

The use of landmarks and panoramic context in the performance of local vectors by navigating honeybees

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Summary

Bees seem to use landmarks to segment familiar routes. They can associate, with a landmark, a memory that encodes the direction and distance of the path segment between that landmark and the next. The expression of the memory results in the performance of a local vector matching the distance and direction of the path segment. The memories of path segments appear to be ‘chained’ together, so that the performance of one local vector is sometimes sufficient to elicit the subsequent local vector, even in the absence of the associated landmark. We have investigated the effect of visual panoramic context on the expression of local vectors. Bees were trained to fly along a narrow channel to collect sucrose from a feeder positioned partway along it. Panoramic context was provided by various types of patterning on the walls. The channel was partitioned into different segments using landmarks of two kinds: a boundary landmark that marked a change in the pattern on one or both side-walls of the channel, and an isolated landmark, consisting of a baffle through which the bee passed, for which the wall

pattern was the same before as after. In tests, we removed the feeder and analysed the search distribution of the bees for various arrangements of landmarks. Altering the spatial relationship between landmarks has different consequences for the two types of landmark. If the final boundary landmark is shifted, the centre of the search distribution shifts by approximately the same amount. Changes in the position of an isolated landmark have a weaker effect. In the absence of the final context, the search is disrupted. We suggest that for local vectors to be expressed the surrounding panoramic context needs to be appropriate. A comparison of search patterns from two different training configurations of landmarks supports the hypothesis that local vector memories merely encode route segments and that global positional coordinates are not linked to landmark memories.

Key words: honeybee, *Apis mellifera*, navigation, landmark, panoramic context, local vector.

Introduction

Insects, such as bees and ants, often follow stereotyped routes when they travel between their nest and a habitual foraging site (Santschi, 1913; Baerends, 1941; Janzen, 1971; Collett et al., 1992; Wehner et al., 1996). The routes appear to be partitioned into segments that are each associated with a prominent feature that serves as a landmark. On recognising a landmark, the insect is reminded what action it should perform next, such as approaching the landmark (von Frisch, 1967), turning left or right (Weiss, 1953; Collett et al., 1992; Zhang et al., 2000) or in a particular compass direction (Chittka et al., 1995; Collett et al., 1998) or searching relative to landmarks or landmark configurations (Tinbergen, 1932; Anderson, 1977; Wehner and Räber, 1979; Cartwright and Collett, 1983).

The present paper focuses on a sub-set of these behaviours for which landmark-associated memories continue to provide navigational information even after the associated landmark is no longer visible. The behaviours, which we call local vectors, employ memories associated with en-route landmarks. The

memories encode directional and distance information from one landmark to a site further along the route (Collett et al., 1993, 1996, 1998; Chittka et al., 1995; Srinivasan et al., 1997). The use of this memory probably involves the normal mechanisms of path integration with a sun-compass (Wehner and Rossel, 1985) and optic flow (Srinivasan et al., 1996, 1997), updating an accumulator to track changes of position. Encountering a familiar landmark on a route may lead to the resetting, or the initiation, of a path integration accumulator that is used for guidance along a local vector (Srinivasan et al., 1997; Collett and Collett, 2000).

Visual cues that change only slightly over large sections of a route may not specify a place with sufficient precision to be used as a landmark, but can nevertheless provide context for local vectors. A ‘panoramic context’, provided for instance by distant or repeated features, can be recognised as familiar over a wide area without necessarily specifying a precise spot. We distinguish two categories of landmark on the basis of the

continuity of the surrounding panoramic context before and after the landmark. An 'isolated landmark' is a prominent feature whose surrounding panoramic context is perceived to be similar before and after the landmark. Examples of an isolated landmark for a honeybee could be a boulder or a tree that it passes in the middle of a large meadow. A 'boundary landmark' is a rapid transition between two panoramic contexts that are perceived to be different. An example could be the point at which a honeybee passes from an open meadow into a wood or next to a tree line.

Local vectors can be associated both with isolated landmarks (Collett et al., 1993, 1996; Srinivasan et al., 1997) and with boundary landmarks (Srinivasan et al., 1997; Collett et al., 1998). Srinivasan et al. (1997) compared the two types of landmark in similar situations. They trained bees to fly along a narrow channel to reach a feeder placed at a set distance from the entrance. The width of the bees' search distribution within the channel increased with the distance of the feeder from the entrance. The search distribution was narrowed if bees were trained and tested with either a boundary or an isolated landmark shortly before the feeder. The area over which the bees search seems to depend upon the length of the local vector that has just been performed rather than upon the distance of the whole journey from hive to feeder. Both boundary and isolated landmarks can thus act to partition a route.

