# Look and turn: landmark-based goal navigation in honey bees

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## Summary

This report describes the piloting mechanisms employed by honey bees during their final approach to a goal. Conceptually applying a bottom-up approach, we systematically varied the position, number and appearance landmarks associated with a rewarded target location within a large, homogenous flight tent. The flight behavior measured under various conditions is well explained with visuo-motor control loops that link perceived landmarks with appropriate turning responses. This view is consistent with the requirement of prolonged reinforcement learning for efficient goal navigation. A simple model is able to provide a comprehensive explanation for diverse flight patterns that range from convoluted searching behavior to highly idiosyncratic approaches, depending on the experimental context. Our results challenge the prevalent notion that honey bees employ image matching for visual guidance toward a goal site. Basic visuo-motor control loops may better meet the high demands for robust and fast flight control, which could serve as a powerful bio-mimetic design principle for micro-robotic aircraft.

Key words: honey bee, *Apis mellifera*, behavior, flight, vision, landmark.

## Introduction

Eusocial insects, such as honey bees, wasps and ants, are well known for their ability to learn visual features of an important location, such as a profitable feeding site, which they repeatedly visit during their lives as foragers (von Frisch, 1967; Wehner, 1981; Wehner et al., 1996; Collett and Collett, 2002; Collett et al., 2003). During the initial approach toward the desired goal, vectors and visual landmarks encountered *en route* and near the goal play a prominent role (for reviews, see Menzel et al., 1996; Giurfa and Menzel, 1997; Collett and Collett, 2002; Collett et al., 2003). Usually, a fairly direct approach flight is followed by prolonged searching at the presumptive goal location, if the desired target, e.g. the food source or the entrance to the colony, cannot be found immediately. In his classic experiments, Tinbergen (1932) exploited experimentally induced searching behavior to explore how a digger wasp represents a configuration of landmarks in its memory. He first placed a circular array of pine cones around the nest entrance and allowed the wasp to familiarize itself with this array. Next, he observed where the wasp searched within modified landmark configurations to explore its internal visual representation of the goal site. Following the same approach, Anderson (1977) applied the 'search paradigm' to honey bees trained with a feeder surrounded with a circular array of tall cylinders. When tested with experimentally manipulated landmark configurations in the absence of the feeder, the bees preferred to search where they were similarly 'surrounded' by landmarks as during training, but not where the landmarks appeared at the habitual retinal positions. These results were challenged by Cartwright and Collett's influential 'snapshot' model (Cartwright and Collett, 1982, 1983). This is also based on measured search distributions after experimental manipulation of landmarks at the feeding site, but proposes an eidetic representation of the landmarks perceived at the goal location. Appropriate steering commands for a goal approach are computed from the mismatch between the current retinal input and the stored retinal template, or 'snapshot'. This approach is highly appealing because it provides testable hypotheses both for the approach behavior during goal navigation, as well as concrete algorithms that can be explored in numeric (Cartwright and Collett, 1983; Nicholson et al., 1999; Möller, 2001) and robotic (Lambrinos et al., 2000; Möller, 2000, 2001; reviewed by Franz et al., 1998) simulations.

Though image matching is widely accepted to underlie goal-directed piloting behavior in bees, a direct verification of the predictions made by the model has been precluded by the technical limitations related to a precise and detailed measurement of flight paths extending beyond the immediate goal location. Such analyses have become possible through the use of pan-tilt cameras and appropriate software, which allows the observation area to be extended several fold without significant loss of spatial detail (Fry et al., 2000; reviewed by

Reynolds and Riley, 2002). We applied this technique in a conceptual bottom-up approach to explore navigational mechanisms in highly defined goal-seeking tasks. Bees entered a large uniform flight, in which one or a pair of landmarks provided prominent visual cues for locating an inconspicuous target associated with a food reward. We acquired the flight paths under standard conditions and in occasional tests with modified landmark positions. In separate experiments, we varied the position, number and appearance of the landmarks for a systematic analysis of the resulting flight paths toward the goal. The results of our experiments show that honey bees combine beacon navigation and an intricate motor behavior for a robust and flexible navigation strategy. A simple rule-based model is able to explain the structure of approach flights measured in various landmark settings, ranging from search-like flight behavior in the absence of a suitable landmark to highly stereotyped, direct approach flights in the presence of a landmark close to or behind the goal. Furthermore, our model is consistent with the gradual effect of operant learning observed during training.

## Materials and methods
### Experimental set-up

We performed our experiments under highly controlled conditions in a large cylindrical tent (Fig. 1; see also Fry and Wehner, 2002) constructed within an indoor laboratory. Homogenous illumination was provided from six halogen lamps (500 W each; not shown in Fig. 1) positioned around the tent. Entry to the tent was provided by a short, narrow tube, which could be blocked off to ensure that bees entered the tent singly when data acquisition was in progress. Flights within the tent were filmed from above using a video camera located at the center of the roof. Bees flew to a 1.9 m-distant hole in the floor (hereafter referred to as the 'food hole'), which gave access to a box with a feeder containing concentrated sucrose solution. Landmark cues were provided by a paper square attached to the side wall and cylinders placed at the locations indicated in Fig. 1 (inset). A simple but effective 'one-way system', consisting of a 1 m-long transparent Plexiglas tube leading from the feeding box toward a window of the room, allowed bees a direct exit from the box but prevented them from returning, as well as preventing naive bees from accessing the feeder from outside the flight tent. Importantly, this feature allowed trained bees to forage in the set-up without manipulation by the experimenter or unwanted disruption of the foraging behavior.

