longer distances with a goal-defining landmark, produced similar results to the initial experiment. One caveat was that, with the removal of the familiar landmark, bees tended to overshoot the training location, relative to the case where bees were trained without a landmark. Taken together, the results suggest that bees assign appropriate significance to odometric and landmark cues in a more flexible and dynamic way than previously envisaged.

Key words: navigation, honeybee, odometry, landmark, *Apis mellifera.*

Introduction

Honeybees *Apis mellifera* use a combination of sensory cues to guide navigation (von Frisch, 1993). These include both long-range (e.g. odometry, compass direction) and short-range cues (e.g. scent, landmark). An unresolved problem is how bees integrate these sensory cues to guide their return to various places in the world, such as the location of a food source. It is often assumed, for instance, that long-range cues are sufficient to guide a bee to the general vicinity of a goal site (e.g. Collett and Collett, 2002), and that landmark cues are used to pinpoint the exact goal location (Cartwright and Collett, 1983). However, few experiments have explored this latter hypothesis in a systematic fashion (cf. Chittka et al., 1995a). This study examines the functional roles and interactions of visual odometry (the distance sense of the bee) and landmark guidance during food search, within the context of a scaled-down foraging environment.

Until recently, it was believed that honeybees use the amount of energy expended on a given flight as an index of distance travelled (von Frisch, 1993). Accumulating evidence now suggests that honeybees use visual information to measure how far they have flown in a particular direction (Cheng et al., 1999; Chittka and Tautz, 2003; Esch and Burns, 1996; Esch et al., 2001; Si et al., 2003; Srinivasan et al., 1996, 1997, 1998, 1999, 2000; Tautz et al., 2004). In particular, distance appears to be measured in terms of the amount of optic flow, or visual motion, that occurs on the eye during a given flight (i.e. integrated optic flow). For example, honeybees trained to forage in an environment rich in optic flow, such as a narrow tunnel lined with a textured pattern, dramatically overestimate the actual distance flown, as indicated by their dance behaviour (Esch et al., 2001; Si et al., 2003; Srinivasan et al., 2000). However, no comparable overestimation occurs when bees fly through an environment impoverished in optic flow, namely, a tunnel lined with stripes oriented along the direction of travel (Si et al., 2003; Srinivasan et al., 2000). Srinivasan et al. (1996, 1997, 1998) showed that honeybees can use visual odometry to guide food search, independently of cues such as visual landmarks, scent, time of flight and energy expenditure. Perhaps the most compelling evidence that bees use integrated optic flow to guide search comes from a control experiment, in which bees were trained and tested in tunnels lined with axially oriented stripes, such as those used in the dance experiments of Srinivasan et al. (2000). In this situation, bees simply flew from one end of the tunnel to the other during their search, indicating that they could not locate the training position with any accuracy in the absence of optic flow.

Once a honeybee enters the general vicinity of a previously visited site, she may navigate by means of visual landmarks (Collett and Zeil, 1998; Collett, 1996). Much evidence supports the view that honeybees are able to locate very precisely the location of a food site by visually matching the constellation of landmarks around the goal with a stored image of the site as viewed from the food source (Cartwright and Collett, 1983; Cheng et al., 1987; Collett and Baron, 1994; Collett and Kelber, 1988; Collett and Rees, 1997; see Judd and Collett, 1998, in relation to ants). Visual landmarks may also play a role in guiding navigation along the path to the food source (e.g. Chittka et al., 1995a,b; Collett, 1996; Collett and Rees, 1997; Collett et al., 1993, 2002; Srinivasan et al., 1997; Zhang et al., 1996). For example, landmarks may serve as long-distance beacons that guide bees to the approximate location of a goal (e.g. Chittka et al., 1995a,b; Collett and Rees, 1997). Another role for landmarks is to elicit a particular sensory-motor behaviour which, when executed alone (Menzel et al., 1998; Wehner et al., 1990), or when nested within a sequence of such behaviours (Collett et al., 1993, 2002; Collett and Collett, 2002; Srinivasan et al., 1997; Zhang et al., 1996), brings the bee closer to the goal. In the later instance, local landmark cues may also function to ameliorate the accumulation of odometric error by resetting the odometer (Srinivasan et al., 1997). Notably, once a set of landmark cues has been learned, bees are able to perform the correct sequence of sensory-motor actions, even in the absence of these cues, albeit with decreased accuracy (Collett et al., 1993; Zhang et al., 1996).

In the present study, bees were trained to forage in textured tunnels, such as those used by Srinivasan et al. (1996, 1997, 1998), with a visual landmark directly above the reward site. By changing the position of the landmark in the test conditions, and the availability of odometric cues during training and test, an attempt was made to tease apart the relative contributions of odometry and landmark cues to navigation and search behaviour. We devised various experiments to address the following questions. Experiment 1: Does the presence of a learned landmark increase the accuracy of search behaviour, relative to the situation in which odometry alone guides search? Do odometry or landmark cues predominate when the two sets of cues are made to conflict, for example, by shifting the position of the landmark at test? Experiment 2: What is the effect of depriving the bees of visual odometry while allowing the use of landmark cues? Experiment 3: Is it necessary that the landmark be present during training (i.e. learned), or do bees use any landmark cues near the goal to guide search? Experiments 4 and 5: Does the tunnel distance to which bees are trained significantly affect the relative significance of odometry and landmark cues?

Materials and methods

Location and equipment

Experiments were conducted outdoors in a relatively open area in the Wallaby Compound of The Australian National University, unless otherwise specified (i.e. Experiment 5), using tunnels either 3.4 m or 7.8 m (Experiments 4 and 5) long, 0.2 m high and 0.22 m wide. The side of each tunnel was marked every 0.2 m, enabling quantification of search patterns. The entire tunnel was covered with either Plexiglass sheets or (on hot days) nylon mesh, to prevent bees from entering or exiting at any location other than through the tunnel.

The landmark was a piece of rigid white cardboard placed on the top of the tunnel, spanning one lateral wall to the other, and encompassing the whole of the 0.2 m unit on which it was placed. Since the landmark spanned the entire unit, bees could make several U-turns within this segment before finally crossing over into an adjacent segment. In this sense then, the recording criterion underestimated the number of U-turns made by bees anywhere in the tunnel, but especially at the landmark site. The landmark being large and dorsal, however, had the advantage of obscuring the bees' views of any external landmarks (e.g. branches of distant trees).

Training

Italian honeybees *Apis mellifera* L. from a single colony were trained to forage at a feeder located at a specified position within a tunnel for a full day (8 h training) before testing began. Bees flew from the hive to the tunnel, located around 50 m away. The feeder was a small plastic container (100 ml capacity), with a flat circular-shaped base through which bees could extract small amounts of sucrose solution. The sucrose concentration was 1 mol l^{-1} at the start of training but was modulated slightly throughout the experiment to keep an approximately constant number of bees coming to the experiment. The tunnel was lined with paper printed with random black and white 1 cm^2 texture elements. In each experiment, approximately 20 bees were marked individually with coloured paint and trained to locate the food reward in the training tunnel. We ensured that nearby landmarks were not visible from the bees' vantage point in the tunnel.