Memories of local vectors can be chained together in a sequence: one local vector priming the recall of the subsequent local vector. In one demonstration, bees were trained along a zig-zag course past two isolated landmarks. Once trained, the bees would fly along the zig-zag, even if the landmarks were removed, although less precisely in the absence of landmarks (Collett et al., 1993). This result suggests that a local vector, primed by the completion of the previous segment, can be recalled and expressed even in the absence of the landmark that normally triggers it. In this paper, we also find evidence of 'chaining' when an isolated landmark is removed. But there is no sign of chaining when a boundary landmark and its associated visual context are missing. We suggest that the change in panoramic context associated with a boundary landmark means that bees respond to the two types of landmark in different ways. The removal of a boundary landmark disrupts the context that follows, whereas the removal of an isolated landmark leaves the context unaltered. To anticipate a little, we will argue that the bee needs to be in the correct visual panoramic context for it to express a local vector so that chaining is only observed for isolated landmarks.

Materials and methods

We have followed Srinivasan et al. (1997) in training honeybees (*Apis mellifera*) to forage within a channel where their visual world can be closely defined. From the bees' perspective, distances flown in a channel are greatly magnified. Because bees measure the distance that they fly through the image motion – the optic flow – that they experience en route, and because the walls and floor of the channel are much closer

to the eyes of the bee than are the ground and vegetation outside, a short distance flown within a channel is perceived as equivalent to a much longer distance flown over open ground (Srinivasan et al., 1996, 1997, 2000). Moreover, since optic flow also controls the bees' flight speed (Srinivasan et al., 1996), flight through the channel is sufficiently slow that a walking observer can monitor a bee's progress over a route that from the bee's perspective is many tens of metres long. Unfortunately, under these circumstances, only the distance component of local vectors is easy to analyse.

Bees were trained to a feeder in a channel that had two landmarks placed between the entrance of the channel and the food. We analysed where the bees searched when the feeder was removed. We used two of the types of landmark that Srinivasan et al. (1997) had employed previously. One was a boundary landmark – a change in the pattern lining the inner wall of the channel, from a random array of black-and-white squares to vertical black-and-white stripes. The panoramic context provided by the changed pattern continued until the pattern changed again. The other was an isolated landmark – a baffle through which the bees flew. The panoramic context was the same either side of the baffle so that, once the bee had passed it, the baffle no longer provided any immediate cue.

Experiments were carried out on a garden lawn in Sussex during July and August 2000. Bees from a nearby hive were trained to fly down either of a pair of identical narrow channels to a feeder. The channels were 20 cm wide, 20 cm high and 14 m long. They were placed side-by-side with a space of 1.5 m between them. Both channels contained a 3 m training section that consisted of an entrance, two landmarks and a feeder. The walls of the tunnel before the entrance to the training section were unpatterned, and the top of the channel was uncovered. The entrance itself was marked by yellow plastic placed as a lintel. From there to the blocked end of the channel, the walls were covered with patterns to provide optic flow, and the roof was covered with fine mesh to prevent the bees from escaping. Starting at the entrance, the sides of the channels were covered by black-and-white textured patterns made of paper laminated with clear plastic sheets and divided into removable sections 1 and 2 m long. Two different pattern types were used. One type consisted of alternating black-and-white vertical stripes ('stripe pattern') with a period of 60 mm. The other ('random pattern') was made of black squares and white squares (width 2 mm) randomly arranged, but preserving 50% black coverage.

There were two training conditions, a 'boundary landmark training' (BLT) and an 'isolated landmark training' (ILT), which are explained below. A separate group of bees was used for each training condition. Bees were marked during the first day of their training. They were trained for two full days before tests were introduced and, except for the single bee being tested, training continued in one channel while bees were tested singly in the other.

Visual context and landmarks during training

In both BLT and ILT conditions, there was 1 m of random pattern after the entrance on both side-walls. At this point, the

