

THE KNOWLEDGE BASE OF BEE NAVIGATION

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Summary

Navigation in honeybees is discussed against the background of the types of memories employed in the navigational task. Two questions are addressed. Do bees have goal-specific expectations, and when are novel routes travelled? Expectations are deduced from (1) context stimuli as determinants for local cue memories, (2) landmark-dependent path integration, (3) sequential learning of landmarks, and (4) motivation- and context-dependent memory retrieval. Novel routes are travelled under two conditions: (1) goal-cue-based piloting and (2) integration of simultaneously activated vector memories. Our data do not support the conclusion that memory

integration in bees is organised by a cognitive map. The assumption of purely separate memories that are only retrieved according to the chain of events during navigational performance also appears to be inadequate. We favour the view that multiple memories are integrated using external and internal sources of information. Such configural memories lead to both specific expectations and novel routes.

Key words: honeybees, navigation, memory, expectation, vector integration.

Introduction

Navigation by a central-place forager such as the honeybee requires learning and memory. The destination of a bee's journey may change as the result of the unpredictable and sudden appearance and evanescence of food sources. Celestial navigation cues are not available under an overcast sky, and local terrestrial cues are not fully reliable either, being subject to visibility. Learning about the multitude of cues provided by the external world and their inter-relationships would allow a foraging animal to guide its way safely under continuously changing environmental conditions. How can it establish a concise and flexible representation of the external world which is resistant to the actual inconstancy of the environment?

Two extremes have been discussed so far: the local rule concept (Wehner, 1992; Collett, 1992, 1993; Wehner and Menzel, 1990; Dyer and Gould, 1981; Dyer, 1991; Dyer *et al.* 1993) and the cognitive map concept (Gould, 1986; Gallistel, 1989). The local rule concept proposes that navigation is guided by multiple and independent memories. In novel situations, the animal's behaviour is dominated by one of these memories. The cognitive map concept proposes, in contrast, that the integration of multiple memories leads to the generation of novel information. In conflicting situations, animals would thus be expected to be able to find effective solutions to navigational problems (Tolman, 1948). Two paradigms are available to test the cognitive map concept, namely goal-specific expectations and novel routes. Under certain conditions, the latter might, but need not, be an indication of a geostable map-like memory organisation.

Although overwhelming experimental evidence favours the

local rule concept of bee navigation (Wehner and Menzel, 1990), two objections need to be considered. (1) If an animal expects particular signals at a particular site or in the sequence of landmarks, local memories may be integrated in the context of external and internal sources of information. Thus, context stimuli and motivational factors need to be incorporated into the analysis. (2) The experimental design applied so far to test the map concept critically may have been unsatisfactory. Bees trained to forage at a single artificial food source may reduce their spatial memory very quickly to include only the signals relevant to this single route. Even attempts to train bees beforehand to other places in order to overcome this problem (Wehner *et al.* 1990; Dyer *et al.* 1993; Menzel *et al.* 1990) may not help because of the fast and effective learning capacity of bees. Thus, the novel route test employed predominantly in experiments investigating the cognitive map hypothesis is not the only crucial paradigm. Do bees have goal-specific expectations? When are novel routes travelled?

Contextual stimuli as determinants for local cue memories

Bees readily learn to fly to different locations to collect food during one foraging bout or at different times of the day. If local cues at the feeders differ, one may ask whether and how contextual parameters, such as time of day and features characterising the location, can be utilised to determine choice behaviour. In one particular experiment (R. Menzel, unpublished results), a group of bees was trained to feed on a

blue target in the morning at a location 40 m northwest, and on a yellow target in the afternoon at a location 55 m northnortheast, of the hive. Dual choice tests with both colour targets presented simultaneously were performed at noon and at the respective feeding times (morning northnortheast, afternoon northwest). The bees chose the colour target according to the location and not the time of day. However, time can also be an effective parameter, since bees learn to choose a scented food source at a particular time of day if they have fed on the scented source at that time and on an unscented source at other times at the same location (Koltermann, 1971). When bees were trained to two sites during one foraging bout, with different local landmarks characterising the location of the feeder, they searched at the correct locations at both sites (Collett and Kelber, 1988; Collett *et al.* 1993).