Food search

Bees were tested in the training tunnel in Experiments 2, 4 and 5. In Experiments 1 and 3, bees were tested in a tunnel in which the feeder was periodically placed at a random location. To accomplish this, the training protocol was interrupted hourly for a period of 5–10 min, during which the training bees foraged in the testing tunnel. At test, individual bees flew through the tunnel towards the position previously occupied by the feeder. At some point during a given flight, the bee began to search for the missing feeder, performing a series of U-turns, each time reversing its direction of travel in the tunnel (Fig. 1). Search flights were quantified by observing the first four U-turns conducted by each bee upon entering the tunnel. A U-turn was defined as a crossing-over between adjacent units in

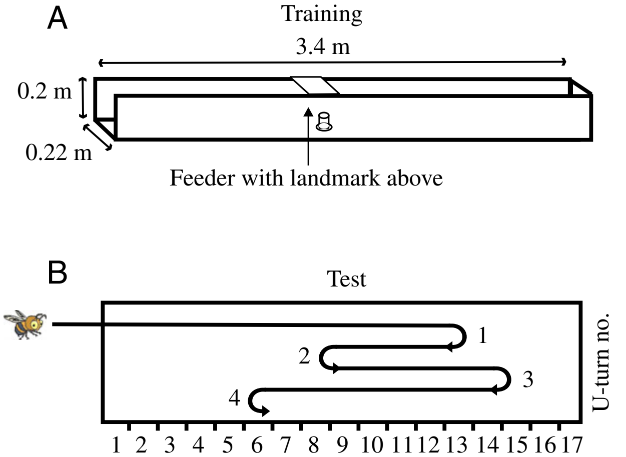

Fig. 1. Schematic illustration of the training and testing set-up. (A) Bees were trained to forage in a textured tunnel (the specific texture was varied throughout experiments) with a feeder at a designated location, and the landmark directly above. (B) In the test situation, bees entered the tunnel individually, and began searching for the removed feeder, repeatedly traversing the tunnel. The cross-section shows the trajectory over four U-turns (note this is not a space-time diagram in the strict sense).

the tunnel (e.g. from 9 to 8), and was recorded manually on paper by the experimenter.

Experiment 1

Bees were trained to forage at a feeder placed in a tunnel lined with a randomly textured pattern, such as that used by Srinivasan et al. (1997). A conspicuous visual landmark was placed directly above the location of the feeder. In the test situation, the feeder was removed and bees' search patterns were assessed (a) when the landmark was removed altogether, (b) with the landmark in place at the training position, or (c) with the landmark displaced relative to the training location, thereby setting up a situation in which odometry and landmark cues were in positional conflict.

Experiment 2

Experiment 2 was similar to Experiment 1 except that the training tunnel was lined with parallel stripes oriented along the main axis of the tunnel. Since such axial stripes do not produce a significant image motion on the eye, bees cannot gauge distance travelled (Si et al., 2003; Srinivasan et al., 1997, 2000). In the present instance, this would apply equally to measurements made either relative to the tunnel entrance or relative to the goal-defining landmark. Experiment 2 thereby assessed what kind of search strategies bees adopt when only landmark cues are available to locate the feeder.

Experiment 3

Bees were trained in a tunnel lined with random texture, but without a landmark at the feeder location. In the test conditions, a landmark was placed at one of several locations in the tunnel to examine how the addition of novel landmark cues affects search behaviour. An additional control condition assessed how bees searched when tested without the novel landmark.

Experiments 4 and 5

Bees were trained to a longer distance than in Experiment 1 in order to examine whether search behaviour would differ from that observed at shorter distances.

Data analyses

The order in which conditions were tested was randomised within blocks, each block testing all conditions; once tested, a condition was excluded until all had been tested. Each block was tested at least twice. For each condition, search distributions were calculated on the basis of the first two U-turns. These U-turns typically provided sufficient information to analyse search behaviour (e.g. Cheng et al., 1999). In cases where the third and fourth turns illustrated important aspects of the bees' navigation strategies, these data were also analysed. The search distribution of a group of bees was calculated for each test condition, as follows. For each flight, all tunnel units between the positions of first and second U-turns were assigned values of one. Each of these values was then divided, or weighted, by the total path length between the first and second U-turns (inclusive). These weighted scores were then summed, for each tunnel unit, across all the flights in an experimental condition, and divided by the total number of flights. Thus, the total area under the curve representing the search distribution was normalized to one. Due to the normalization with respect to path length (i.e. distance from first to second U-turns), each flight segment contributed the same area to the curve. That is, shorter path lengths (associated with the more accurate searches) contributed the same bulk to the search distribution as longer path lengths. However, shorter (more accurate) path lengths contributed more to the height of the search distribution, because the value associated with each tunnel unit was higher.

All figures also show the positions of first and second U-turns normalized to the total number of flights, giving the relative frequency of U-turns across all units. When analysing only the first two U-turns the flight path-segment between first and second U-turns for each individual flight were displayed graphically, which supplemented the histogram representations of U-turns (which do not give information about individual flight paths). Indeed, displaying individual flight paths makes it immediately possible to visualise the link between U-turn position and the search distribution.

Statistics

Statistical analyses (analysis of variance, ANOVA) were conducted for each experiment on the first and second U-turn data, and in appropriate cases, on the third and fourth U-turn data. These analyses indicated whether the position of the landmark at test had an overall effect on the means of U-turns 1 and 2 across conditions. The results of these *en bloc* statistical analyses are stated only briefly in the text; details can be found in the Appendix. In special instances, where a comparison between similar conditions in different experiments was of particular importance, individual statistical tests were undertaken as stated in the text. Analyses were performed using Matlab software, Version 6.1 (MathWorks, Inc.) and Genstat for Windows, Release 6.1 (USN International, Ltd).

Results

Experiment 1

The data from this experiment are shown in Fig. 2. The positions of first and second U-turns are plotted as frequency histograms (normalized to flight number), and the search distribution, calculated as described in Materials and methods, is overlaid on top. The path segments between the first and second U-turns, for each flight, are plotted above the histograms and search distributions, showing the positions of first and second U-turns, and for each flight, the line joining these positions indicates the length of the path segment.

The data show clearly that the presence and position of the landmark had a dramatic effect on where bees searched. An ANOVA revealed a significant effect of landmark position on the mean ($F_{3,166}$=59.78, P<0.001) of search. In the absence of the landmark (Fig. 2A), bees searched very broadly for the food, whereas search was very accurate with the landmark in place at the training location (Fig. 2B). When the landmark was shifted towards the tunnel end (Fig. 2C) or entrance (Fig. 2D), bees generally searched near the position of the landmark, rather than at the training distance, meaning that landmark cues tended to override odometry. The overall difference between conditions, in terms of both mean search position and spread of search, was highly significant. The individual conditions are examined further below.

No landmark

The search distribution in this condition shows a very broad peak in the general vicinity of the training location (Fig. 2A). Indeed, the search distribution appears much broader than those previously obtained with bees trained to the same tunnel location (e.g. Srinivasan et al., 1997). As indicated by the pattern of first U-turns, the errors were typically in the direction of overshooting rather than undershooting the training location. It is therefore possible that these bees were seeking the missing landmark. Interestingly, the pattern of individual flight path segments shows that, in many instances, bees did not pass over the training location on the transition from first to second U-turns.

Landmark at unit 9

With the landmark present at the training position, bees searched almost exclusively at this location (Fig. 2B). Essentially, bees never performed U-turns away from the immediate vicinity of the landmark. This result therefore confirms the hypothesis that landmark cues can significantly improve search accuracy, relative to the case where only odometric cues are available (see above).