In previous experiments (e.g. Cartwright and Collett, 1983), the location of the feeder and the associated landmarks were repeatedly shifted to different locations during training to compel the bees to rely on the presented landmarks rather than uncontrolled cues, including, in particular, pheromone markers. We avoided this procedure in our experiments due to its potential influence on the motor components of a bee's natural navigation strategy. Although control experiments indicated that olfactory cues were relatively unimportant in the context of our experiments, we took extra precautions to
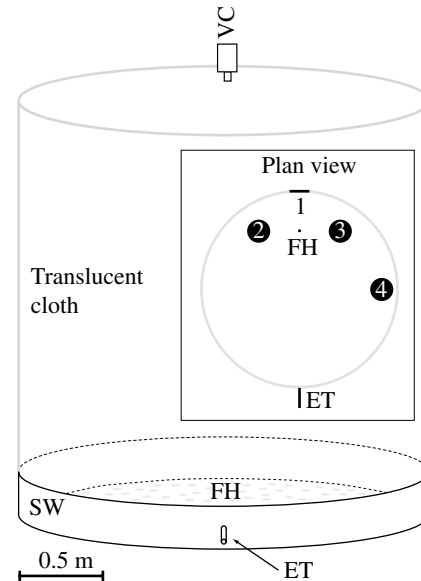


Fig. 1. Cylindrical flight chamber (height and diameter, 2.4 m). The circular floor is filmed from above using a video camera (VC). Bees entered the tent through the entry tube (ET), attached to a white painted side wall (SW). Bees flew to the 1.9 m-distant food hole (FH), which gave access to a feeder (not shown). Discs on the floor provided visual feedback. The inset shows a plan view of the set-up with the locations of the landmarks used in the experiments: (1) paper square (side length, 25 cm); (2, 3) cylinder (diameter and height, 25 cm) located 0.5 m to the side of the food hole; (4) same cylinder, located 1 m to the right of the center.

preclude their use in the present experiments. We covered the food hole with a transparent Plexiglas disk (diameter 10 cm), which we frequently washed with hot soapy water. The same was done with the feeding box and the feeder. Furthermore, we prevented airborne pheromones from entering the tent from the feeding box by expelling the air with a fan.

### Training and testing procedures

Bees were trained using the standard procedures described by von Frisch (1967). A small group of bees was recruited from a permanent feeding station installed on the balcony outside the laboratory and guided into the laboratory-based flight tent by stepwise displacement of a feeder that contained highly concentrated sucrose solution. Inside the tent, the artificial landmarks were present in the final training situation, and the food hole was marked with a conspicuous yellow paper ring. During this phase of training, the bees took off from the temporary feeder, where they were observed to perform short learning flights ('turn-back-and-look': Lehrer, 1991, 1993; Lehrer and Bianco, 2000), and were manually released from the tent. Next, the bees were trained to enter the feeder box through the food hole and to exit it through the Plexiglas tube. In the course of the subsequent training phase, the bees were marked individually with pigmented shellac solution, and the marker around the food hole was reduced in size until it became visible to the bees only in the close vicinity of the food hole.

We typically began our measurements of flight paths from the third day of training, when the bees showed a consistent flight behavior. In most cases, we filmed the bees' approach flights without altering the experimental conditions. In some tests, we covered the food hole with an inconspicuous disc attached to a thread. After a trained bee had searched for a few seconds, we drew the disc away to give the bee access to the food hole. Covering the food hole had no noticeable effect on the bees' approach flights, indicating that it was not used as a cue until the bees were close to it.

### Data acquisition and analysis

In a first series of experiments, we filmed the bees using a standard video camera (Panasonic F-10; $f$=10.5 mm, equipped with a 7× wide-angle converter) and recorded the data on video tape. We used custom software based on LabView (National Instruments, Austin, TX, USA) in order to extract the 2-D position of the bee measured at intervals of 1/50 s. We later performed our measurement using Trackit 2D (BIOBSERVE GmbH, Bonn, Germany) equipped with a Sony LSX-PT1 pan-tilt camera (Fry et al., 1998, 2000). Using this system, we were able to automatically acquire the position and the orientation of the bee's body axis at 50 Hz in 2-D coordinates. Parallax errors resulting from the bees' changes in flight altitude were insignificant due to the elevated position of the camera.

Analysis of the flight data was performed using custom programs developed in Matlab (R14, The Mathworks, Inc., Natick, MA, USA). During the approach flights, the bees typically flew at a velocity above 0.5 m s$^{-1}$, except for a brief period just after take-off and before landing or searching. At the elevated speeds observed, the bee's body axis was closely aligned with the flight direction, as confirmed by Trackit 2D measurements (Fig. 4). For reasons of consistency and simplicity, we therefore inferred the body axis direction from the measured flight direction. On the basis of these data, and further assuming that

the bee's head does not move significantly with respect to the body, the azimuthal retinal landmark positions can be determined. Portions of the flights during which the speed was below 0.5 m s$^{-1}$ were excluded from the analyses, because during these parts the bees' body axis might have deviated from the flight direction. For the largest part of the data, our recording method provides a robust and sufficiently precise way of measuring retinal landmark position within the context of the present experiments.

## Results
### *Visuo-motor learning with a single frontal landmark*
### *Effective goal-seeking behavior results from prolonged learning*

