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Honey bees store landmarks in an egocentric frame of reference

Abstract Honey bees are well known to rely on stored landmark information to locate a previously visited site. While various mechanisms underlying insect navigation have been thoroughly explored, little is yet known about the degree of integration of spatial parameters to form higher-level spatial representations. In this paper we explore the basic interactions between landmark cues and directional cues, which stand at the basis of our understanding of piloting mechanisms. A novel experimental paradigm allowed us independent manipulation of each parameter in a highly controlled environment. The approach taken was twofold: cue-conflict experiments were first conducted to examine the interactions between positional cues and directional cues. The bees were then successively deprived of sensory cues to question the dependence of landmark navigation on context cues. Our results confirm previous findings that landmark cues are used in concert with external directional cues if present. Conversely, the bees' ability to locate a food site was not disrupted in the absence of an external directional reference. Thus, bees store landmark memories in an egocentric frame of reference and only loose and facultative associations between visual memories and compass cues are formed.

Keywords Honey bee · Landmark · Visual learning · Memory · Flight

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Introduction

Central place foragers, such as bees and ants, have evolved a variety of navigational strategies that allow them to successfully navigate between the nest and previously discovered food sites (von Frisch 1967). Using dead reckoning, a bee is able to locate a site based on knowledge of the distance to and direction of a location relative to its own position. Such egocentric cues are subject to cumulative error, however, and therefore an additional mechanism based on geocentric cues, i.e., piloting, is also required. It is well established that bees are able to form visual memories and pinpoint a goal guided by local landmarks (Cartwright and Collett 1982, 1983).

Despite this basic understanding of foraging behavior, we still know little about the insects' representation of space. The key to understanding higher forms of spatial representation lies in elucidating the ties formed among stored visual memories and other parameters, such as directional cues (Dickinson 1994). It is well established that in some situations insects rely on eidetic (retinal) images (Wehner 1972; Wehner and Flatt 1977; Collett and Cartwright 1983; Dill et al. 1993), and that landmark guidance is complemented with directional information from celestial (Lindauer 1960) or terrestrial cues (Dyer and Gould 1981; Dyer 1987).

Previous studies have consistently shown directional cues to be used by insects during goal navigation (Lindauer 1960; von Frisch 1967; Dyer and Gould 1981; Dickinson 1994; Collett and Baron 1994). The influential snapshot model proposed by Cartwright and Collett (1983; p 537) suggests that successful image matching depends critically on the use of external directional cues (see also Collett 1992). Close integration between landmark memories and directional cues is also suggested in models of higher order spatial representations (Gould 1986; Cartwright and Collett 1987). More recently, Collett and Baron (1994) found that bees approaching a goal tend to keep their heading direction constant,

suggesting that stored retinotopic views and compass information may be more loosely linked in an associative way. Distinguishing between these alternate possibilities has important implications for proposed models of navigational mechanisms and spatial representation.

In this report we explore the interactions between landmark and directional cues in a twofold approach: First, the importance of different directional and landmark cues (visual and olfactory) are pitted against each other in cue-conflict experiments to determine their relative importance in a goal-seeking task. Second, we successively eliminate each of the cues available to the bees to elucidate how and to what degree piloting depends on an external directional reference. We are able to show that external directional cues can be used by the bees, but are not required for piloting, suggesting that landmark memories are stored in an egocentric frame of reference.

Materials and methods

Laboratory experiments were performed in a cylindrical flight chamber (height: 2.4 m, diameter: 2.4 m). The flight chamber consisted of a large cylindrical tent that covered the *arena*, consisting of a circular floor board with a side wall of 25 cm height, standing on legs 43 cm above ground. The inside of the arena was painted white and the floor covered with gray discs of 5 cm diameter in a quasi-random pattern, which was required by the bees to perform stable flight.

Three *entry holes* were drilled into the side wall of the arena, separated by 120°. During training, a conspicuously marked narrow tube (the *entry tube*) was fitted in the entry hole facing the balcony door (Fig. 1A). In tests, bees crawling through the tube could be caught by blocking off both openings with a small divider and the tube fitted to one of the alternative entry holes (E_1 and E_2 in Fig. 3A and C, respectively).

The apparatus was illuminated from one side by two lamps (Lowel, 650 W each) from a distance of approximately 2 m, such that a light gradient without sharp contrasts was formed on the tent. While the light gradient served as a potent directional cue, it did not provide strong cues for local search of the food source (data to support this are shown in Fig. 2B). A second pair of lamps pointed towards the tent from a different direction. In tests, the lamps used during training could be switched off and the tent illuminated from the alternative position (e.g., Fig. 3A).