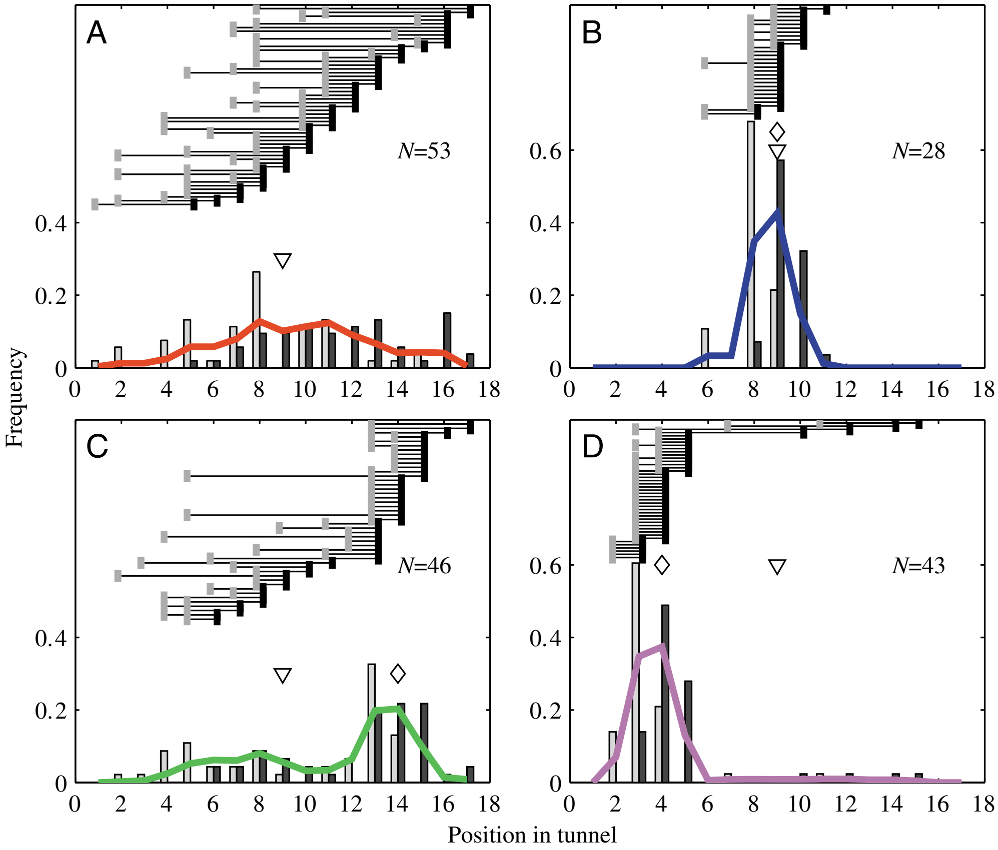

Fig. 2. Results of Experiment 1. (A) Bees tested with no landmark conducted a broad search. (B) With the landmark at the training location, bees searched very accurately. (C) When the landmark was shifted to unit 14, bees searched either at the landmark or the training location. (D) Bees searched at the landmark when it was shifted to unit 4. Black bars, first U-turns; grey bars, second U-turns; coloured lines, search distributions; inverted triangles, training location; diamonds, landmark position; N=flight number. Note different y-axis scales in A,C and B,D.

Landmark at unit 14

A more complex pattern of results emerged when the landmark was positioned at unit 14 (Fig. 2C). On most flights, bees searched at the position of the landmark, but there was a small group of flights in which bees searched in the vicinity of the training position. This division of behavioural outcomes most likely arose because, in many cases, bees overshot the training location and subsequently sighted the landmark. Once acquired, bees did not often disengage visually with the landmark, as shown by the pattern of second U-turns. By comparing the pattern of first U-turns in the current condition with that obtained in the 'No landmark' condition, it is possible to deduce the distance at which bees first detected the landmark. This comparison therefore quantifies the extent to which the landmark acted as a beacon (e.g. Chittka et al., 1995a; Collett and Rees, 1997).

Fig. 3 plots the first U-turns for both conditions, along with the cumulative distributions obtained by summing (and normalizing to the total number of U-turns) the number of U-turns performed at, or before, each unit in the tunnel. These cumulative distributions differ overall (Kolmogorov–Smirnov test, P=0.0187). Pairwise comparisons at different tunnel units show that the two cumulative distributions differ statistically at unit 11 (two-tailed Fisher exact test, $P<0.05$) and at unit 12 (two-tailed Fisher exact test, $P<0.01$), meaning bees began to detect the landmark from at least 0.6 m away. The cumulative distributions diverge slightly earlier than unit 11 (though the differences are not significant), indicating that some bees may have detected the landmark before reaching unit 11.

Landmark at unit 4

When the landmark was shifted to unit 4, bees searched almost exclusively at this location (Fig. 2D). On a few flights (8/43), bees went past the landmark on first U-turns but there is insufficient data to conclude whether these bees were searching in accord with odometry or were simply lost. What is clear is that on most flights bees preferred to search in accord with the landmark cue. The pattern of results is therefore very similar to the 'Landmark at unit 9' condition.

Experiment 2

The rationale of the following experiment was to eliminate the search component driven by odometry, thereby isolating the mechanism that depends only on landmark cues. To this end, bees were trained at unit 9 in a tunnel lined with black and white stripes oriented along the tunnel axis (axially striped tunnel). The experimental protocol was the same as in Experiment 1, except that bees were tested in the training tunnel.

We found that the position of the landmark cue again had a strong effect on search behaviour in terms of the mean ($F_{3,152}$=55.16, $P<0.001$) search position. In the absence of landmark cues, the search distribution appears approximately flat (Fig. 4A), and as the pattern of first and second U-turns shows, this distribution was due to the tendency for bees to fly from one end of the tunnel to the other during search. There was a slight tendency for bees to make U-turns near the training location, possibly indicating the effect of scent cues. In general, however, these findings agree with previous results insofar as odometry appears to play little role in bees' search behaviour in axially striped tunnels (Srinivasan et al., 1997).

In all cases where the landmark was present, however, a different pattern of results emerged. Regardless of whether the landmark was positioned at unit 9 (Fig. 4B), unit 14 (Fig. 4C), or unit 4 (Fig. 4D), bees nearly always performed first U-turns at the site of the landmark (see Appendix for levels of statistical significance). However, of the flights in which bees made first U-turns at the landmark, not all bees made a second U-turn at this site. Indeed, there was a strong tendency to break visual contact with the landmark, and in many cases, to fly all the way back to the tunnel entrance. This tendency to fly a long distance from the landmark is not unexpected because bees would have been unable to measure distance travelled relative to the landmark. However, the initial tendency to break visual contact with the landmark is an unexpected outcome.

Do odometric cues affect landmark fidelity during search?

A comparison was conducted between Experiments 1 and 2 to assess whether odometric cues can influence bees' fidelity

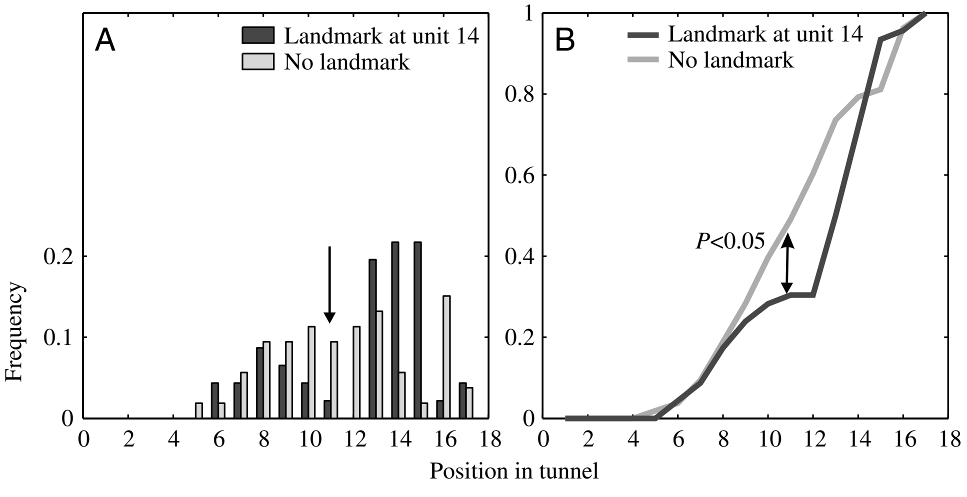

Fig. 3. Comparison between the 'Landmark at unit 14' and 'No landmark' conditions reveals the point at which bees were drawn towards the landmark (i.e. a beacon effect). (A) Reproduction of first U-turn distributions. (B) Cumulative frequencies were tested statistically, and found to be different at unit 11 (see text), meaning that bees were drawn to the landmark from this point onwards.