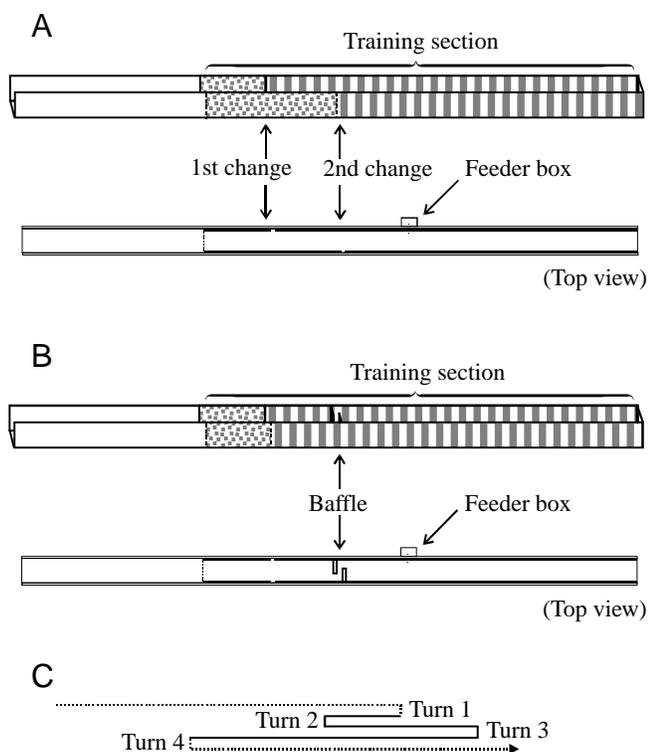


Fig. 1. Methodology. (A) Channel for boundary landmark training (BLT) viewed obliquely and from above showing texture changes on the wall and the position of the feeder box. (B) Channel for isolated landmark training (ILT) viewed obliquely and from above showing texture changes on the wall, the baffle and the position of the feeder box. (C) The bees' path through the channel, illustrating individual turns and the path segment (solid line) that each test flight contributes to the search distribution.

pattern changed, producing a boundary landmark. The next 1 m of pattern and the following landmark were different for the two training conditions. For the BLT, the pattern on the left side of the channel changed to stripes, while the right side continued for an additional 1 m with random pattern. At the end of the second metre, the right side also changed to stripes, thus producing a second boundary landmark (see Fig. 1A), and both sides remain striped to the end of the channel. For the ILT, after the first 1 m, both sides changed to stripes. In this case, 1 m after this first landmark, there was a baffle through which the bees flew. This baffle provided an isolated landmark because the same stripe pattern continued beyond the baffle to the end of the channel (see Fig. 1B). In both training configurations, the feeder was placed 1 m beyond the second landmark so that the context for the feeder was a pattern of stripes on both walls.

So that bees would learn the position, and not merely the appearance, of the feeder, which was larger than the feeder used previously (see Srinivasan et al., 1997), we located the feeder in an opaque box attached to the outside of the channel. A hole 10 mm in diameter in the left-hand wall, raised 20 mm above the floor of the channel, led into the box containing the feeder. The hole was located on a black stripe of the stripe pattern (see

below) and had a small (10 mm wide) square of yellow tape above to help guide bees at close range into the hole.

It was necessary to eliminate the interfering effects of trees surrounding the lawn, which the bees tended to use as overhead landmarks. The training section within each channel was therefore moved over a range of 8 m, with training sessions alternating between the two channels every 20 min. At each alternation between the channels, the training configuration was moved along the channel by at least 2 m so as not to coincide with either of the previous two positions. There was always at least 1 m of bare channel before the entrance to the training section and at least 4 m of patterned channel after the feeder.

Testing

Tests were carried out in the channel that was not at that time used for training. There was no feeder in the test channel, and the 2 m section of striped pattern around the feeder hole was replaced with a section without a hole. The position of the testing configuration of landmarks was varied over 1–4 m, ensuring that the expected centre of search did not coincide with the actual or previous position and was at least 3.5–7.5 m from the end of the channel.

A test began when a single marked bee was allowed into the test configuration; other bees were prevented from entering. A test bee flies from the entrance and at some point turns back towards the entrance (turn 1). In most tests, the bee turns again before reaching the entrance (turn 2). This search sequence can continue for a variable number of cycles before the bee lands on the wall or the roof or flies to the entrance to leave the channel. We recorded no more than the first four turns. Lines on the channel floor every 20 cm defined the basic unit of resolution for measuring turns (Srinivasan et al., 1997). We considered a bee to have turned if it re-entered a 20 cm section it had just left. A search was not included if the first turn occurred within the first 1 m after the entrance, as in these cases the bee had generally been disturbed by the testing arrangement and was attempting to leave the channel.

Data analysis

What features of these turn data provide the best estimate of the position of the feeder within the channel? Srinivasan et al. (1996, 1997) used the peak of a search distribution that was composed of the total flight path between the first and fourth turns (Fig. 1C). Cheng et al. (1999) reanalysed the data reported by Srinivasan et al. (1997) to determine whether the best estimate was given by the first or second turn or their midpoint. They concluded that the first turn gives the most accurate estimate. To determine whether our data were similar to theirs, we examined the means and standard deviations of all four turns from tests with landmarks in the training configuration. Pooling the ILT and BLT test data, the values are: turn 1 (mean distance from feeder 38 ± 75.6 cm, $N=72$), turn 2 (36 ± 88.4 cm, $N=70$), turn 3 (66 ± 91.6 cm, $N=69$) and turn 4 (28 ± 133.6 cm, $N=61$) (means \pm s.d.). The feeding site is straddled quite precisely by turns 1 and 2, and the standard deviation increases markedly with turn number.