In an initial experiment, we explored how increasing experience with a landmark affects goal-directed flight behavior. For this, we trained a single bee with a square landmark located directly behind the food hole, as viewed from the entry (position 1 in inset of Fig. 1). This training took place in two phases. We first trained the bee to locate the food hole by moving a feeder stepwise toward the food hole between consecutive foraging trips (arrows in Fig. 2Ai). The bee reached each new feeder location with slow, tortuous flight paths (Fig. 2Ai). Once the bee was able to locate the
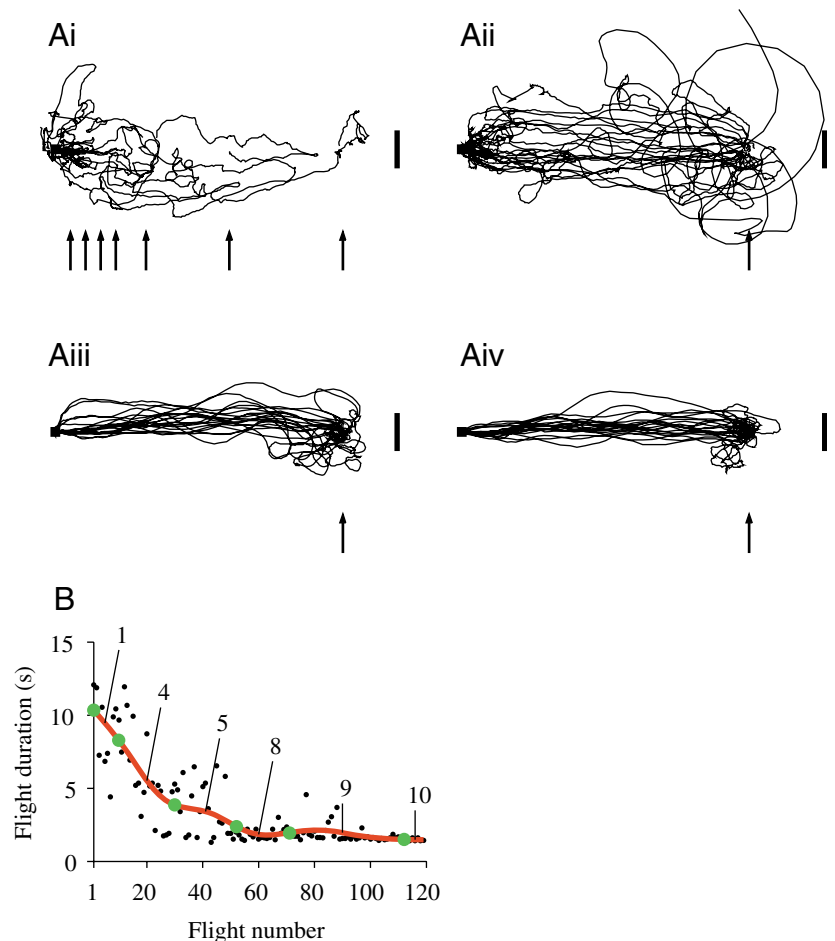


Fig. 2. Learning experiments. (A) Successive flights of a bee trained with a single landmark. (i) Flights to a feeder while it was moved toward the final training position. The feeder was moved on the connecting line between entry (black square) and center of landmark (thin line at far right). Arrows point to feeder positions. A single unsuccessful flight was excluded. (ii) Flights 1–20 performed after the bee learnt the final feeder position. (iii) Flights 51–70. (iv) Flights 101–120, after which the bee ceased to return. (B) Flight duration over successive flights after training. The duration of the approach to within 25 cm of the food hole of 119 successive flights is shown as dots, together with a smoothed spline function to emphasize the trend. Five unsuccessful approach flights were excluded from the analysis. Numbers with lines indicate days at which experiments were performed.

food hole and forage from a feeder located below the floor board, we took precautions to prevent the bee from using odor cues to locate the food hole (see Materials and methods). We then filmed 119 consecutive flights to the food hole until the bee ceased to return. With increasing experience, the bee performed increasingly smooth and direct flight paths (Fig. 2Aii–iv: flights 1–20, 51–70 and 101–120, respectively).

Flight duration continually decreased with increasing experience from about 10 s to a stable plateau at around 2 s from the 50th flight onward (red trace in Fig. 2B). The flight speeds of experienced bees reached up to ~1.2 m s$^{-1}$.

The large number of repetitions required before an effective approach behavior is learned indicates a possible role of operant conditioning. To be considered biologically relevant, a model for a landmark-based goal navigation should therefore be consistent with the observed gradual increase of performance over time.

## Use of a single landmark as a directional and positional reference

The previous results raise the question of whether the experienced bees indeed relied on the landmark cue in an explicit way, or if they instead substituted its use with a different navigational strategy, such as dead-reckoning. To explore this fundamental question, we trained a bee to fly to the food hole with the landmark in the same position as in the previous experiment. We then tested the bee with the landmark displaced 10 or 20° to either side of the food hole or left it in the training position as a control. We also temporarily covered the food hole with a white disk to induce searching at the presumptive goal location. Only just after the onset of flight did the bee tend to head in a consistent direction within the tent, whereas the remaining flight path and subsequent searching were governed entirely by the presence of the landmark cue (Fig. 3A,B). This finding is consistent with our observation that bees tested in the absence of a landmark never
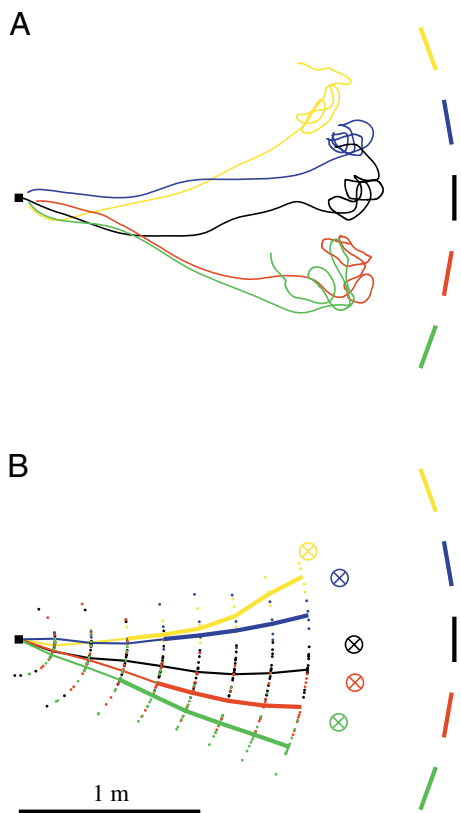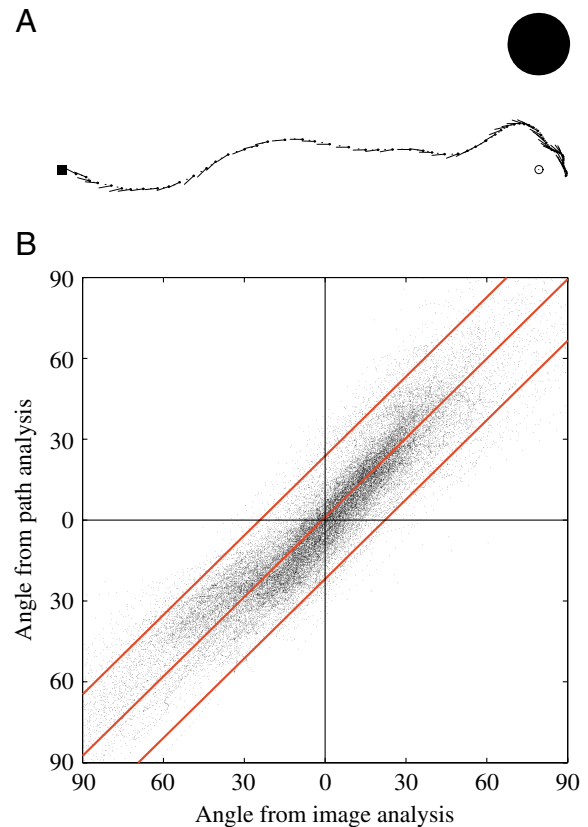