A feeder containing concentrated sucrose solution was located in a small box beneath the arena. Access to the feeder was through a small hole in the arena floor, hereafter referred to as the *food hole*. Having fed, the bees exited the food box via a Plexiglas tube (about 1 m in length and 1 cm in diameter). The tube prevented bees from entering the feeding box through the exit hole.

Several measures were taken to minimize unwanted odor cues. First, an inconspicuous Plexiglas disc (diameter 10 cm) with a hole and a short tube at its center was fitted over the food hole. The disk, as well as the food box and the feeder were frequently replaced and washed with hot soap water to remove pheromone markings. Second, a ventilator extracted the polluted air from the feeding box. Ventilation holes in the arena wall prevented air from being drawn into the flight chamber from the feeding box due to convection. Precautions were taken to ensure that they were inconspicuous to the bees.

At the beginning of each training session, bees were recruited from a permanent feeding station located on the balcony and trained to fly into the laboratory using standard methods (von Frisch 1967). By moving the feeder in small steps, bees were trained to land on the entry tube, crawl through it, and fly to the feeding
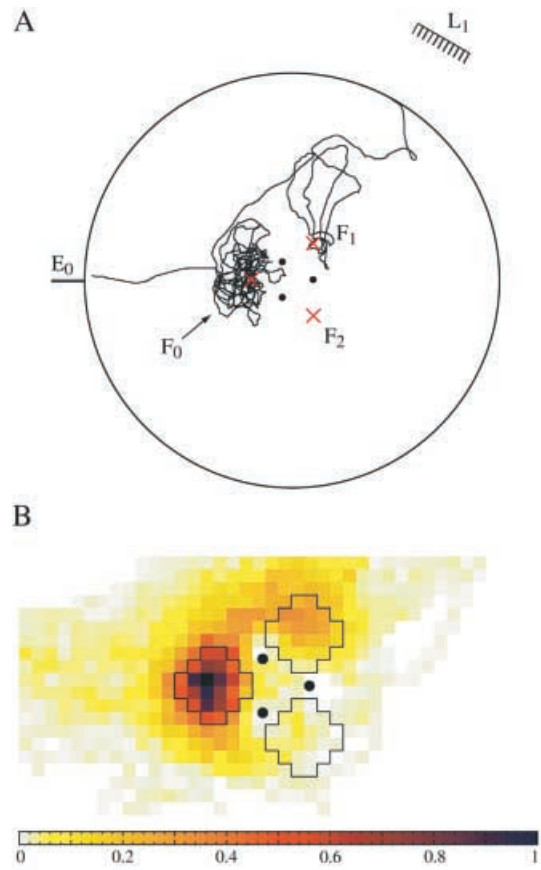

Fig. 1A,B Control experiment. **A** Top view of the flight chamber (*large circle*) and a typical search flight, obtained by blocking the food hole in F_0. *Filled circles*: cylindrical landmarks. The entry tube (*short line*) was attached at entry position E_0. L_1: position of the lamps (actual distance to arena was 2 m) during training and control experiment. *Crosses* mark the hypothetical search areas F_0, F_1 and F_2. **B** Search density distribution computed from 23 flights. Area shown: 2 m×1 m. For each square the number of traverses was counted and the highest score normalized to 1. Bees entered on the left and searched mostly in front of the landmark array. *Outlined areas*: search areas around the hypothetical food holes

hole marked by one or several landmarks, through which they accessed the food box with the feeder. As soon as the bees had learnt to reliably forage in the flight chamber, the lights and ventilation were turned on as required. Bees used in the experiments were marked individually with colored shellac.

Flights were recorded by a PAL VHS video camera (Panasonic F10), located centrally above the arena, and stored on video tape for later analysis. The camera was equipped with a wide-angle lens ($f = 10.5$ mm) and a wide-angle converter (factor 0.7), which allowed a view of the entire arena. Digitization of the video tapes was performed semi-manually with special-purpose software developed using LabView software.