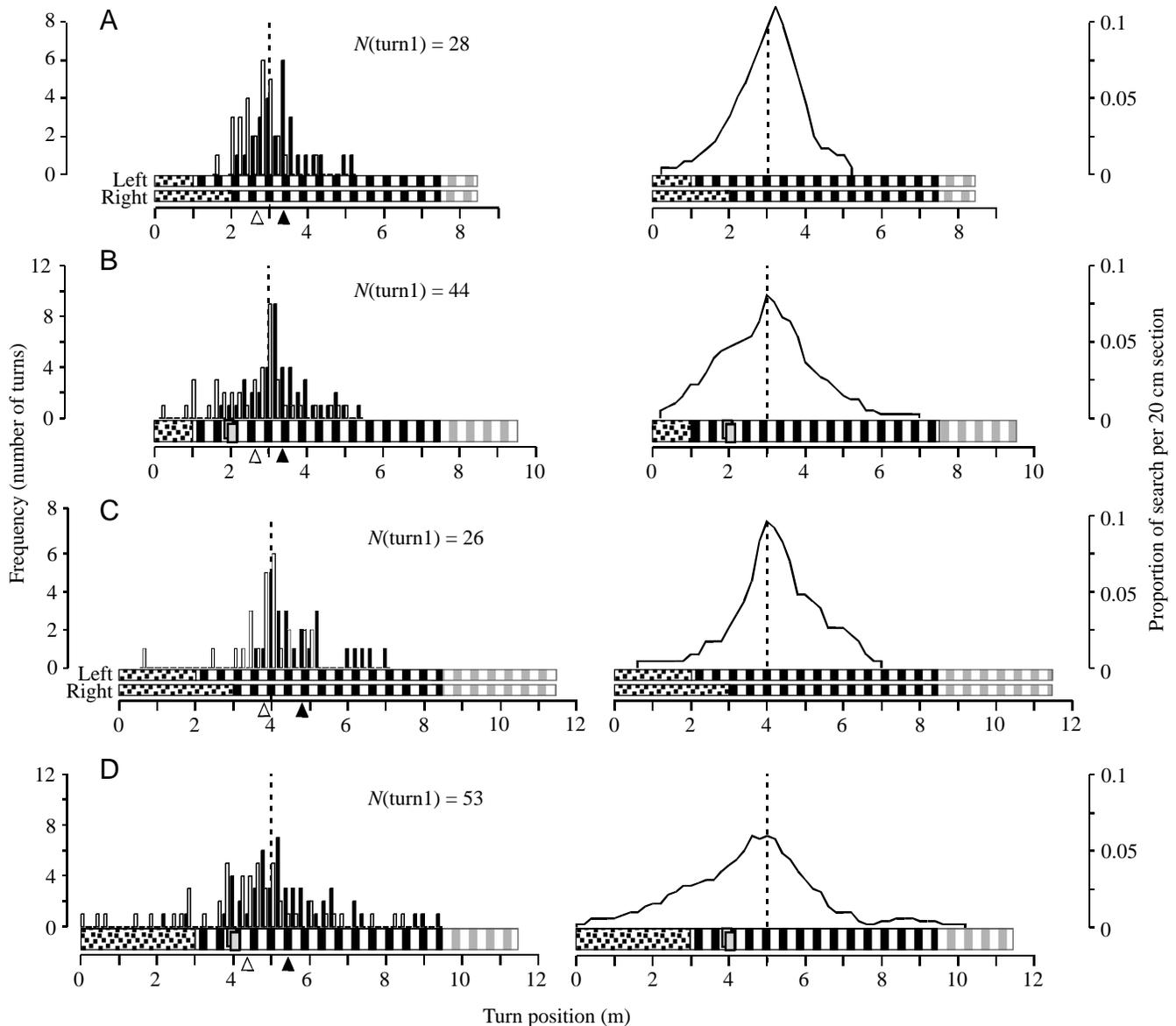


Fig. 2. Search distributions when the relationship between the landmarks is as in training. (A) Boundary landmark training (BLT) with landmarks in the training configuration. (B) Isolated landmark training (ILT) with landmarks in the training configuration. (C) BLT with landmarks shifted 1 m away from the entrance. (D) ILT with landmarks shifted 2 m away from the entrance. Left: distribution of first turns (filled columns) and second turns (open columns) above a sketch showing the arrangement of landmarks on the walls of the channel. Bin size is 20 cm. Filled and open arrowheads show the mean position of the first and second turns respectively. Right: search distribution as defined by Srinivasan et al. (1997) and described in the Materials and methods section. The dashed vertical line in this and subsequent figures shows the position, relative to the closest boundary landmark, of the feeder in the training configuration. The pattern beneath each graph shows the succession of landmarks and panoramic contexts from the entrance at the left. The section of lighter pattern at the right shows the range of the positions of the channel end.