Fig. 3. Approach flights of a single bee trained with a black square landmark located behind the food hole (shown in black; position 1 in inset of Fig. 1) and tested with the landmark shifted to –20° (yellow), –10° (blue), 0° (black, control), 10° (red) and 20° (green) with respect to training position, as seen from the entry position (small black square). (A) Typical sample flights. (B) Median approach flights. Trajectories are shown with thick lines where the approach direction differs significantly from the control (Watson–Williams test for two samples, P=5%; Zar, 1999). Total number of flights analyzed was 47.



Fig. 4. Analysis of body axis orientation. (A) Sample flight of a bee, measured at intervals of 1/50 s (dots). Lines associated with larger dots indicate the body axis direction, as measured from image analysis. For clarity, body axis direction is only shown at intermittent positions. (B) Correlation between body axis direction as measured from image analysis and inferred from path analysis. The analysis is based on 437 flights (obtained from five bees, of which data are shown in Figs 6 and 8). Portions of flight at speeds below 0.5 m s$^{-1}$ were omitted. The coefficients of the regression (y=ax+b) are: a=0.982, b=0.96; r$^2$=0.993. Red lines indicate 95% confidence intervals.

approached the food hole (data not shown). The results indicate that the observed approach paths result from a visuo-motor control strategy that is intimately linked with the landmark cue, which provides the prerequisite for exploring the mechanisms underlying landmark-based goal navigation in the given task. It would be interesting to employ recently developed technology under field conditions (e.g. Riley et al., 2005) to explore if the same or additional mechanisms, such as dead reckoning, play a more prominent role at a much larger spatial scale.

### Estimation of azimuthal retinal landmark positions from flight paths

While foraging paths do provide important insights into an animal's navigation strategy, a mechanistic model of visuo-motor control requires knowledge of the relevant stimulation as it is experienced by the animal. In our experimental situation, the relevant visual cue is well described by the azimuthal retinal position of the landmark as perceived by the bee during its approach toward the goal. These retinal landmark positions can be calculated trigonometrically from the measured body position and direction, assuming that head movements are comparatively small. Using Trackit 2D, we obtained simultaneous measurements of the bee's position and the orientation of the bee's body axis (Fig. 4A) for a large sample of approach flights. For flight speeds exceeding $0.5\,\mathrm{m\,s^{-1}}$, the directly measured body axis directions are closely correlated with the flight directions (Fig. 4B). Individual measurements of body axis directions can be determined from the measured approach paths within a range of $\pm24°$ (95% confidence limits). In the context of the present stimulus situations and experimental paradigms, the calculation of time-averaged distributions is highly robust toward this error and allows for a sufficiently precise assessment of landmark positions within the bee's visual field.