The food hole was marked either by three identical cylinders (30 cm tall, 5 cm diameter) arranged as an equilateral triangle (Fig. 1A) or by a single landmark of the same type at the center of the arena (Fig. 5A). The feeding hole F_0 was located on the line connecting the entry hole and the centre of the arena. The triangular landmark array appeared the same in three positions, F_0, F_1 and F_2, due to its symmetrical properties. In the case of a single landmark, the bee required additional cues to determine in which direction of the cylinder to search for the food. By manipulating the position of the entry hole, the direction of the impinging light, the presence or absence of odor cues, as well as the arrangement of
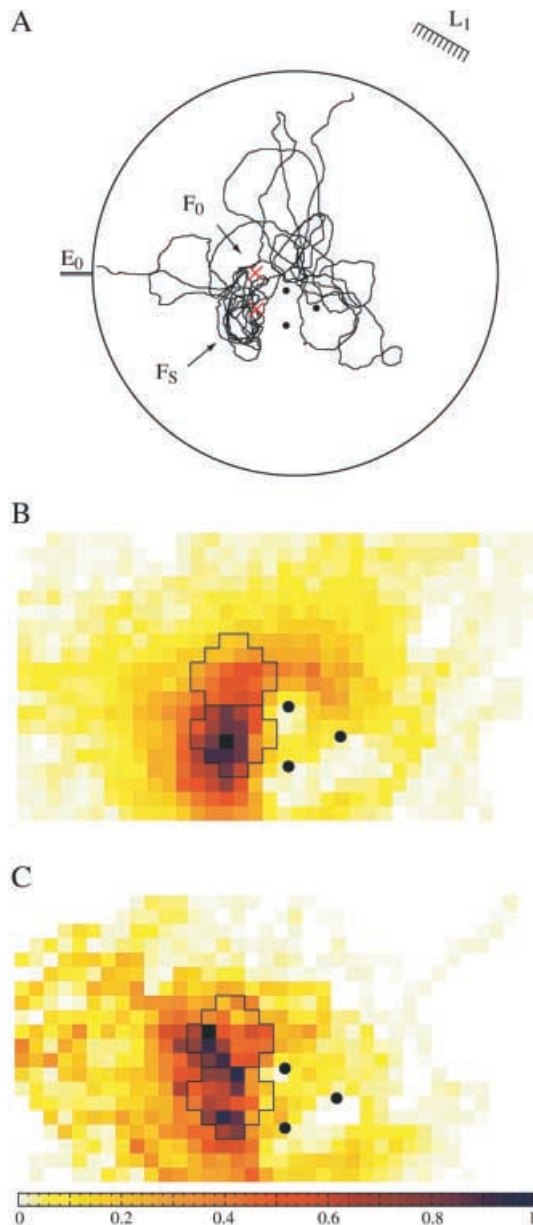
Fig. 2A–C Landmark array shifted to a new position. **A** Set up and sample flight. F_0: position of blocked food hole; F_S: hypothetical search area if bees relied on landmark array during searching. **B** Search density distribution of 26 flights. Bees searched primarily in front of the landmark array, indicating that the local landmarks governed the location of their search. **C** Search density of 11 flights obtained from bees trained and tested without odor extraction. Searching was divided between the actual location of the food hole and the location marked by the landmark array

landmarks it was possible to analyze how the bees used different cues in a piloting task. Furthermore, this paradigm permitted extensive control experiments.

Two types of analyses were performed on the resulting data. Search density distributions were calculated by covering the arena with a virtual grid (distance between grid lines: 5 cm). Traverses through each square were counted and the maximum score normalized to 1. In a second type of analysis, three circles with a radius of 10 cm were defined around each of the food sites F_0, F_1 and F_2. Every time a bee passed through one of the circles a "visit" was scored. Within the same flight, a visit to a different circle had to occur before another visit in the same circle was scored.

Results

Bees use external cues to resolve position ambiguity

Bees were trained to enter a flight chamber and fly to a food hole marked with an array of three cylindrical landmarks, arranged as an equilateral triangle in the center (Fig. 1A). Entry was through E_0. A light gradient (L_1) was established at an angular distance of 120° as seen from the center of the arena. The chosen landmark array offered an ambiguous visual cue for the bee with respect to the position of the food hole, as there were three positions (F_0, F_1 and F_2) from which the landmark array appeared the same. However, there were three additional cues that the bees could, in principle, use to choose the rewarded site. First, the light gradient could serve as a directional reference. Second, the position of the entry hole could be used to select the food site directly in front (e.g., by dead reckoning). Third, external directional (e.g., magnetic) cues, or local (e.g., olfactory) cues could be used.

Individual bees were allowed to enter the flight chamber and tested with the food hole covered, as in all the following tests. Figure 1A shows a typical example of a flight path. The bee approached the landmark array (from left to right) and searched near the covered food hole (F_0). The bee then traversed to one of the other fictive food holes (F_1), where it continued its search for a short while before flying towards the light and landing on the cloth. A search density distribution of 23 search flights of three individual bees is shown in Fig. 1B. Searching was not distributed evenly among the three fictive food holes, but was concentrated around F_0, indicating that the bees used direction cues to resolve the ambiguity caused by the symmetry of the landmark array. A smaller proportion of searches took place in F_1. Searching close to the brighter side of the flight chamber was generally observed and is most easily explained by phototaxis. This finding is corroborated further by the observation that searching typically ended with bees heading towards the light, as in the example shown.