In Figs 2–4, we plot in the left column the distributions of first and second turns for each test. For direct comparison with the results of Srinivasan et al. (1997), we also plot in the right column the search distribution (Fig. 1C). As did Srinivasan et al. (1997), we entered a score of 1 in a particular 20 cm segment each time the bee passed through or turned in that segment. Each histogram combines the scores of all the tests conducted with the same configuration of landmarks.

Results

In the following, we compare the search behaviour in equivalent test configurations of bees trained with a baffle as the landmark closest to the feeder (ILT) with that of bees for which the final landmark was a change in the wall pattern (BLT). It is important to remember that moving or removing the final landmark for BLT bees shifts or removes the panoramic context that in training contains the feeder.

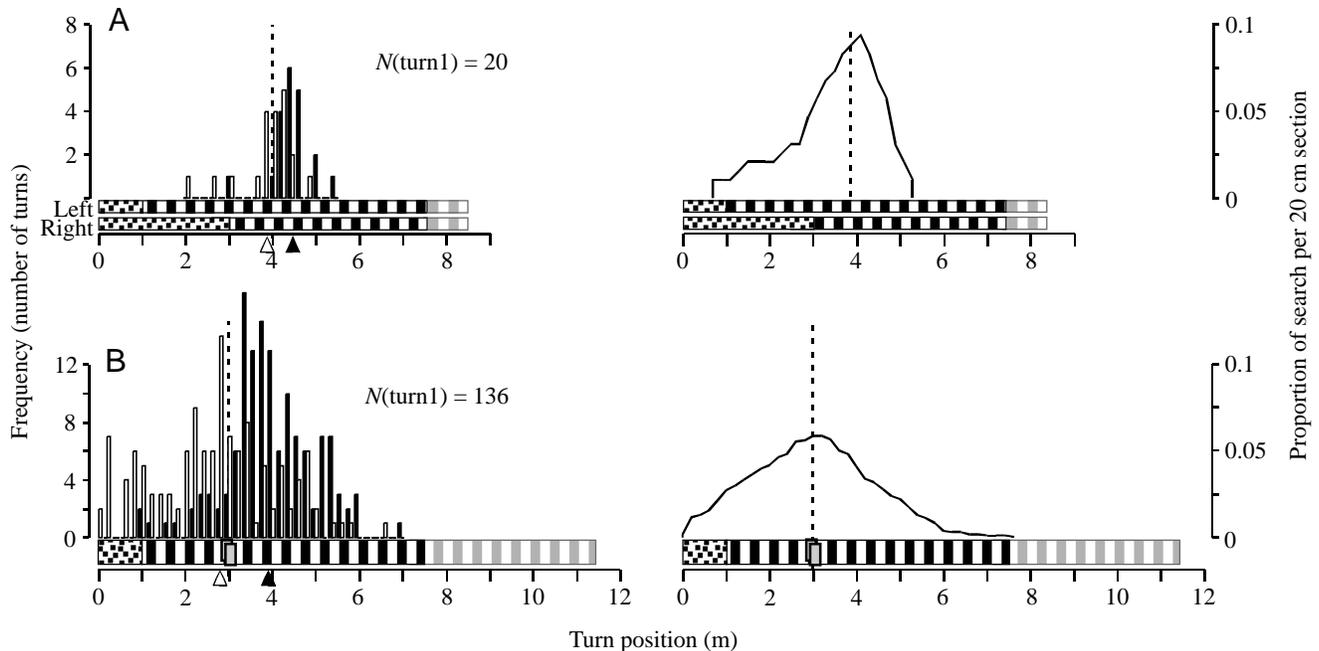


Fig. 3. Search distribution when the final landmark is moved 1 m away from the channel entrance. (A) Boundary landmark training (BLT). (B) Isolated landmark training (ILT). Data presented as in Fig. 2.

Local vectors

When bees were tested with landmarks arranged as in training, they searched in the expected position of the feeder relative to the two landmarks in the tunnel (Fig. 2A,B). Consequently, their search could be governed either by the position of the landmarks or by the apparent distance from the nest. To distinguish between these possibilities, we performed tests in which the distance from the channel entrance to the first landmark was extended beyond its usual length (Fig. 2C,D). Bees continued to search in the same position relative to the landmarks, confirming earlier findings (Srinivasan et al., 1997) that the search for the feeder is controlled by a local vector guided by landmarks.