### Beacon navigation provides a basis for motor learning

For a detailed analysis of the piloting mechanisms, we trained four bees in the same task, measured their approach paths to the food hole (Fig. 5Ai–Di) and calculated the retinal coordinates of the landmark as perceived by the bees during their approaches (Fig. 5Aii–Dii). The food hole was covered briefly so as to allow us to measure the location of the bee's
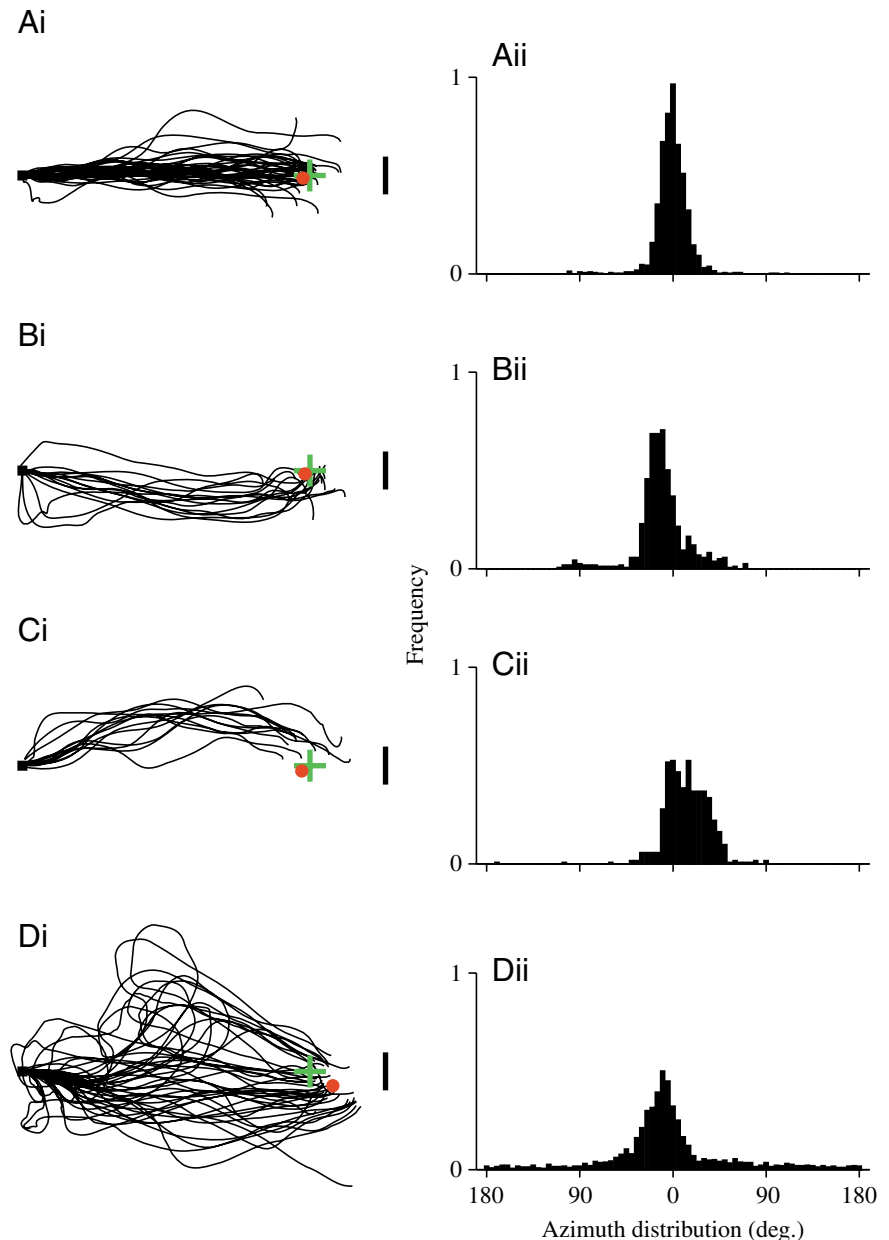


Fig. 5. Experiments with a single frontal landmark. (i) Approach flights of four bees (A–D; $n$=16, 13, 41, 40, respectively). The location of the food hole is indicated by a green cross, the median search position with a red dot. (ii) Landmark azimuth distributions (bin width: 5°). 0° indicates frontal; negative and positive angles represent the left and right visual field of the bee, respectively.

search paths (red dot in Fig. 5Ai–Di). Each bee approached the food hole in a typical, highly stereotyped flight pattern. In one case, a bee approached the landmark with exceedingly straight flight paths and searched precisely over the location of the covered food hole (Fig. 5Ai), while it kept the landmark continually within a narrow range of about $\pm30°$ of its frontal (0°) direction of view (Fig. 5Aii). Two other individuals exhibited flights that were slightly biased to one side, leading to a skewed distribution of the azimuthal positions of the landmarks (Fig. 5B,C). Finally, in 30 out of 41 cases (73%),

one bee approached the food hole in a slightly curved path but occasionally performed a small clockwise loop just after take-off or a much wider anti-clockwise loop at a slightly later stage of its flight (Fig. 5Di). In the latter case, the bee deviated far to the left and then approached the landmark from various directions along a straight path. The lopsided distribution of retinal positions resembles those of the two previous examples, except for a plateau extending over the entire visual field, due to the 360° loops (compare Fig. 5D with Fig. 5B,C). On the one hand, the bees showed a common tendency to fixate the landmark with the near-frontal retina, and hence treated it as a beacon. On the other hand, the stereotyped approach flights of individual bees indicate a probabilistic learning scheme, such as operant conditioning of visuo-motor patterns.

### Beacon navigation is combined with biased detours

Having established basic principles for the use of a single landmark located directly behind the goal and thus in front of the approaching bee, we performed similar analyses with bees trained with a black cylinder (height and diameter, 25 cm) placed to the side of the food hole. In one experiment, we trained a bee with the cylinder located at an angular distance of 15° from the food hole, as seen from the bee's starting position (position 2 in the inset of Fig. 1; Fig. 6Ai). The bee did not approach the food hole directly but instead headed in the direction of the cylinder. As it did so, it occasionally performed detours toward the side of the food hole. Near the cylinder, the bee consistently turned left and searched at the location of the covered food hole (Fig. 6Ai). The distribution of the azimuthal retinal positions of the landmark peaks around 0° and is skewed toward the right visual field. The results are well explained with a combination of beacon navigation and biased detours in the direction of the goal, similar to the previous results. Hypothetically, the bee could have relied on alternative strategies to solve the task. First, the bees could have fixated the landmark at a retinal position of 49.6° for a curved approach in the form of a logarithmic spiral. Second, the bees could have approached the hole more directly by relying on image matching of sequentially recalled snapshot memories (Judd and Collett, 1998; Collett et al., 1998). Neither alternative is supported by our data.