From a psychological point of view, one can interpret local cues, such as odour or colour, as conditioned stimuli (CSs) which gain control over choice behaviour as conditioned responses in an operant learning situation. Parameters such as time of day or landmarks cannot by themselves elicit the conditioned response, but can control different behaviours (image-matching, navigation, timing of motivation to forage). Thus, they become determinants of choice behaviour. To acknowledge the different roles played by landmark or time cues compared with 'ordinary' CSs, the former might be qualified as contextual stimuli (Rescorla *et al.* 1985). Two questions arise from such an interpretation. (1) Do memories of context affect storage or retrieval of CS memories? (2) What is the nature of the associations that are established: associations of context and reward, of context and CSs or of context and CS-reward relationships (Rescorla *et al.* 1985)?

Landmark-dependent path integration

The role that landmarks, as context cues, play in navigation was investigated recently (Chittka *et al.* 1995b) in a study concerned with the learning of a new flight route. The experiment was carried out in an area devoid of natural landmarks (Fig. 1), where a feeder 175 m north of the hive was positioned at 8° to a car (as the only landmark in an otherwise featureless environment) 150 m from the hive. Bees flying towards the feeder steered towards the car and then made a turn to the left to reach the feeder. After feeding, the bees' vanishing bearings were determined. They flew straight back towards the hive (Fig. 1, training).

In the first test situation, both feeder and car were displaced by 30° to the left (Fig. 1, first test). Bees departing from the hive flew first along the trained vector, then in a curve towards the car, and then to the feeder. Upon leaving the feeder, they chose the same compass bearing as during training, indicating that they had not learned the new vector from the hive to the new location. However, if only the feeder, not the car, was displaced by 30° (Fig. 1, second test), bees were observed to fly towards the car first, as they did during training, and only then to start searching laterally for the feeding place. The distribution of vanishing bearings of these bees was

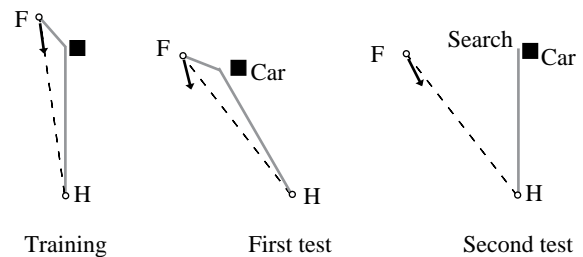


Fig. 1. The role of a landmark (a car) in the learning processes underlying path integration was tested in a flat area devoid of natural landmarks (after Chittka *et al.* 1995b). In the training situation, the bees flew towards the feeder (F) positioned 175 m north of the hive (H) and saw a car 150 m to the right. The flight route to the feeder is indicated by a thick grey line. The direct route from F to H is marked with a dashed line. In the first test, both feeder and car were moved 30° to the left; in the second test, only the feeder was moved 30° to the left. The vectors indicate the mean flight direction from the feeder calculated from the angular distribution of vanishing bearings seen from the feeder. Bees do not respond to the lateral shift if both landmark and feeder are moved (first test) but compensate for the lateral shift when only the feeder is moved (second test), and thus have learned only during the search flights.

significantly different from both other distributions, and the 95% confidence interval included the direction straight towards the hive, which was not the case in the first test. Thus, only under the latter conditions was the bees' path integration learning switched on.

The results shown in Fig. 1 indicate that if bees experience the expected relationship between landmark and feeder, they do not learn the new flight path. However, they do learn the new flight path if this relationship deviates from what they expected. Learning depends on the difference between the expected and the actual stimulus conditions (Rescorla and Wagner, 1972; Sutton and Barto, 1981). Blocking experiments in olfactory conditioning (Smith and Cobey, 1994) and experiments in which bees match choice frequency with the profitability of food sources (Greggers and Menzel, 1993) provide evidence for the applicability of the difference rule to bee learning. We might conclude, therefore, that they have expectations about the stimulus conditions both in conditioning experiments and in navigational tasks.