Landmark cues predominated over external position cues

To rule out the possibility that imperfections of the flight chamber provided local cues and thus were causing the elevated intensity of searching in the vicinity of F_0, bees were tested with the landmark array shifted to a new position (Fig. 2A). Bees searched primarily in the shifted position, albeit somewhat less focused than in the previous experiment (Fig. 2B). Thus, landmarks were the predominant local cue used by the bees.
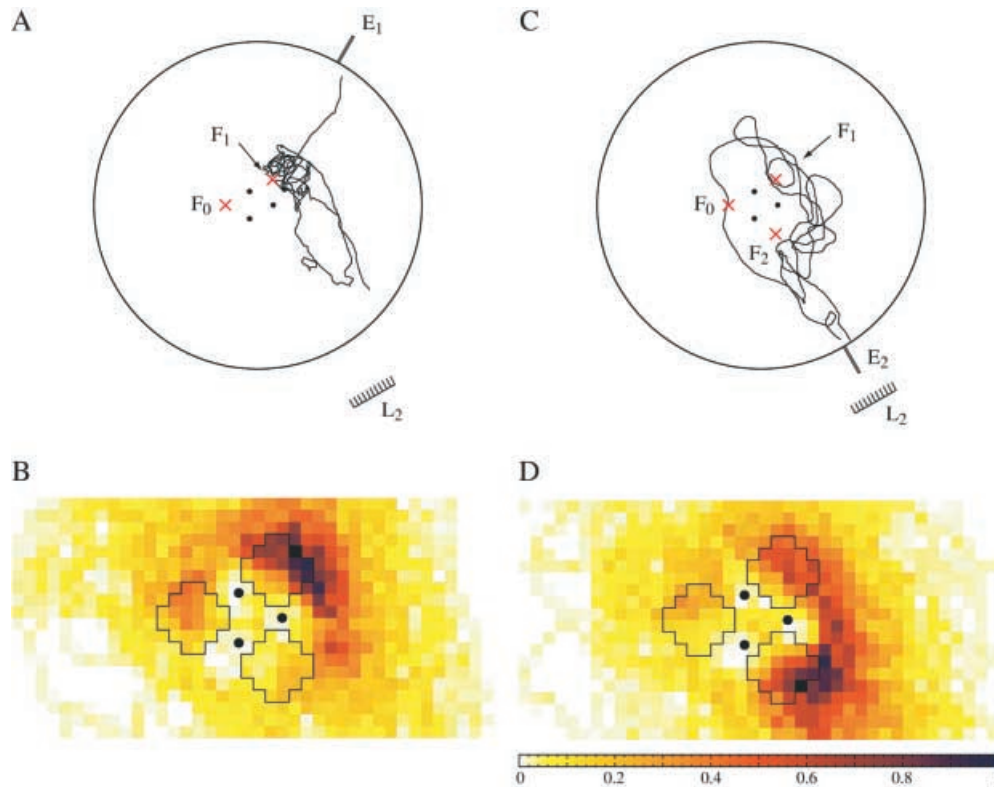
Fig. 3A–D Cue-conflict experiments with triangular landmark array. **A** Set-up and sample flight with the entry position and the position of the lights rotated clockwise by 120°. E_1: new entry position; L_2: position of lights; F_0: food hole position during training, conforming to geostationary and uncontrolled cues; F_1: hypothetical search area, if the position of the entry hole and the lights were used. **B** Search density distribution of tests performed using the set-up shown in **A**. Twenty-six flights were analyzed. Bees searched at the same position relative to the entry hole and lights, while disregarding geostationary and uncontrolled cues. **C** Set-up as in **A**, except that the entry position is rotated by an additional 120° to E2. F_1: hypothetical search area according to the position of the lights; F_2: hypothetical search area according to the entry position. **D** Search density distribution calculated from 30 flights. The searches were concentrated in front of the entry hole, despite the conflicting cues from the lights. To a lesser degree, bees also searched in F_1, where the lighting cues were in register

Odor cues can become as important as landmark cues

Bees are very effective at marking a rewarding food site with pheromone (von Frisch 1967). The experimental paradigm used in the previous experiment provided a good opportunity to examine an interesting side aspect, namely, to examine if odor markings can serve as equally effective local cues as visual landmarks. The previous experiment was repeated with a different group of bees under the same experimental conditions, except that the ventilator was not in operation. The behavior of bees tested with the landmarks in the training position showed a similar behavior to that observed in bees trained in the absence of odor cues (data not shown). However, bees tested with the shifted landmark array searched over a much broader area including both the

training and the shifted position (Fig. 2C). Thus, odor near the goal also served as an important cue to the bees.