Moving the final landmark

For one series of tests, the landmark closest to the feeder was shifted 1 m further into the channel, placing it, relative to the first landmark, in a position that is usually occupied by the feeder. The search distribution of BLT bees in these tests shifted by the same distance that the landmark was moved (Fig. 3A). Srinivasan et al. (1997) found a similar shift in search distribution on moving a boundary landmark towards the channel entrance. Shifting the final landmark (the baffle) for ILT bees had a different effect. Foragers tended to turn soon after passing the baffle, generating a search distribution that centred on the baffle (Fig. 3B). The bees' search seems to have been triggered by a cue encountered before they reached the baffle and, consequently, the local vector associated with the baffle was not performed. The search distributions of Fig. 3A,B, nonetheless, have one feature in common, they are centred at the distance of the feeder from the final boundary

landmark. In other words, both ILT and BLT bees search at the trained distance along the visual context that contains the feeder.

Removing the final landmark

In the last series of tests the final landmark was removed. The consequence for BLT bees is that nowhere in the channel can bees find the visual context that is associated with the feeder. Their first turns were mostly towards the end of the channel. This point is best appreciated from search data plotted with respect to the end of the channel (Fig. 4A), rather than the entrance (Fig. 4B). The search distribution plotted with respect to the channel entrance is broad, without a well-defined peak, and the means of turns 1 and 2 are widely separated (Fig. 4B), suggesting that, in the absence of the panoramic context appropriate for the feeder, bees do not perform the same type of search as at the end of the local vector seen in Fig. 2A. Instead, the majority of turns occur within approximately 2 m of the end of the channel (Fig. 4A), at which point the looming of the end of the channel is unlike anything they would have experienced during training. The bees seem content to continue along the penultimate panoramic context for a distance much longer than the trained distance until the channel end makes the visual surroundings inconsistent with the trained route.

In contrast to the BLT bees, the search distribution of ILT bees when the baffle is missing has a peak that is located 2 m after the change in background (Fig. 4C). The bees seem to have sufficient information to reach the feeder without needing the final landmark to trigger its associated local