Sequential learning of landmarks

In another recent study (Chittka and Geiger, 1995; Chittka *et al.* 1995a), the role of landmarks in the bees' estimation of the distance between hive and feeding site was tested. Bees were trained along a row of artificial, movable landmarks (four tents, each 3.5 m high) in an otherwise structureless environment. The tents were placed equidistant from each other during training (75 m apart), and the feeding place was located halfway between the third and fourth tent. To determine whether bees search for the feeding place according to its absolute distance, or whether they also take its location relative to the sequence of landmarks into account, tests were

conducted in which the distance between tents was either increased or decreased. An empty feeding dish was placed at the correct absolute distance and the respective correct relative positions, and the number of bees arriving at each dish during a test was recorded. Bees searched for the feeding place significantly more frequently at shorter distances when the space between the tents was reduced and at greater distances when the space was enlarged. This result indicates that bees learn the sequence of prominent landmarks that they pass and relate their distance estimates, at least partially, to the sequential position within the landmark arrangement. It is tempting to conclude that they expect to find the feeding place after the third landmark. Similar experiments with a series of visually distinguishable landmarks show (a) that bees expect a particular landmark at the distance at which it was encountered during training, and (b) that they form specific expectations about the sequential arrangement of the landmarks passed *en route* (Chittka *et al.* 1995a).

While the above results might in a sense be interpreted to indicate that bees have acquired a positional representation of their surroundings, this is certainly not the most parsimonious explanation. We favour the interpretation that points along the route are memorised without their coordinates on a map, but are retrieved in a context-dependent fashion. The correct context can be, for example, having flown a given distance after which it is reasonable to expect a particular landmark, or having passed a panorama that usually precedes the encounter of that landmark. The retrieval of context-dependent memories does not require a map – one can get from A to B *via* C and D (using instructions such as ‘look for C after B’ or by passing a sequence of similar landmarks), without having access to the complete arrangement of these positions at any point in the journey.

Motivation- and context-specific retrieval of vector memories

At any given time, only a small fraction of the stored memories are behaviourally relevant. In order to behave appropriately, animals must store their memories in a way that would allow them to retrieve the ‘correct’ memory items selectively and to move them into a working memory stage that leads to a specific behaviour. It is one of the most challenging issues in learning research to understand the processes by which this selective retrieval comes about (Luria, 1979; Squire, 1987). Both internal and external factors are involved. Internal factors are the motivational and attentive states, external factors are the local and contextual signals which are associated with different memories.

Each foraging bout by a bee is characterised by a regular sequence of two flight phases (inbound, outbound) and four transitional periods (arrival at hive, departure from hive, arrival at food source, departure from food source), the motivational states of which are well defined. For example, there is ample evidence showing that outbound bees (bees departing from the hive) apply a working memory of the flight vector towards the

feeding place, and that inbound bees (bees departing from a food source) apply a working memory of the flight vector which guides them back to the hive. Furthermore, bees arriving at the hive have a working memory activated which leads them back to the hive and continues to guide their behaviour, even when they are captured and released at a different site immediately after arrival at the hive (Wehner and Menzel, 1990).

The interactions between motivational and context-dependent forms of memory were studied in recent experiments (R. Menzel, J. Joerges and U. Müller, in preparation) in which a group of bees was trained to fly 630 m to the southeast in the morning (F1) and 790 m to the northeast in the afternoon (F2) (Fig. 2). F1 was placed in an open and flat agricultural area, without any landmarks nearby, whereas