No uncontrolled geocentric directional cues were used

The previous results show that the landmark array was the dominant local cue in the absence of odor cues (in all of the following experiments odor cues were removed). Therefore, the bees used the directional cues provided by the flight apparatus to identify the search area over the food hole. The two following experiments were performed to identify which directional cues were important to the bees in this task. In the first experiment, we asked if the bees were relying on the manipulable directional cues of light gradient and entry position, or if other cues, such as the Earth's magnetic field were used. Bees were released from entry position E_1, which corresponded to a 120° clockwise rotation in respect to the center of the arena (Fig. 3A). From this vantage point the landmark array did not appear different from the training situation, due to its symmetric properties. A corresponding rotation of 120° was also applied to the direction of the impinging light by switching from the training position L_1 to L_2. Bees entering the arena in E_1 encountered exactly the same conditions as during training, as far as the controlled cues were concerned. However, all other geostationary cues appeared rotated by –120°. Figure 3B shows the results of this experiment. Bees searched mostly in F_1, where the controlled cues were in register, while only very little searching occurred in F_0. Therefore, the entry position and the light gradi-

ent were sufficient to guide the bees to the food source. Uncontrolled cues, as well as geostationary cues, such as magnetic cues, were ignored by the bees.

An external directional reference is not required for piloting

Apart from the landmark array itself, two directional cues remain that could have been used by the bees as a directional reference: The light gradient and the position of the entry hole. We explored the importance of these two cues by presenting them in conflict with each other. Lights were shining from L_2 as in the previous experiment, however in this test bees were displaced to the entry hole E_2 (Fig. 3C). If the lights were used as a directional reference, the bees were expected to search near F_1, as in the previous experiment (Fig. 3B). Conversely, if the bees relied on their entry position, searches near F_2 were to be expected. The bees concentrated their searches around F_2 and paid little attention to the unusual direction of illumination (Fig. 3D). A smaller search density peak in F_1 does indicate that the light gradient was perceived and used to a lesser extent. The results show that the bees were able to perform landmark navigation while disregarding the external directional reference provided by the light gradient.

The light gradient was disregarded during the first approach

It was observed that the bees seemed to always approach F_2 directly, whereas F_1 was approached only after some searching had taken place. This observation was confirmed by a more detailed analysis of the bees' flight behavior, in which the sequence of approaches to the fictive food hole positions F_0, F_1 and F_2 was analyzed. Approaches to less than 10 cm to a fictive food hole position were scored and the sequences of all flights computed. Bees released in E_1 (with the light gradient in L_2) flew directly to F_1 in 24 of 25 cases ($E_1{\rightarrow}F_1$: 96.0%; also see Table 1 and Fig. 3A, C). The choices of bees released in E_2 (with conflicting lighting cues in L_2) were significantly different, with only 3 out of total 28 flights directed towards F_1 ($E_2{\rightarrow}F_1$: 10.7%; $\chi^2 = 35.10$, $df = 1$, $P < 0.001$). All other flights were towards F_2. Thus, the entry position, but not the light gradient, determined the position reached immediately after the release into the flight chamber.

During searching the bees preferred the site corresponding to the training conditions

In the cue-conflict experiment, bees arriving in F_2 from E_2 had the choice of flying to either F_1 or F_0 (Fig. 3C). Bees could have randomly flown toward either of the food sites, and searched more persistently where the

Table 1 Summary of sequential analysis of flight paths. Data from previous experiments with entry positions E_1 (Fig. 3A) and E_2 (Fig. 3C) are compared with each other in columns E_1 and E_2. Rows $E–F_x$: number of flights from the entry positions (E_1 or E_2) to the search areas around the hypothetical food hole locations (F_0, F_1 and F_2, outlines are shown in Fig. 1). Lower six rows show the number of flights between the search areas. For example, bees flew from F_2 to F_1 12 times in the experiment with the entry position at E_1 and 28 times in the experiment with the entry position at E_2