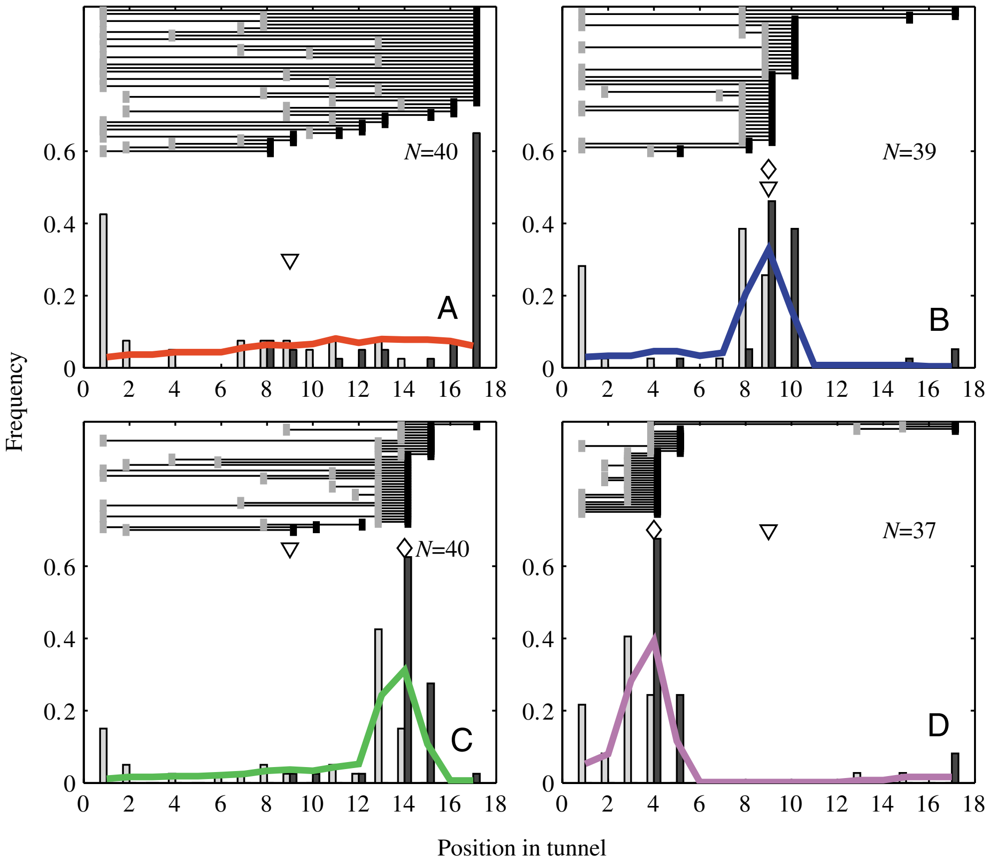

Fig. 4. Results of Experiment 2. Bees were trained and tested in an axially striped tunnel. (A) Bees tested without the landmark generally flew from one tunnel end to the other. (B–D) Bees tested with the landmark at the training site (B), shifted to unit 14 (C) and shifted to unit 4 (D), all made first turns near the landmark then tended to break visual contact on second turns (and often flew back to the entrance). For an explanation of figure layout and symbols, see Fig. 2.

for a landmark cue; that is, the tendency for bees to remain faithful to the landmark cue throughout the four U-turns (Fig. 5). For each experiment, the three conditions in which the landmark was present were included in the analysis. Flights in each experimental condition were then classified according to whether a bee performed its first U-turn within one unit either side of the landmark. The number of flights fitting these criteria were then divided by the total number of flights, giving a ratio that measures how strongly bees were attracted to the landmark. Flights showing the strongest attraction were selected for further analysis, while the others were excluded from the analysis.

Of the remaining flights, the same criteria were applied to the second, third and fourth U-turns, with one additional caveat: only those flights in which bees had the opportunity to turn within one unit either side of the landmark were included. For instance, if the landmark was at unit 9, a bee making its first U-turn at unit 8 could not subsequently perform its second U-turn within the set criterion (i.e. one unit either side of unit 9), since a U-turn was defined as a crossing from one unit to an adjacent unit (see Materials and methods). Such flights were therefore also excluded from further analysis. Taken as a whole, the analysis provides an indication of bees' affinity to the landmark over the four U-turns for each condition across the two experiments.

To compare these results quantitatively, the data were pooled across all four U-turns and all three conditions within each experiment. The proportions of bees performing U-turns within the set criteria were then calculated for each experiment and compared statistically. The analysis revealed a highly significant overall difference between Experiments 1 and 2 (two-tailed Fisher exact test, $P<0.001$), meaning that the availability of odometry has a powerful effect on landmark fidelity. Interestingly, an overall difference (i.e. for all U-turns) was also found between the 'Landmark at unit 9' condition, and the remaining two cue-conflict conditions, within Experiment 1 itself (two-tailed Fisher exact test, $P<0.05$), meaning the conflict between landmark position and odometry decreased bees' overall affinity for the landmark. These fascinating results are considered in further detail in the Discussion.

Experiment 3

The results of the first experiment suggest that bees use landmark cues at the feeder to narrow the area of search. However, it is not clear whether the landmark must be learned during training, or whether bees are intrinsically drawn towards any landmark in the vicinity of the training location. Indeed, it is well-known anecdotally that bees are attracted to novel objects in their environment. How do bees handle a situation in which a novel landmark cue is added to the training site at test? To examine this issue, bees were trained to unit 9 in a randomly textured tunnel containing no landmark, and tested with an unfamiliar landmark in the tunnel. The test

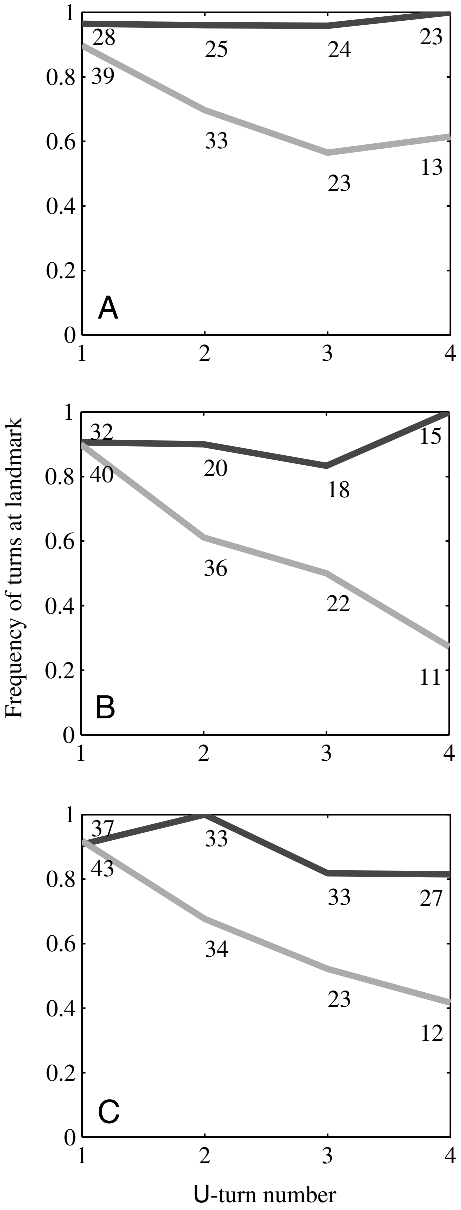

Fig. 5. Comparison of landmark fidelity, i.e. the tendency for bees to stay faithful to the landmark during search, with odometry (black line) and without odometry (grey line). Bees with odometry remained faithful on all four U-turns, whereas bees without odometry progressively gave up searching at the landmark, in all conditions. (A) Landmark in place at the training site, (B) landmark shifted to unit 14, and (C) landmark shifted to unit 4. Numbers given indicate the number of bees considered when calculating the observed frequency.

protocol was identical to that used in Experiment 1 (i.e. bees tested in a tunnel in which the feeder was randomly positioned for short time periods to distribute scent equally).