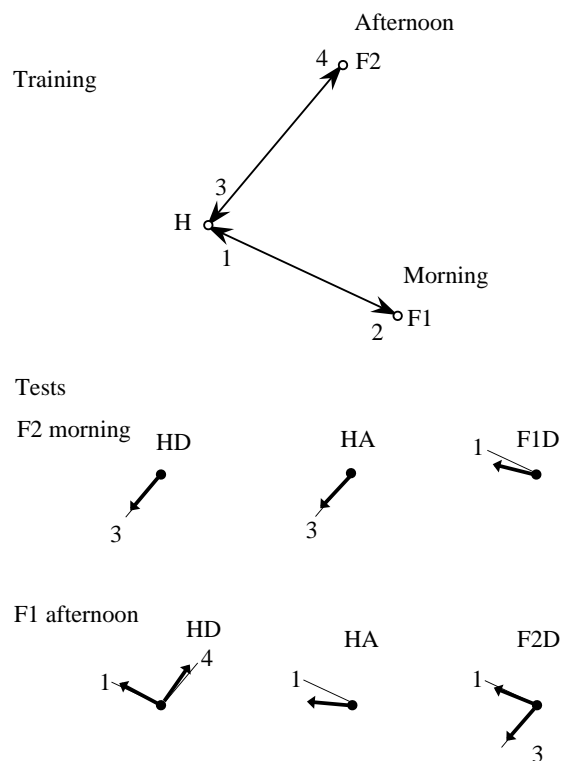


Fig. 2. Context- and motivation-dependent memory retrieval. A group of bees was trained to forage at F1 (115° SE, 630 m from the hive H) in the morning (09:00–12:00 h) and at F2 (40° NE, 790 m from the hive H) in the afternoon (14:00–17:00 h). Tests were performed by releasing bees at F2 in the morning and at F1 in the afternoon. Bees in three motivational states were tested: bees departing from the hive (HD), bees arriving at the hive (HA) and bees departing from the feeder (FD). The flight directions for these motivational states are indicated with numbers in the upper diagram. The lower part of the diagram gives the results in the form of mean vectors calculated from the angular distributions of the vanishing points for the two test conditions. The thin lines with numbers mark the flight directions which are interpreted to be expressed in the respective mean vector. Statistics: V-test (Batschelet, 1981 p. 58); all distributions are significantly different from random ($P < 0.01$). In the case of bimodal distributions, we applied the broken axis approach (Holmquist and Sandberg, 1991) (after R. Menzel, J. Joerges and U. Müller, in preparation).

F2 was characterised by small bushes and a conspicuous distant mountain peak just behind it when approached from the hive. Bees were then captured upon arriving at the hive (HA bees), departing from the hive (HD bees) or departing from the feeder (FD bees), and they were released at F2 in the morning and at F1 in the afternoon.

All HD and HA bees released at F2 vanished towards the hive, irrespective of their motivational state. They thus switched from their original vector memory (HD: $H \rightarrow F1$; HA: $F1 \rightarrow H$) to the vector appropriate for the release site ($F2 \rightarrow H$). HD and HA bees released at F1 behaved differently. HA bees showed a broad distribution of vanishing bearings with a rather imprecise direction towards the hive. HD bees flew in two directions, $F1 \rightarrow H$ and their original vector, $H \rightarrow F2$. Feeder-departing bees navigated either according to their original working memory (F1D released at F2) or according to their original working memory and their memory appropriate for the release site (F2D released at F1). No outbound motivated bees flew according to a map-like memory ($F1 \rightarrow F2$ or $F2 \rightarrow F1$), a direction one would expect if they had kept their original motivation and steered towards the intended goal along the shortest route.

Obviously the landmarks characterising F1 and F2 activate the vector memory for the correct return flight from the release site to the hive in most bees, although a different vector memory is active in the working memory. The potential to switch off the existing working memory and replace it with the one relevant for the particular location is different for the two locations and for the motivational states. F2, with its stronger landmarks features, has a higher potential than F1, which lacks any conspicuous landmarks. Furthermore, hive- and feeder-departing bees appear to have a stronger working memory than hive-arriving bees, as is evident from the finding that many of them vanished in the direction corresponding to the flight vector stored in their working memory. These results indicate that the four vector memories established in these bees can be activated and repressed by external and internal factors and, thus, appear as a flexible set of addressable memories.

When are novel routes travelled?

Cue-based piloting over longer distances rarely occurs in bees, probably because compass navigation dominates and because cue-based piloting requires a certain degree of generalisation of the picture memory adopted for the final goal location (Collett, 1996).