We then trained and tested three more bees with the cylinder positioned 40° to the side of the food hole (position 4 in Fig. 1; Fig. 6B–Di). In this situation, beacon navigation should be detrimental for rapid approach flights, and, indeed, the bees' flights were no longer headed toward the cylinder. Furthermore, the flight paths no longer showed the stereotyped structure observed in previous experiments. Nonetheless, the flights share in common that the cylinder's image was consistently placed within the right visual field. A simple visuo-motor strategy could account for this observation. The bees could have kept to the left side of the landmark by responding to right-to-left motion of the landmark with a strong corrective turning
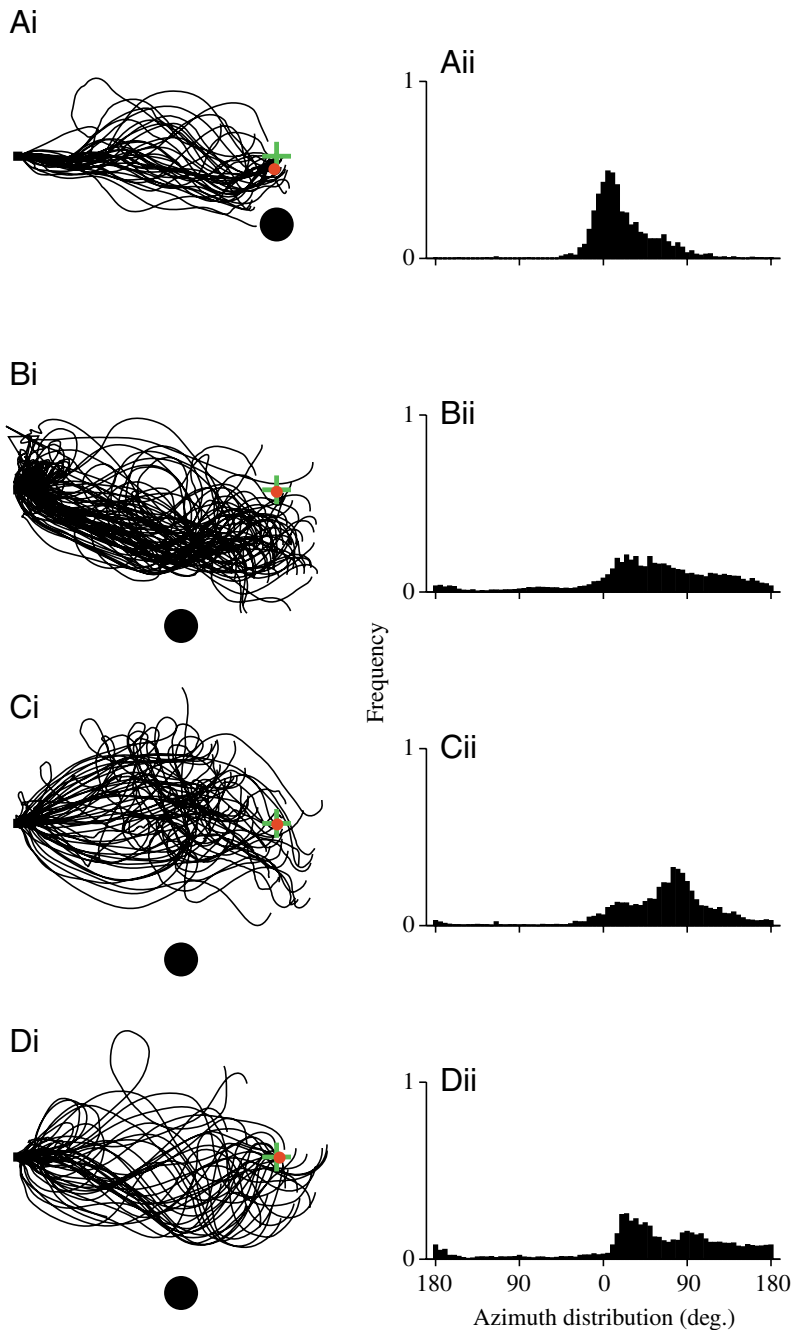


Fig. 6. Experiments with a single lateral landmark. (Ai) 40 successive approach flights of an individual bee with a cylinder positioned at an angular distance of 15° from the food hole. (Aii) Landmark azimuth distribution. (B–D) Same as in A, except that the cylinder was located at an angular distance of 40° during training and test. Also see legend of Fig. 5 for further details.

maneuver toward the left. They could still have been drawn toward the cylinder by responding to left-to-right motion of the cylinder with (a much weaker) corrective maneuver toward the right. This simple look-and-turn strategy would effectively restrict a bee's flight behavior to leftward turns and anti-clockwise loops, bringing the bee successively closer to its desired goal. This model is described in more detail in the Discussion (also see Fig. 9).

### Navigational strategies with two symmetrical landmarks

Under more natural conditions, a bee is likely to encounter two or more landmarks close to the goal. To test whether the bee then resorts to alternative mechanisms, such as image matching, we trained bees with two black cylinders placed on either side of the food hole (positions 2 and 3 in inset of Fig. 1; Fig. 7Ai,Bi).

Representative examples of approach flights from seven bees are shown in Fig. 7Ai. The bees tended to approach the food hole in a more or less direct path. Only occasionally did they approach one of the cylinders (e.g. the red trace in Fig. 7Ai). Fairly direct approaches toward the goal are documented in Fig. 7Bi (see azimuthal retinal positions of the right and left cylinders in red and black in Fig. 7Bii, respectively). This result would again be consistent with a simple visuo-motor strategy. The bees could have reacted to right-to-left motion of the landmarks with a strong leftward turning response, as in the previous experiment (see above), but with an equally strong rightward turning response to perceived left-to-right motion. As a result, the bees would be 'trapped' between the cylinders and would approach the food hole in a more or less direct approach, as was observed. However, the bees' behavior could also be explained by a successive matching-to-memory strategy. Therefore, we conducted additional tests in which one of the two cylinders was removed. According to the above-mentioned visuo-motor strategy, the bees were now expected to approach the remaining cylinder by fixating it with their frontal retina. By contrast, an image-matching strategy would place the cylinder in a lateral retinal position, so that the bees should fly in a wide arc around the remaining cylinder. The bees indeed approached the remaining cylinder (Fig. 7Ci,Di) and hence behaved as predicted from our previous results.