Traverse	Entry position	
	E_1	E_2
$E{\rightarrow}F_0$	1	0
$E{\rightarrow}F_1$	24	3
$E{\rightarrow}F_2$	0	25
$F_0{\rightarrow}F_1$	10	7
$F_1{\rightarrow}F_0$	15	12
$F_0{\rightarrow}F_2$	6	6
$F_2{\rightarrow}F_0$	5	4
$F_1{\rightarrow}F_2$	18	16
$F_2{\rightarrow}F_1$	12	28

light gradient conformed to the training situation. The data, however, show that of the 21 flights measured, significantly more flights were directed towards F_1 than would be expected by chance ($E_2{\rightarrow}F_2{\rightarrow}F_1$ versus $E_2{\rightarrow}F_2{\rightarrow}F_0$: 19/21 or 90.5% ($\chi^2 = 13.76$, $df = 1$, $P < 0.001$). Thus, the smaller peak in Fig. 3D was caused by more frequent flights from F_2 to F_1, and not merely by more persistent searching. It is intriguing -and remains unexplored- how the bees used the light gradient as perceived near F_1 to preferentially fly towards F_2.

Choices were independent of previously flown path

So far, we have tacitly assumed that the bees' decisions depended solely on the perceived stimuli, and not on the history of the previous decisions made during the search. This need not necessarily be so. For instance, desert ants searching for the nest entrance rely on path integration to repeatedly return to the origin of their search (Müller and Wehner 1994), a strategy causing the ant's search to remain focused on the same spot. If the bees relied on a similar strategy, their choices could have been biased toward the previously visited site, possibly confounding the interpretation of the data. We tested this possibility by comparing the choices made by bees at F_1, depending on their previous flight path. In the first case, flights of bees that had flown to F_1 directly from E_1 were considered (Fig. 3A). The sequence $E_1{\rightarrow}F_1{\rightarrow}F_2$ was flown 13 times, and $E_1{\rightarrow}F_1{\rightarrow}F_0$ was flown 4 times (Fig. 4A). The relative proportion of flights to F_2 was $F_2/(F_0 + F_2) = 76.5\%$. These data are compared to choices made by bees arriving at F_1 from F_2, after having entered at E_2 (Fig. 3C). Eight flights (66.7%) were performed in the sequence $E_2{\rightarrow}F_2{\rightarrow}F_1{\rightarrow}F_2$ and 4 flights in the sequence $E_2{\rightarrow}F_2{\rightarrow}F_1{\rightarrow}F_0$ (Fig. 4B). The proportion of flights toward F_2 was not higher if this site had been previously visited (n.s.: $\chi^2 = 0.03$, $df = 1$, $P > 0.80$),
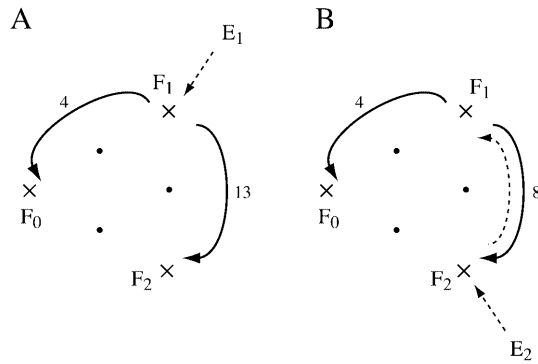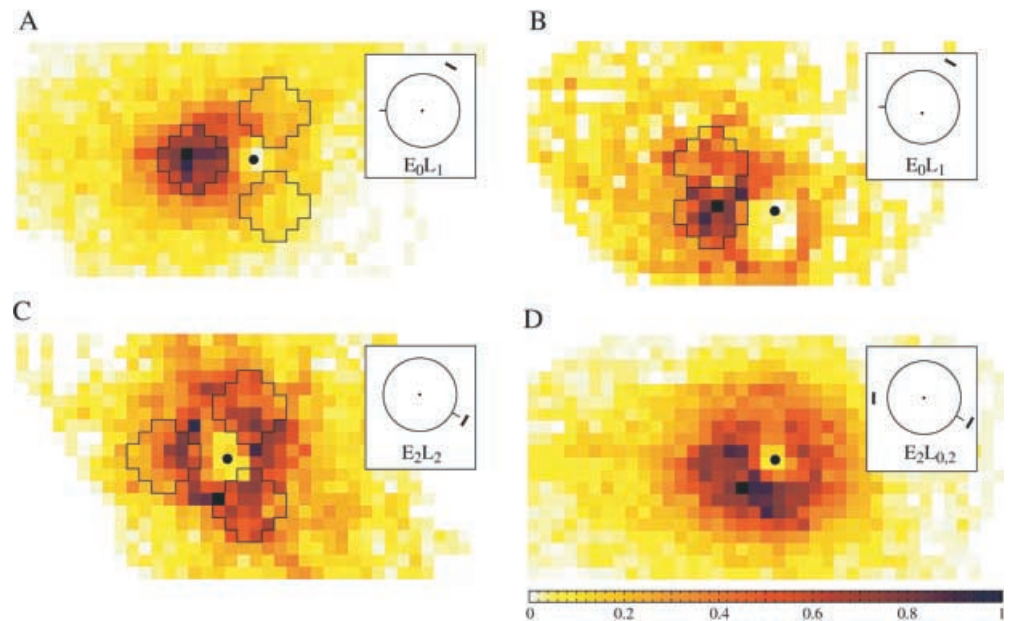
Fig. 4A,B Sequence analysis. *Dotted arrows* show approach paths to F_1, the *arrows and numbers* show flights from F_1 to F_0 and F_2, respectively. **A** Choices of bees in F_1 after release in E_1 (position not shown to scale). Of the 17 flights leaving F_1, 4 were led to F_0 and 13 to F_2. **B** Choices of bees that had returned from F_2. Bees were released in E_2, flew to F_2 and on to F_1. From there, 4 flights were directed to F_0 and 8 flights led back to F_2. The bees' preference for F_2 over F_0 was not higher if they had already visited that site during their search flight (n.s.: $\chi^2 = 0.03$, $df = 1$, $P > 0.80$)