Fig. 6 shows that the experimental manipulation was again effective (mean: $F_{3,173}$=9.67, P<0.001). Of particular interest here is the condition in which bees were trained and tested without a landmark (i.e. ‘No landmark’ condition; Fig. 6A). This condition is comparable to the ‘No landmark’ condition of Experiment 1, wherein bees were trained with a landmark but tested without. The question of interest is whether search performance was different in these two conditions. A statistical comparison of first U-turns shows no overall difference between conditions (Kolmogorov–Smirnov test, $P\geqslant 0.1$). Thus, there is little evidence to support the hypothesis that bees overshoot the feeder position when trained with a landmark and tested without (Experiment 1), any more than they would when trained and tested without a landmark.

The overall pattern of results obtained with the novel landmark in place was qualitatively different from that seen in Experiment 1. In contrast to Experiment 1, bees tended to search just short of the landmark (see below for quantification) in the ‘Landmark at unit 9’ (Fig. 6B), the ‘Landmark at unit 14’ (Fig. 6C), and to a lesser extent in the ‘Landmark at unit 4’ condition (Fig. 6D). In all three cases, the search distributions appear truncated near the position of the landmark. In the ‘Landmark at unit 4’ condition, bees sometimes flew past the landmark and searched in the tunnel region just beyond the training distance. Since this consistent tendency to overshoot the training site was unexpected (see Discussion), more test flights were recorded in this condition than in the others.

Comparison with Experiment 1

To quantify the apparently different effects of familiar and novel landmarks, a conjoint analysis was performed on Experiments 1 and 3. Only first U-turns were used for this analysis because they provide information about the bees’ initial reaction to the landmark cue. For each condition in both experiments, the number of U-turns made in the tunnel unit occupied by the landmark (e.g. unit 9) and the unit just beyond the landmark (e.g. unit 10) was calculated. A second measure counted the number of first U-turns performed in the two tunnel units preceding the landmark (i.e. units 7 and 8). The ratio of these two numbers (i.e. turns 7,8/turns 9,10) provides a measure of the tendency for the novel landmark to repel bees rather than attract them. That is, we interpret U-turns performed at units 8 and 9 as resulting from an attraction effect, while U-turns performed at units 7 and 8 are interpreted as being due to a repulsive effect. By comparing these data across experiments, it may be possible to deduce the relative behavioural significance that bees assign to novel and familiar landmarks positioned at the goal.

The data are plotted in Fig. 7. Black and grey bars show the ratios of bees repelled by the landmark to those attracted by it for each condition in Experiments 1 and 3, respectively. The figure shows clearly that, regardless of the landmark’s tunnel location, bees were far more likely to turn just before reaching the novel landmark than was the case with the familiar landmark. The red line in the figure indicates the ratios of bees in Experiment 3 that turned in the two units preceding the landmark relative to all units beyond the landmark (i.e. not including the landmark unit). This ratio therefore measures the absolute tendency for bees to be repelled by the novel landmark in each condition of Experiment 3.

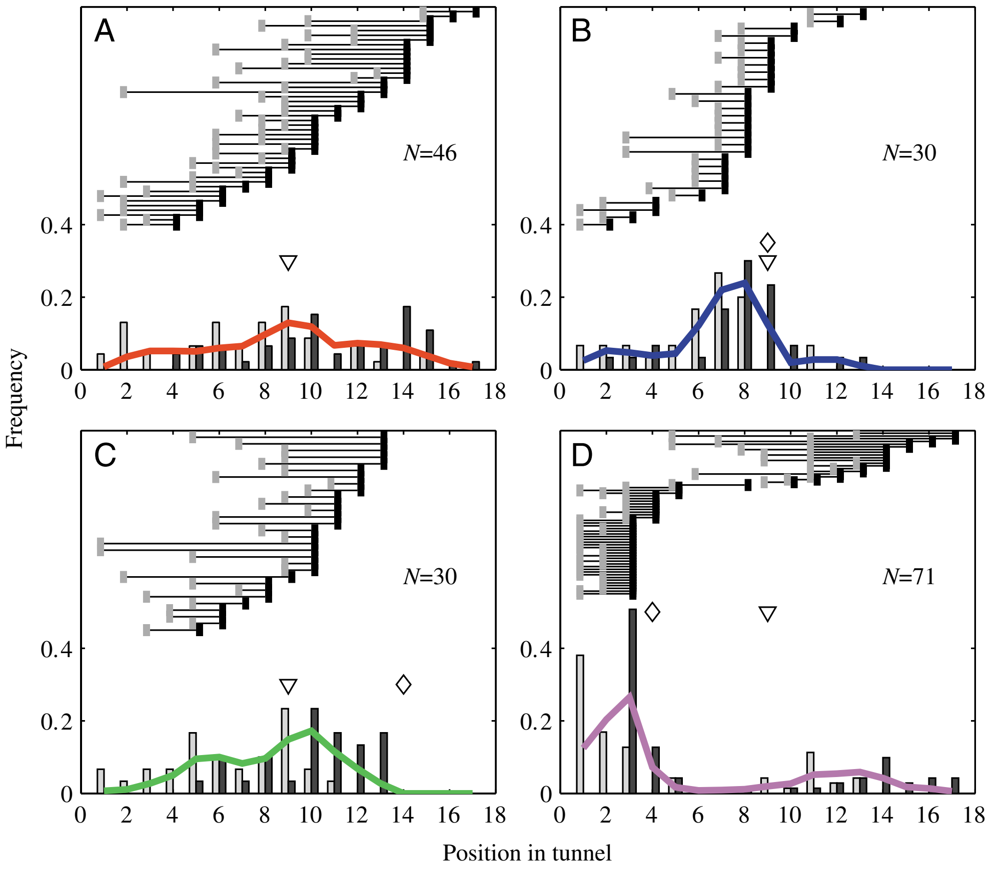

Fig. 6. Results of Experiment 3. Bees were trained without a landmark and tested with a landmark. (A) Bees tested without the landmark searched broadly in the tunnel. (B–D) Bees tested with the landmark (B) at the training site, (C) shifted to unit 14, and (D) shifted to unit 4, all tended to make first turns before reaching the landmark. This effect suggests that bees are repelled by the novel landmark placed along a familiar path. For an explanation of figure layout and symbols, see Fig. 2.

To obtain a quantitative measure of the repulsion effect relative to the attraction effect (i.e. bars in Fig. 7), the frequencies shown in Fig. 7 were pooled across all conditions within each experiment. A statistical test performed on these overall frequencies shows a highly significant difference between experiments (two-tailed Fisher exact test, $P<0.001$). The strength of the absolute repulsion effect (i.e. within Experiment 3 itself) was ascertained by comparing the proportions obtained for the ‘Landmark at unit 4’ condition and the ‘Landmark at unit 14’ condition (i.e. the strongest and weakest effects). The comparison shows a significant difference in the strength of the effect (two-tailed Fisher exact test, $P<0.05$).