### Navigational strategies with two differently colored landmarks

Taking the stance of devil's advocate, the relevance of the previous results with two identical landmarks might appear questionable, given that under more natural conditions bees
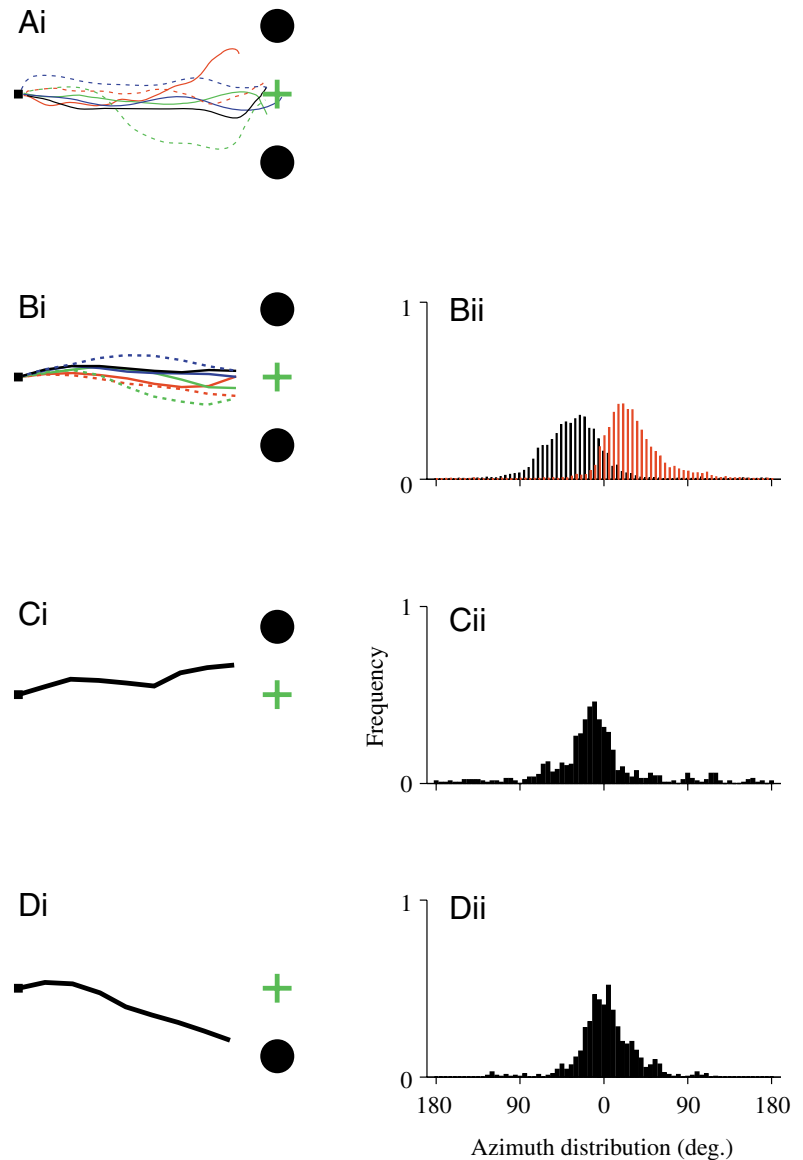


Fig. 7. Experiments with two black landmarks. (A) Examples of training flights. A typical flight of each of seven trained bees is shown. (B) Data obtained under training conditions, based on 116 flights performed by seven bees. (Bi) Median approach flight of each bee. (Bii) Distribution of landmark azimuths of the left and right training landmark (as seen from the approaching bee's perspective), shown in black and red, respectively. (C) Experiment with right landmark removed. (Ci) Median approach trajectories ($N$=7, $n$=13) tested with the right landmark removed. (Cii) Azimuth of the left landmark. (D) Experiment as in C, but with the left landmark removed ($N$=7, $n$=25). The location of the food hole is indicated by a green cross.

might use additional cues, such as shape, color or texture, to distinguish between landmarks. We therefore trained bees under the same conditions as in the previous experiment, except that the right and left cylinder were wrapped in green and blue paper, respectively (Fig. 8Ai). Approach flights of two bees tested in the training configuration revealed that the bees used the green cylinder as a beacon, apparently ignoring the blue cylinder (red and black traces in Fig. 8Ai,ii). The
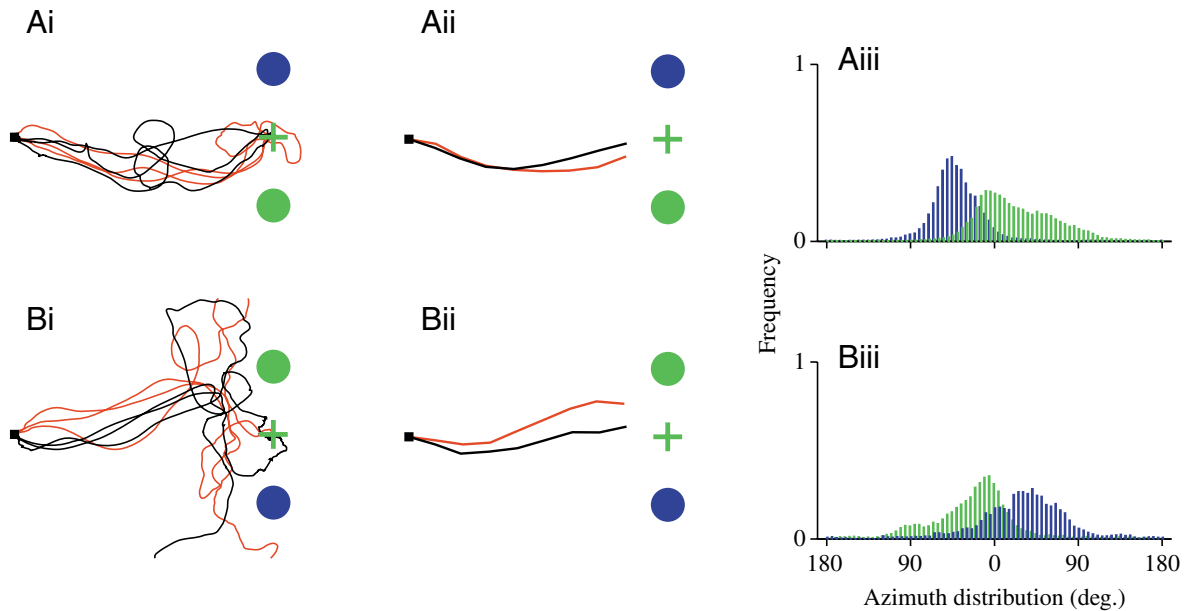
Fig. 8. Experiments with two differently colored landmarks. (Ai) Sample flights from two bees under standard conditions. (Aii) Median approach flights of the two bees (*n*=135, 175). (Aiii) Azimuth of the green and blue cylinders, shown in their respective colors. (B) Same experiments as in A but with landmarks interchanged (*n*=27, 29).