indicating that path integration was not used by the bees in this context. Similarly, bees searching for a known (but displaced) food site were shown not to use path integration cues, whereas bees exploring novel food sources did (Chittka et al. 1995).

The results of the sequence analysis can be summarized as follows. Bees entering the flight chamber approached the array of landmarks directly, disregarding the lighting cues. In the case of conflicting cues, the light gradient was used to guide the bees to the location where all parameters were in register. The searching behavior did not depend on the previously visited locations.

Single landmark experiments

The previous results have revealed that the bees derived directional information primarily from the entry position and the landmark array, which restricted searching to the three axes of symmetry. To explore if the bees were able to derive directional information from the landmark array, experiments were performed by training a new group of bees with a single cylinder (of the same type), located at the center of the arena in otherwise identical conditions as during the previous experiments. Again, bees entered the flight chamber through entry hole E_0 and flew to the food hole F_0, with lights shining from L_1 (inset of Fig. 5A). As usual, tests were performed with the food hole blocked. Figure 5A shows searching was confined to an area around the fictive food hole (F_0), although the single landmark no longer provided directional information. Compared to the analogous experiment with three landmarks (Fig. 1), the searches covered much larger an area, presumably due to the decreased information content provided by the single cylinder.

The bees were then tested with the landmark shifted to a new position (inset of Fig. 5B). The bees searched most intensely in same relative position to the landmark (Fig. 5B), indicating that the cylinder was the prominent location-defining cue. In both cases the bees were able to search on the correct side of the landmark, indicating the use of landmark independent directional cues. To a lesser degree, the bees searched in all directions from the landmark, disregarding directional cues. Interestingly, the bees were still able to perform piloting to the extent that they were able to extract distance information from the landmark, in disregard of a directional reference.

Fig. 5A–D Experiments with a single landmark. *Insets* show the set-up used in the specific test. Symbols are used as in the previous figures. **A** Control experiment with food hole blocked. **B** Experiment with shifted landmark. **C** Bees were released in E_2 and lights positioned in L_2. **D** Bees were released in E_2 and lights were shining in L_0 and L_2, providing a broad patch of light. Conventions are the same as in the previous figures

In analogy to a previous experiment, in which the light gradient and the entry position were pitted against each other in a cue-conflict experiment (Fig. 3C), bees entering from E_2 were presented with the lights shining from L_2 (Fig. 5C). Contrary to the results obtained with the triangular array, the bees' searches were scattered in all directions around the landmark, suggesting that they failed to use directional cues under these conditions. Without additional directional cues from the landmark as was the case with the triangular configuration, the bees searched at the correct distance, but in all directions from the cylinder. In a slightly different test bees could be persuaded to search in a location, where none of the learnt directional cues were in register. Bees were again released in E_2, but now additional lamps were switched on in L_0, resulting in a much broader (and brighter) light gradient, centered in an intermediate position between L_0 and L_2 (Fig. 5D). In this situation the bees focused their searches closest to the patch of light, obviously attracted by it, similar to earlier observations. This result exemplifies that the bees' ability to search at the correct distance from the landmark remained intact in the absence of a clear directional reference.

The results from the tests with a single landmark differ from the three-landmark experiments in an interesting way. In the case of a single landmark and conflicting directional cues, searches became undirected, while the bees were still able to determine their distance from the landmark. Conversely, the array of three landmarks provided the bees with the directional cues allowing them to restrict their searches to a small region.