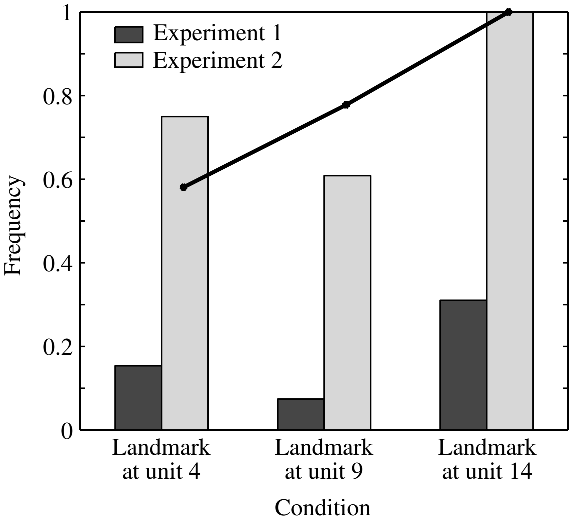

Fig. 7. Assessment of the tendency for a novel landmark to repel bees. Ratios of bees turning just before the landmark to those turning at the landmark; black bars, familiar landmark; grey bars, novel landmark. The black line shows the ratios of bees turning before and after the landmark in Experiment 3 only. The conditions were ‘Landmark at unit 4’, ‘Landmark at unit 9’ and ‘Landmark at unit 14’.

In summary, the behaviour adopted by bees encountering a novel landmark at the training position is very different from that observed with a familiar landmark. The novel landmark tends to truncate the search, perhaps because the presence of an unexpected landmark cue indicates to the bees that they have overshot the training site and so are in the wrong place (see also Discussion).

Experiment 4

Do the results of Experiment 1 generalize to longer training distances? In an attempt to answer this question, bees were trained at unit 21 with a landmark placed above the feeder. The tunnel was 7.8 m long and lined with a randomly textured pattern. Bees were tested in the training tunnel under one of four conditions: ‘No landmark’, ‘Landmark at unit 21’, ‘Landmark at unit 30’ and ‘Landmark at unit 12’.

Fig. 8 shows that, as in the previous experiments, landmark position strongly affected search behaviour (mean: $F_{3,152}=79.87$, $P<0.001$). When bees were tested in the ‘No landmark’ condition (Fig. 8A) there was a tendency for them

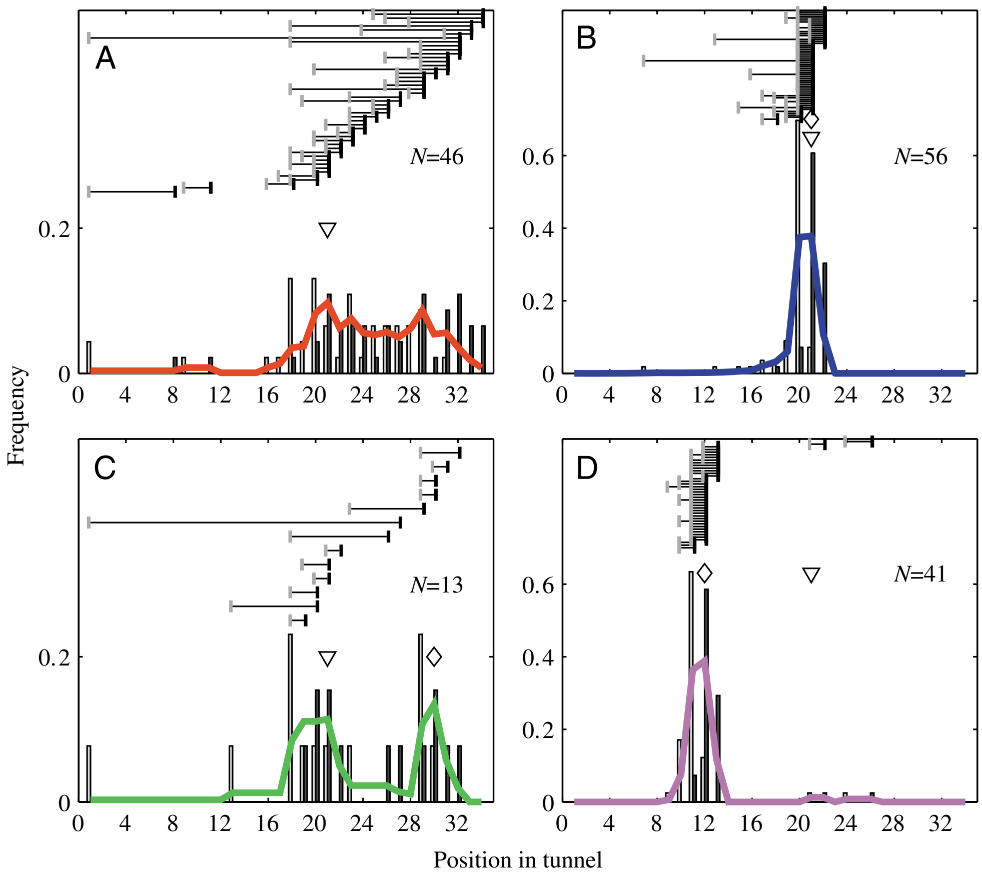

Fig. 8. Results of Experiment 4. Bees were trained at unit 21 with a landmark. (A) Bees tested without the landmark searched either near the training location or at the end of the tunnel. (B–D) Bees tested with the landmark (B) at the training site, (C) shifted to unit 30 and (D) shifted to unit 12, all tended to search at the landmark, or sometimes (as in C) before reaching the landmark. Note the different *y*-axis scales in A,C and B,D. For an explanation of figure layout and symbols, see Fig. 2.

to search both at the training location and at a location towards the tunnel end. That is, bees often overshot the training location considerably. Of the 46 flights in this condition, bees made their first U-turn at or beyond unit 28 (an arbitrary cut-off) on 21 occasions. On 16 of the 46 flights, the average of the first two U-turns equalled or exceeded 27.

In the ‘Landmark at unit 21’ condition (Fig. 8B), the pattern of search appears very similar to that obtained in Experiment 1 with the landmark in place at the training location. The distribution is quite narrow and peaks at the training unit, although there is perhaps slightly more scatter in the positions of second U-turns than in Experiment 1. This increased scatter is to be expected given that the training distance, and hence odometric error, was substantially greater in the present experiment. The results of the ‘Landmark at unit 30’ condition (Fig. 8C) are also quite similar to the analogous condition of Experiment 1. Indeed, the search distribution appears bimodal, as was the case in Experiment 1. One peak occurs in the vicinity of the training location, while the other peak occurs at the position of the landmark. Unfortunately, the number of flights in this condition was quite low (*N*=13) due to inclement weather, which ended the experiment early.

In the ‘Landmark at unit 12’ condition (Fig. 8D), bees searched predominantly at the location of the landmark. On only two flights did bees make first U-turns beyond the landmark. In this sense, the results of the present condition seem to mirror those obtained in the ‘Landmark at unit 4’ condition of Experiment 1. While the results of the present experiment were generally comparable with those of Experiment 1, there was one major difference, manifested in the ‘No landmark’ condition, where bees exhibited a proclivity to search near the end of the tunnel. However, third and fourth U-turn data (not shown above) indicate that bees in the ‘Landmark at unit 21’ and ‘Landmark at unit 12’ conditions also searched at the end of the tunnel after breaking visual contact with the landmark.

Fig. 9 plots these data for the third and fourth U-turns in the same form used throughout this study for first and second U-turns. It is clear from the figure that, in both the ‘Landmark at unit 12’ (Fig. 9A) and ‘Landmark at unit 21’ conditions (Fig. 9B), bees were drawn away from the landmark, and towards the tunnel end, on third U-turns. Bees were also drawn towards the tunnel entrance (fourth U-turns) in the ‘Landmark at unit 21’ condition. The reason(s) for this seemingly anomalous behaviour remain unclear (see Discussion). The behaviour did, however, suggest the need to replicate the present experiment.