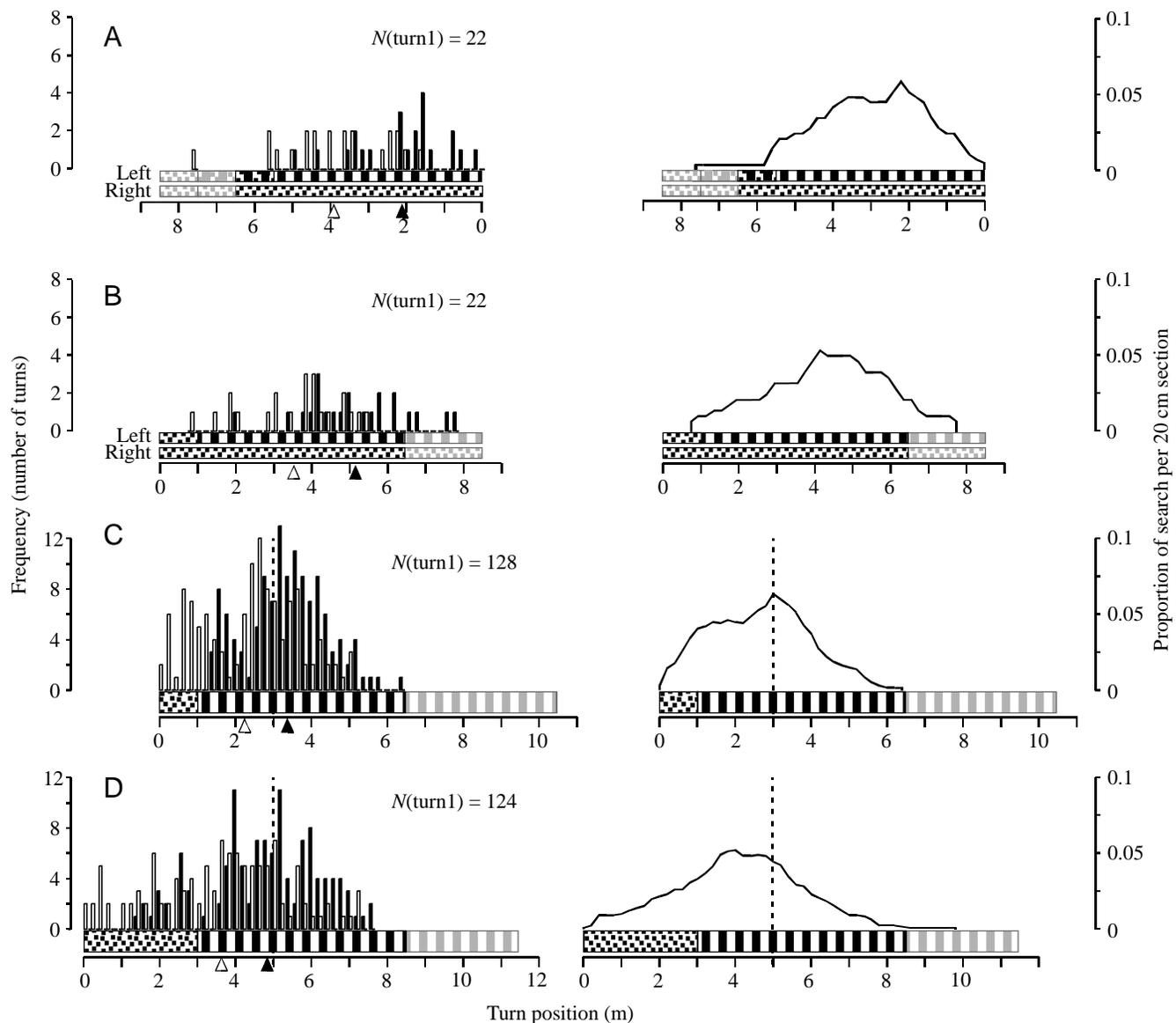


Fig. 4. Searching with the final landmark removed. (A,B) Boundary landmark training (BLT). (A) Search distributions plotted relative to the end of the channel. The lighter portion shows the range of positions of the entrance and first landmark relative to the channel end. (B) Search distributions plotted (as elsewhere) relative to the entrance of the channel (C) Isolated landmark training (ILT). (D) ILT with an additional 2 m of random pattern before the first landmark. For further details, see Fig. 2.

vector. The spread of turns when the baffle is removed is notably greater than when the baffle is present. The standard deviation of the distribution of first turns with the baffle in its normal position is 79.4 cm (Fig. 2B). Without a baffle (Fig. 4C), the standard deviation is 106.7 cm. The two values differ significantly ($F_{127,43}=1.805$, $P<0.014$). That the information used for the search is provided by the penultimate landmark (the change in wall patterns), rather than the apparent distance from the hive or the channel entrance (which can also be considered to be a boundary landmark) is shown by adding an extra 2 m of random texture at the entrance (Fig. 4D). The peak is less well-defined but has a mean located well beyond the trained distance from the channel entrance.

Discussion

The major finding of this paper is that, in a variety of test configurations in which the spatial relationships between landmarks are altered from those in the training situation, bees fly through the trained length of the panoramic context that surrounds the feeder and search at the trained distance from the final boundary landmark (Fig. 5). In the cases that we tested, if an isolated landmark is moved in relation to a boundary landmark, it no longer determines the centre of the search distribution. Nonetheless, it is clear that isolated landmarks are used when they remain in the same position relative to the preceding boundary landmark as in training. The search distribution is then much tighter than when the isolated landmark is removed (compare Fig. 2B,D with Fig. 4C,D).

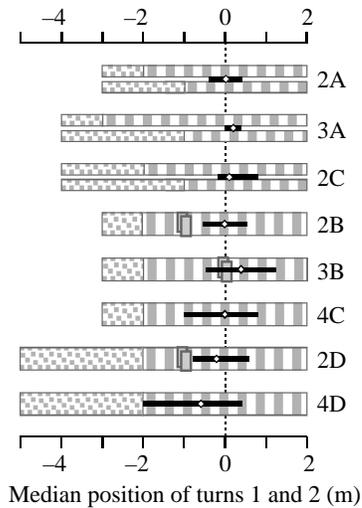


Fig. 5. Summary of experimental results for test conditions that included the final panoramic context. The open diamond shows the median value of the midpoints of turns 1 and 2. Distances are relative to the trained length through the final panoramic context. Bars show the first quartile of midpoints either side of the median. The lettering on the right indicates the figure in which the results are presented. The dashed vertical line shows the position, relative to the closest boundary landmark, of the feeder in the training configuration.

The correct panoramic context seems to be necessary for a local vector to be properly expressed. If the final boundary landmark is removed, so that bees never reach the accustomed panoramic context of the feeder, they tend to continue towards the end of the tunnel (Fig. 4A,B). This behaviour is reminiscent of observations from desert ants trained to a feeder along a channel (Collett et al., 1999). If the end sections of the channel are removed, foraging ants continue far beyond the trained position of the feeder without performing the normal search pattern. Here, too, search for a food source appears not to occur without the appropriate panoramic context.

Local vectors reflect procedural rather than positional memories

Landmarks can, in principle, provide an insect with two distinct forms of navigational information: procedural and positional. Global path integration could conceivably give the coordinate positions of landmarks relative to the nest or a food site. Memories of landmarks could then be linked to memories of the appropriate coordinate position (Cartwright and Collett, 1987; Gallistel, 1990; Menzel et al., 1996). If this were the case, we would expect to see landmarks providing information about the position of the goal with respect to the landmark. The global path integration accumulator would be reset to the stored coordinates of the landmark, making it possible to produce a vector from the landmark to the goal (Collett and Collett, 2000). Alternatively, landmarks could simply be associated with memories of what to do in the subsequent path segment. Evidence of local vectors produced by such procedural memories has come from studying path segments that do not end at the feeder (Collett et al., 1993, 1996).