We have so far observed three conditions under which a bee selects a novel route: (1) when local cues are seen close up (in the range of less than 2 m) and from a viewpoint close to the usual final flight path when approaching the hive (Fig. 3A); (2) when celestial cues are not available and the release site is at an 'impossible' location, e.g. at the end of a pier looking out to sea (Fig. 3B); and (3) when celestial cues are not available and the horizon is unreliable owing to frequent and variable screening by deep clouds and fog (Fig. 3C). The latter situation occurred in a steep Alpine valley. These three cases reflect a

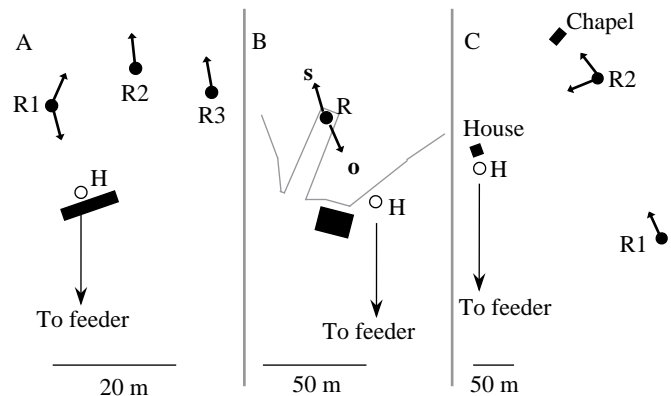


Fig. 3. Three examples of local cue-based piloting in bees. The bees were captured when leaving the feeding place and released at the indicated locations (filled circles). Only the vectors calculated from the distribution of vanishing bearings are given. The sketches are arranged in such a way that the flight path between feeder and hive (H) points downwards. The three figures are not to scale (see scale bars). Local cues close to the hive are indicated by black boxes. (A) Bees are released under sunny conditions at three sites close to the hive. They are guided towards the hive by local cues (a pile of logs) only when very close to the hive (Geiger *et al.* 1995). (B) Bees are released at the end of a pier looking out to sea, either under sunny conditions (vector *s*) or under a fully overcast sky (*o*). They fly towards the hive only under the latter conditions (Menzel, 1989). (C) Bees are released under a fully overcast sky in a narrow Alpine valley. At release site R1 they steer towards a chapel which resembles features of the house close to the hive, but is larger. The mean vector direction is significantly different from that chosen under sunny conditions (not shown). At R2, bees show a bimodal vanishing bearing distribution with one mode centred on the chapel and the other on the house (Geiger *et al.* 1995).

rather basic orientation mechanism, namely navigation according to a cue at the goal which is visible from the distance. The novel routes travelled on the way to the goal, therefore, do not require more than a memory for extended landmarks close to the goal.

If novel routes were travelled over longer distances in the absence of goal cues, they might be indicative of integration mechanisms at the level of spatial memories. It is essential that these spatial memories are represented simultaneously in working memory.

In the experiment described in Fig. 2, two vector memories are established in long-term memory. A location which has some features resembling both feeding sites, F1 and F2, might have the potential to activate both inbound vector memories simultaneously. Release site R3, halfway between F1 and F2, turned out to be such a location (R. Menzel, J. Joerges and U. Müller, in preparation). Fig. 4 demonstrates that a novel flight route close to the vector $R3 \rightarrow H$ is indeed chosen by HD bees. 41% of the HD bees released in the morning at R3 and 40% released in the afternoon flew towards the hive (vector 5 in Fig. 4), the remaining bees followed their original vector memory (vectors 2 and 4 in Fig. 4). Several controls support the conclusion that the distribution of vanishing bearings at R3