Experiment 5

The following experiment was similar to the previous one, in that bees were trained at unit 21 with the landmark above the feeder. In the control condition, a separate set of bees was trained to unit 21 without a landmark and tested under the same conditions. For bees trained with the landmark in place, there

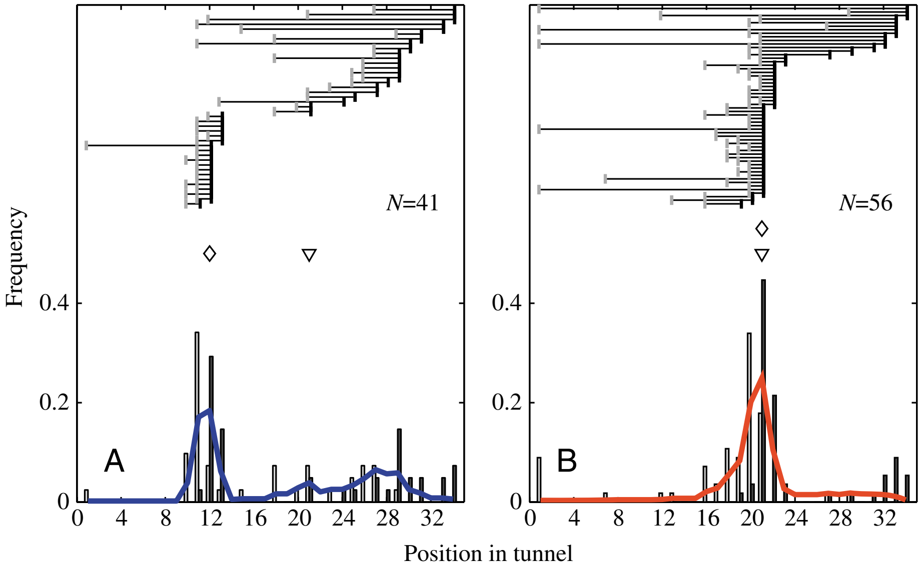

Fig. 9. Third and fourth U-turns, plotted for two conditions of Experiment 4, show that bees that strayed away from the landmark often searched near the tunnel end. This occurred with the landmark (A) shifted to unit 12, and (B) in place at the training location.

were two test conditions: a 'No landmark' condition, and a second condition in which the landmark was present at the training site ('Landmark at unit 21'). Bees were again tested in the training tunnel. There were also two other important differences relative to Experiment 4. The experimental site was changed to a more open field, due to the overgrowth of trees at the previous site, and the pattern lining the tunnel walls and floor was changed from a random texture to a checkerboard. Since the checkerboard pattern is entirely regular (self-repeating) it mitigates against any tendency for bees to pinpoint the goal location by matching micro-patterns in randomly textured tunnels.

The results were in line with the previous experiments in showing an overall effect for the mean ($F_{2,97}$=8.61, P<0.001) search position. Bees in the 'Train with and test without landmark' condition (Fig. 10A) clearly overshot the training location on first U-turns. Indeed, on no occasion did a bee turn at or before unit 21 (see also below). Interestingly, the pattern of second U-turns shows that bees almost always came back to the training site on second U-turns, unlike the analogous condition of Experiment 4 where bees often continued to search near the tunnel end. The results of the 'Test with landmark' condition (Fig. 10B), however, are in agreement with the first two U-turns of bees in Experiment 4, insofar as bees searched accurately at the landmark, albeit with perhaps a slightly greater tendency to overshoot the landmark position on first U-turns. Nor was any evidence found that bees behaved radically differently on third and fourth U-turns (data not shown).

The results of the 'Train and test without landmark' condition (Fig. 10C) are particularly interesting because the pattern of search appears quite different to that obtained in the 'Train with and test without landmark' condition (Fig. 10A). In particular, it appears as if the first U-turn distribution in the latter condition (Fig. 10A) was shifted by about three units beyond the training position, relative to the present condition (Fig. 10C). No bees in the 'Train with and test without landmark' condition turned at or before unit 21, whereas the proportion in the present condition was 16 of 39. These proportions are highly significantly different (two-tailed Fisher exact test, P<0.001), suggesting that the absence of a familiar landmark can, in certain circumstances, cause bees to overshoot the training location. In summary, there was little hint of the anomalous behaviour described in Experiment 4; namely, the tendency to search at the tunnel end. Although bees sometimes overshot the training location on first U-turns, they almost always came back to the training site to perform second U-turns.

Discussion

The experiments presented herein confirm the hypothesis that familiar goal-defining landmark cues combine with odometry to ensure that bees search very accurately at the goal location. These results are therefore broadly consistent with previous findings on the role of visual landmarks, positioned *en route* to the goal location, in the tunnel environment (Collett et al., 2002; Srinivasan et al., 1997). The finding that familiar landmark cues override odometry when the two sources of information are set in conflict is also consistent with previous studies conducted under more natural foraging conditions (Chittka et al., 1995a).

Landmark fidelity and odometric context

Several novel findings also emerged during the course of the study. For example, it was found that bees were more likely to continue searching near a familiar landmark, even after initially failing to find food, when odometry was available (Experiment 1) than when it was absent (Experiment 2). Why were bees more likely to break visual contact with the landmark when odometric cues were unavailable? One reason may be that landmark infidelity prevents bees from searching in the vicinity of a landmark for too long in the absence of an odometric cue that confirms to the bees that they

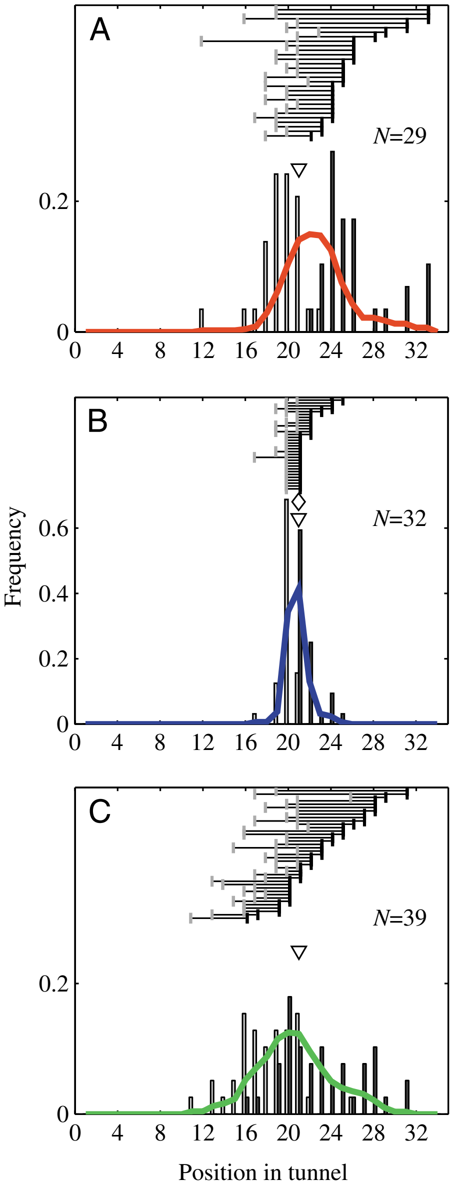

Fig. 10. Results of Experiment 5. Bees were trained at unit 21 with a landmark, and (A) tested without the landmark, or (B) with the landmark at the training site, searched in accord with odometry and landmark cues, respectively. (C) Bees trained without a landmark and tested without a landmark also showed no signs of the anomalous behaviour observed in Experiment 4. Note the different *y*-axis scales in A,C and B. For an explanation of figure layout and symbols, see Fig. 2.

are in the correct place. In natural environments, landmark cues at different locations may appear very similar, and so could easily be confused. One role of odometry then, might be to distinguish similar-looking landmark cues by acting as a context-setting cue (e.g. Collett et al., 1997, 2002), providing bees with information about the expected location of a landmark.