In the training for which the feeder follows an isolated landmark that follows a boundary landmark (the ILT), the bees search at the appropriate distance from the preceding boundary landmark irrespective of whether the (final) isolated landmark is in the training configuration, shifted or removed (Figs 2B, 3B, 4C). This independence of the centre of the search from the isolated landmark implies that there exists sufficient information associated with the (penultimate) boundary landmark for a forager to arrive at the feeder position. By itself, this result could be interpreted both positionally, in terms of a single local vector that spans the entire distance from the boundary landmark to the feeder, and procedurally, in terms of concatenation of local vectors extending from landmark to landmark to feeder. The increased variance of search with the removal of the final landmark in the ILT situation (Fig. 4) does not exclude either possibility. The increased variance is consistent with the ‘chaining’ of local vectors, since the variance of the search would be related to the sum of the variances of the last two local vectors. Also, since the variance of the search distribution increases with distance flown (Srinivasan et al., 1997), increased spread is consistent with the use of a single local vector that spans the distance between the first landmark and the feeder. What may allow us to distinguish between these two possibilities is the comparison of the ILT with the BLT situations.

Since baffles and texture changes are equally effective at triggering local vectors (Fig. 2) (see also Srinivasan et al., 1997), we find it likely that there is the same sequence of local vectors in the ILT (Fig. 1B) as the BLT (Fig. 1A). The difference in search behaviours associated with shifting the two types of final landmark (Fig. 3) supports the conclusion from previous results (Collett et al., 1993, 1996) that local vectors express path segments, and that the performance of one local vector can prime the expression of the following local vector. If the search immediately after the isolated landmark (Fig. 3B) had been caused by a local vector extending from the first landmark to the feeder, BLT bees should also have searched immediately after the shifted second boundary landmark. Instead, the search of the BLT bees is delayed until they have flown the trained distance from that landmark (Fig. 3A). From the absence of a single vector spanning the distance between the penultimate landmark and the feeder in the BLT bees, we deduce a similar absence in the ILT bees and conclude that the ILT search must have been produced by a concatenation of local vectors. Thus, instead of landmarks providing positional (coordinate) information, we find landmarks that provide procedural information about the path segment. Srinivasan et al. (1997) showed that the local vectors are probably controlled with path integration and that the final landmark does reset a path integration accumulator. However, the accumulator that is reset is a local accumulator, associated with the path segment, rather than the global accumulator for the entire trip.

Landmark reliability and contextual cues

Landmark use requires both that a landmark can supply information that is specific to its precise location and that the landmark can be found and identified reliably. There is a

potential trade-off between precision and reliability, but it can be circumvented to some extent by remembering both a precise landmark and the broader more reliable context surrounding that landmark. The context, as well as the landmark, becomes associated with the appropriate behaviour. Although context is not the precise indicator of the exact timing of a behaviour that a landmark is, its identification can be a reliable indicator of what behaviours are appropriate.

The association between context and behaviour can be sufficiently strong that the specificity or even presence of a precise trigger such as a landmark can be rendered unnecessary. This reduces the probability that appropriate behaviour will not be expressed because the landmark is missed or mis-identified. In the experiments reported here, we found that the presence of isolated landmarks is not required for the expression of the associated local vector. Presumably, the end of the previous local vector can determine when the next begins. The ability to chain local vectors together in the correct panoramic context means that routes can continue even if a landmark has been missed, for instance, by an inadvertent change to a foraging path or because the landmark is masked by shadows. A similar example is given by bees encountering a landmark in a familiar context which is of a different colour or shape from what they normally find in that context. The bees then respond to the landmark as though its shape and colour were correct (Collett and Kelber, 1988; Collett et al., 1997), ignoring the aberrant detail because the context is appropriate. Context in these cases improves reliability by reducing the probability of a false negative match (i.e. being misled by an absent or slightly altered landmark).

Contextual cues also increase the reliability of an insect's behaviour by preventing an insect from being misled by a false positive match, i.e. responding to something that is not there or to a landmark that appears in the wrong context (Menzel et al., 1996; Srinivasan et al., 1998; Fauria et al., 2000). Panoramic context, by definition, remains correct over a relatively large area. Thus, while a particular panoramic context does not, by itself, provide precise information about when to start a local vector, it is also little affected by small differences in foraging paths or by minor changes to isolated landmarks. Whereas missing a landmark may be insufficient reason not to express a local vector, the absence of its panoramic context is probably a good reason to suppress it. The absence of the appropriate panoramic context can prevent a false positive match in one of three possible ways: (i) the end of the previous local vector does not prime the next local vector; (ii) the local vector is not updated; or (iii) searching is not initiated at the end of the final local vector. Our current evidence does not help decide which of these possibilities is correct.

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