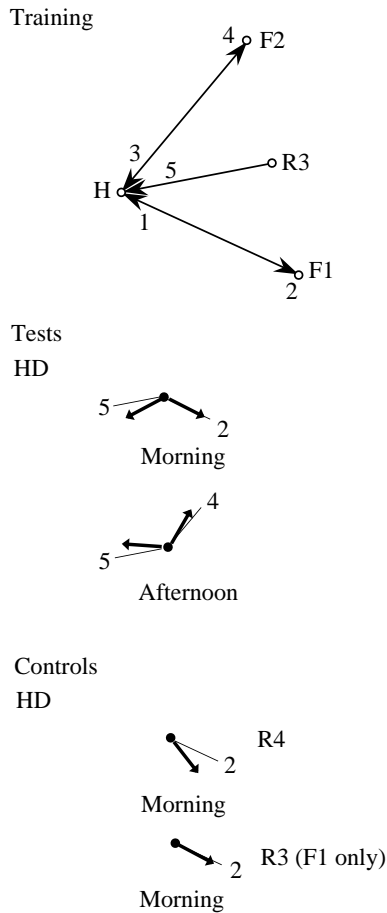


Fig. 4. Integration of two simultaneously activated vector memories. Training situation as in Fig. 2. Tests were performed by releasing HD bees at R3 in the morning and in the afternoon. R3 is a location halfway between the training sites F1 and F2. Two control experiments were performed: HD bees were released in the morning at R4 (not shown), which marks a release site far away (4km) from the training site and at a different relative position to the mountain. The other control refers to bees which foraged only in the morning and thus only have memories related to F1. Abbreviations and basic statistics as in Fig. 2. Statistical comparisons of the control group (HD morning) with the relevant test groups are based on the χ^2 -test (Batschelet, 1981, p. 109). Both control groups are oriented significantly differently from the test group ($P < 0.01$).

indeed indicates an integration of both vector memories. (1) Bees that foraged only at F1 or F2 either in the morning or the afternoon did not choose this direction at R3, but instead chose exclusively the one corresponding to their respective original vector memories. This result excludes the possibility that bees might have used local landmarks close to the hive, which might be visible from R3, to guide their flights directly towards the hive. (2) Bees that foraged at both F1 and F2 did not choose the R3→H direction when released at a site (R4) far away from the training site. They chose the directions corresponding to their originally activated respective vector memories. This result excludes the possibility that bees might simply switch on all inbound vector memories if they find themselves at an

unknown location. (3) Feeder-departing bees (F1D and F2D) flew according to their respective working memories (F1→H or F2→H) and not directly towards the hive when released at R3 (not shown in Fig. 4). This result is to be expected because the working memory of feeder-departing bees is strong and rather resistant to changes caused by context-specific updating (see Fig. 2). Most importantly, HD bees released at R3 never flew directly towards F1 (in the morning) or F2 (in the afternoon) as one would expect them to do if they had retained their motivation and followed a map-like route. This result corroborates the findings reported above for release sites F1 and F2.

Integration of two remote vector memories when simultaneously activated in working memory can be interpreted on two levels of complexity: (1) as an extension of the dead-reckoning process which guides the bee automatically on a small scale, or (2) as an indication of relating egocentric vectors to learned landmarks and, by doing so, fixing vector information to geostable features with the potential to construct a vector map. Since context-specific expectations and memory retrieval have been demonstrated in our experiments, the latter interpretation appears more suitable.

Conclusion

Middle-scale navigation between multiple, highly unpredictable food sources and a central place relies on many forms of learning which lead to multiple sets of memories (Menzel, 1990). But how are these memories related and used in navigation? The behaviourist view would be that separate memories are linked when retrieved by the chain of events as associated during initial learning. The cognitive view would be that separate memories are configured on the basis of common contextual stimuli. Activation of a configured memory would make the navigational process rather robust to disturbance, would lead to expectations about later stages and would integrate conflicting information so that novel behaviours result. Such innovative and novel behaviours would also be more economical than the sequential activation of chain associations. As the history of the debate between cognitive and behaviourist psychologists shows, there is no simple way of distinguishing between these two levels of interpretation. Since goal-specific expectations exist in bee navigation, and because bees indeed travel on novel routes resulting from integration of information acquired from simultaneously activated vector memories, a cognitive interpretation might be more adequate than a behaviourist one. However, none of the experiments reported here indicates that bees operate on the level of abstraction required by the cognitive map hypothesis. Although an integration of memories appears to take place, the generation of novel information from the configured memories is rather basic.

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