Discussion

Insects employ several strategies that allow them to navigate reliably in a complex and variable environment (reviews: Wehner 1981, 1992; Collett 1992, 1993, 1996). In recent years, the mechanisms by which insects form spatial memories have been met with renewed interest (Anderson 1977; Cartwright and Collett 1983; Gould 1986; Dyer 1991; Wehner and Menzel 1990; Collett and Baron 1994; Wehner et al. 1996; also see Tinbergen 1932; van Beusekom 1948; van Iersel and van den Assem 1964; Lindauer 1970).

In spite of the vast amount of behavioral data available today and the important insights gained this field, systematic analyses of the crucial links that need to be forged to compose forms of higher spatial representations have rarely been performed. By training bees in a highly controlled environment we were able to assess the interactions among a small number of parameters in a closely defined piloting task. In this reduced artificial environment the bees made use of directional cues to search in a defined direction from a triangular array of landmarks or a single cylinder (Figs. 1, 5A). We were able to show that it was possible to eliminate odor cues (and other local cues) to the extent that they became

insignificant to the bees (Figs. 2, 5B). We were also able to show that without the precautions taken to avoid scent marking, odor cues will be established and can serve as powerful a cue to the food source as visual landmarks. Unlike visual cues that require past experience, pheromone marks at a food source provide a potent cue, enabling newly recruited bees to pin-point the goal after having reached the environs of it using dead-reckoning.

The next step consisted of assessing which cues were being used by the bees in the given task. By displacing the bees to an unusual entry position we showed that the flight behavior was controlled solely by three parameters, all of which we could control experimentally: (1) the position of the entry hole; (2) the direction of the impinging light; and (3) the type of landmark array used. No evidence was found that other geocentric cues, such as the magnetic field, were used. Similarly, Dickinson (1994) found no evidence of the use of magnetic cues in a similar experimental paradigm (but see Collett and Baron 1994). By confronting the bees with conflicting cues we could show that during the initial approach and the early phase of searching the light gradient was ignored, while is was used as a secondary cue during prolonged searching (Fig. 3D). Especially during the initial approach, when the bees' behavior is most directly under control of the landmarks, external directional cues play a minor role, if any. This finding has important implications for the mechanisms presumed to underlie landmark guided goal navigation. Cartwright and Collett (1983) tested five computational models in an attempt to replicate the results obtained from searching bees. Interestingly, only the models with rotation-invariant snapshots performed sufficiently well. This finding led the authors to suggest that the bee needs to 'maintain its snapshot in the correct orientation' (Cartwright and Collett 1983, p 537). Using an external directional reference, the model brought the stored snapshot and the perceived image into register prior to computing the simulated bee's motion. In other words, for snapshot navigation to work, an external directional reference was required. In our experiments, however, the bees showed the ability to make use of the directional cues provided by the landmark array itself, while disregarding external directional cues (compare Fig. 3D to Fig. 5C), a finding that has been corroborated by field experiments (Dyer and Gould 1981; Geiger et al. 1995). Similarly, desert ants relied on landmarks rather than on celestial cues when searching for the nest entrance in the case of conflicting directional cues. Ants returning to the nest were caught and released near the landmark array, which had been rotated by 180°. Irrespective of the release position, the ants disregarded the strong celestial cues and searched in the same relative position of the landmarks as during training, rather than in the correct compass direction with only a partial match of the landmarks (Wehner et al. 1996). The snapshot model – as formulated by Cartwright and Collett (1983) – is

consequently not sufficient by itself to explain the observed behavior.

How, then, could landmark navigation be organized? In a natural context, a goal is most likely to be associated with a goal vector and the landmarks serve to reduce the errors associated with dead-reckoning. If the discrepancies are slight (as in our experiments), the bee is able to approach the food site more or less directly. During this approach it suffices that the landmarks appear in the usual position (relative to the bee) and weak directional cues are disregarded. Landmarks in this context may be used in a relatively straightforward way, e.g., as beacons. Similarly, bees approaching a pair of landmarks differing in shape (Collett 1996) or color (Fry et al. 1998) treat the individual landmarks as independent beacons, rather than applying a pattern matching strategy (Fry 1999).

After the bee has reached the goal location, it begins to search for the flower, or feeder, dramatically changing its behavior. It is during this time that other cues, such as the directional cues, become increasingly important and help the bee locate the true food location, if it has missed it on the first approach. Detailed analyses of the way in which different cues are used by the bees at different times during their flight towards and search near the food site promises to unravel some of the complex interactions between sensory stimuli on the one hand, and neural mechanisms on the other.

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