In the absence of such contextual information, the estimated probability that a bee is in the wrong place might increase rapidly following the initial failure to find food, since the landmark has lost much of its power to predict the presence of food. Thus, a reasonable strategy would be to break visual contact with the landmark in order to search for similar landmarks nearby. This would be a particularly useful property in environments where odometric cues are very sparse, as when bees fly over still water, since it would prevent bees from persevering with a cue that is itself ambiguous (for the properties of odometry in differently textured tunnel environments, see Si et al., 2003). This property may also suggest a need to revise extant models of landmark guidance (e.g. Cartwright and Collett, 1983), which do not necessarily capture the flexible interaction between odometric and landmark cues.

Interestingly, the conflict between odometric and landmark cues, caused by shifting the landmark in Experiment 1, affected bees differently from the complete absence of odometry (Experiment 2). In the cue-conflict conditions of Experiment 1, a small but constant proportion of bees tended to break away from the immediate vicinity of the landmark, over all four U-turns, relative to the cue-congruent condition. Why should the number of bees breaking away stay constant? Why should bees not rapidly switch back to searching in accord with the available odometric information?

Here it may again prove useful to consider that bees can only estimate the probability that a landmark is in the correct place (i.e. that it is the correct landmark), since odometric error prevents bees from knowing exactly where they are at any given time. After the initial failure to find food, this probability does not change as rapidly as it would in the complete absence of odometric cues, because odometry provides a contextual cue that is roughly consistent with the bees being in the correct place. The information available to the bees therefore favours persevering with the landmark cue. Importantly, the difference between the cue-congruent and cue-conflict conditions suggests that the landmark cue did not reset the odometer (e.g. Chittka et al., 1995b), such that bees behaved as if they were actually at the training site. That is, why should bees break away from the landmark on second, third and fourth U-turns, when their odometric value has been adjusted to that associated with the training site? Indeed, the break-away property suggests just the opposite; that bees do not reset the odometer value, at least relative to the tunnel entrance. Collett et al. (2003) reached a similar conclusion for global path integration in ants.

Landmark repulsion and undershooting

Another significant new finding was that novel landmark cues did not have the same effect on bees as familiar landmark cues (Experiment 3). Rather than having an attractive effect, the novel landmark appeared to repel bees instead, causing them to initiate search closer to the tunnel entrance, than in the case of the familiar landmark. This finding defines another sense in which a landmark cue can take behavioural precedence over odometry, and may reflect another useful behavioural strategy in natural foraging circumstances. In particular, the presence of a novel landmark on a familiar route might indicate that the bee has overshot the location of the food source (or, more generally, that she is in the wrong place). Therefore it may make sense that bees turn back and begin searching at a shorter distance.

In support of this hypothesis, it was also found that the absolute strength of the repulsion effect varied with the position of the landmark in the test tunnel. That is, the closer the landmark was to the tunnel entrance, the greater the probability of bees making U-turns beyond it. This result makes ecological sense because bees encountering the landmark near the entrance would (on average) have smaller odometer readings than bees encountering the landmark at or beyond the training site. Smaller odometer readings would provide evidence to the bees that they had not overshot the training site, making them less likely to turn back. Conversely, bees encountering the novel landmark beyond the training site would (on average) have larger odometer readings, and so be very likely to turn back.

If this hypothesis were correct, then the subset of bees flying past the landmark (i.e. ignoring it) in any given condition would (on average) have smaller odometer readings than bees that turn back. These bees would then tend to overshoot the training site because they would need to fly a little further before their odometer readings matched the one stored in memory. This is exactly what was found in the ‘Landmark at unit 4’ condition of Experiment 3. The subset of bees that flew past the landmark searched a little beyond the training distance. This effect appeared so striking during the experiment that a large number of flights were recorded in that condition in order to confirm the result. The effect is unlikely to be due to resetting of the odometer at the novel landmark: additional experiments, not presented here, showed that bees tended to overshoot the training location even further when the novel landmark was placed closer to the tunnel entrance. The resetting explanation would predict the opposite result: namely, bees would be expected to search at about 9 units beyond the landmark, at a position nearer the tunnel entrance.

Landmark expectation and overshooting

A third novel finding was that the absence of a familiar goal-defining landmark can cause bees to overshoot the training site, compared to the case in which bees were trained without the landmark (Experiment 5; but see below). In this context, the absence of the expected goal-defining landmark had the opposite effect of a novel landmark cue. The failure to find the familiar landmark may have provided evidence to the bees that they had not yet reached the appropriate distance (i.e. that odometry had brought them up short). Bees did, however, return to the training site to perform second U-turns. This is an important observation because it shows that bees re-adjusted their behaviour in response to the failure to find the landmark in the region just beyond the training site. Thus, bees exhibited two behavioural adjustments in rapid succession: as an initial adjustment to the absence of the expected landmark, bees flew a little further than odometry would have permitted; then as a second adjustment to the failure to find the landmark, bees reverted back to the learned odometric distance. This result itself exemplifies the amazing behavioural flexibility of the honeybee.

Interestingly, the overshoot behaviour observed in Experiment 5 did not arise in the experiments involving the shorter tunnels (Experiments 1 and 3). The failure to find a positive result may have occurred for several reasons. For instance, it is possible that bees are likely to exhibit odometric fidelity at shorter training distances, leading to a diminished effect of the familiar landmark’s absence. Further experiments are required to resolve this issue.

Why was search often so broad?

Further experiments are also required to assess whether bees behave differently in indoor and outdoor environments. In particular, the search performance of bees in some of the present experiments (e.g. Experiments 1 and 3), all of which were conducted outdoors, was considerably less accurate than would be suggested by the results of comparable experiments conducted indoors (e.g. Srinivasan et al., 1997). In general, there are many uncontrollable variables in outdoor environments (e.g. cloud cover, temperature), which appear to influence bees’ behaviour in the tunnels. Indeed, several experiments had to be aborted because bees apparently failed to learn, or ignored, the various cues. One example was included herein, partly to illustrate the point that bees can sometimes behave anomalously in the test situation (Experiment 4). Specifically, bees often failed to search in the vicinity of the training site, and instead searched near the end of the tunnel. This also occurred in other experiments not included here, and was not clearly related to phototaxis or any other obvious cue (although bees did often appear to fly quickly in the tunnel in these experiments, perhaps preventing them from learning the cues properly; see Chittka et al., 2003). Since the present work focused on the interactions between odometric and landmark cues, the results of these experiments were not included in the paper. Further study is clearly required to understand why bees can behave differently in indoor and outdoor environments. One speculative possibility is that conditions in the hive itself may influence foraging behaviour differently in indoor and outdoor environments (Groh et al., 2004; Tautz et al., 2003).

Conclusions

In summary, the present work reveals several strategies employed by bees to search for food. Bees assess the relative significance of odometric and landmark cues, often quite dynamically, and assign to each cue a behavioural weight that is appropriate to the situation. However, further experiments are required to investigate why bees do not always appear to pay attention to (or fail to learn) the sensory cues available at the feeder site. Additionally, it is currently uncertain how the present results might generalise to the scale of foraging in natural outdoor environments.

Table A1. *Effect of landmark position on mean search position*

	Landmark position				
Experiment	None	Unit 9/21	Unit 14/30	Unit 4/12	LSD
1	9.68	8.66	11.12	4.15	1.2
2	10.21	7.9	11.93	4.31	1.25
3	8.98	6.93	8.23	5.49	0.79
4	23.97	20.23	22.92	12.13	1.15
5	20.62†	22.71†	20.83†	–	0.54

Two conditions are statistically different if their mean values vary by more than the LSD, a measure that is twice the standard error of the differences of means.

†The respective conditions for Experiment 5 were: trained and tested without landmark; trained with, tested without landmark; trained and tested with landmark.

Appendix

ANOVAs reported in the main text revealed significant effects of landmark position on mean search position in all five experiments. Although the ANOVAs showed that the position of the landmark had a significant effect on where bees searched, they did not specify exactly which conditions differed. Here we tabulate the mean search positions, enabling comparison between pairs of conditions with a simple least significant difference (LSD) test.

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