retinal azimuth of the green landmark peaks around 0° and is strongly skewed toward the right visual field, strikingly similar to the data obtained from a single, lateral cylinder (compare green distribution in Fig. 8Aiii with Fig. 6Aii). This result is again in conflict with image matching, which predicts a straight approach path (Möller, 2001), irrespective of whether or not color information was used. Given the above evidence, we predicted that if the colored landmarks were exchanged during tests, the bees should approach the green cylinder in the new position and hence deviate far away from their habitual flight path, not unlike in earlier experiments with a displaced single landmark (Fig. 3). This was indeed the case. The bees flew left toward the green landmark and even performed their habitual left turns, after which they turned back and successfully located the food hole (Fig. 8Bi). The median approach flights reveal that after heading in the habitual direction for a short distance (similar to the flights shown in Fig. 3), the bees steered toward the green landmark in its new position (Fig. 8Bii). During the approach, the green landmark was kept in a near frontal position, whereas the blue cylinder now appeared far out in the right visual field (Fig. 8Biii). Interestingly, the distribution of the green cylinder was skewed toward the right visual field under standard conditions and toward the left visual field when the cylinders were interchanged (Fig. 8Biii). Possibly, the blue landmark was not completely ignored, but the turning responses weighted far lower than in the case of the green cylinder. How the bees managed to locate the food hole after having been brought off-course must remain speculative. A possible explanation is dead-reckoning, assuming that a path integrator was registering the bees' deviation to a novel location (Chittka et al., 1995). Alternatively, the bees could have applied some form of

landmark guidance that did not depend on the landmarks' spectral properties.

In conclusion, the results obtained with two differently colored landmarks provide further evidence in favor of a simple visuo-motor control loop underlying approach flights toward a goal. The precise visual processing mechanisms underlying the observed behavior remain unknown, but future experiments based on our experiments could further insights into the underlying neural processing mechanisms. For example, a compelling experiment would be to repeat our experiments with landmarks that do not provide luminance contrast to the (color-blind) motion processing pathways to explore their involvement in the given task.

## Discussion

We explored navigational strategies employed by honey bees during their approach toward a goal site marked by one or by a pair of landmarks. Applying a conceptual bottom-up approach in a set of experiments, we systematically varied the position and number of landmarks and measured the approach flights performed by bees under training or experimentally modified conditions. The results are consistent with a set of rules describing visuo-motor control loops. This set of rules is able to explain the gradual transition between searching in the absence of a suitable landmark and highly stereotyped approach flights in the presence of a landmark close to the goal. Our model is also consistent with the finding that rapid approach flights require prolonged operant learning. The flexible combination of basic navigational strategies to navigate within an unpredictable environment is likely to reflect a general principle in insect navigation. Our findings

could serve bio-mimetic design principles for robust navigation in autonomous robots and aircraft.

### Look-and-turn: goal navigation from visuo-motor control loops

Our results are well explained with a simple rule-based model based on visuo-motor control loops. In the absence of landmarks, the bees performed unstructured search flights covering a broad area (data not shown). In presence of a landmark, the bees tended to fixate it with their frontal retina, and hence treated it as a beacon. Beacon navigation appears to be a strong, innate disposition of bees, which have been observed to approach novel landmarks spontaneously (von Frisch, 1967; Frank Bartlett, personal communication). Relying on a beacon near a food site allows newly recruited bees to approach it with a consistent flight pattern, which is reinforced during successive foraging trips (Fig. 2). Even under ideal conditions, reinforcement learning reaches a stable plateau only after ~50 flights. As a result, experienced bees are able to approach the goal fast, reliably and along consistent routes. This behavior is likely to support foraging efficiency and to avoid the risk of predation.

If a landmark is present at or behind the goal, the bee can fixate it with its frontal retina for a direct approach of the goal. Frontal fixation implies compensatory turning maneuvers, whenever the landmark moves toward the lateral visual field (Fig. 9A). Biased turning could be achieved likewise, but with an asymmetrical weighting of the compensatory maneuvers. For example, in the experiments with a single cylinder placed to the right side of the food hole (Fig. 6), the bees' turning behavior was strongly biased. Such behavior could be generated from a strong compensatory reaction to a leftward moving landmark, combined with a much weaker compensatory reaction to a rightward moving landmark (Fig. 9B). As a result, the bee would tend to fixate the landmark frontally but would also make occasional left turns. The final turning toward the food hole after the bees have arrived close to the cylinder is likely to be part of a collision avoidance response to a looming stimulus, similar to the behavior recorded in flies (Tammero and Dickinson, 2002). The same scheme holds for the experiments with two black cylinders (Fig. 7). In the standard configuration, symmetric compensatory reactions would cause the bees to approach the food hole directly. When one cylinder was removed experimentally, the bees fixated the remaining cylinder with their frontal retina (Fig. 9C). Finally, when trained with two differently colored cylinders, the bees performed asymmetrical compensatory maneuvers for one of them (green arrows in Fig. 9D) and did not react noticeably to the other cylinder (blue arrows in Fig. 9D). Consequently, the bees approached one cylinder directly, irrespective of its relative position to the
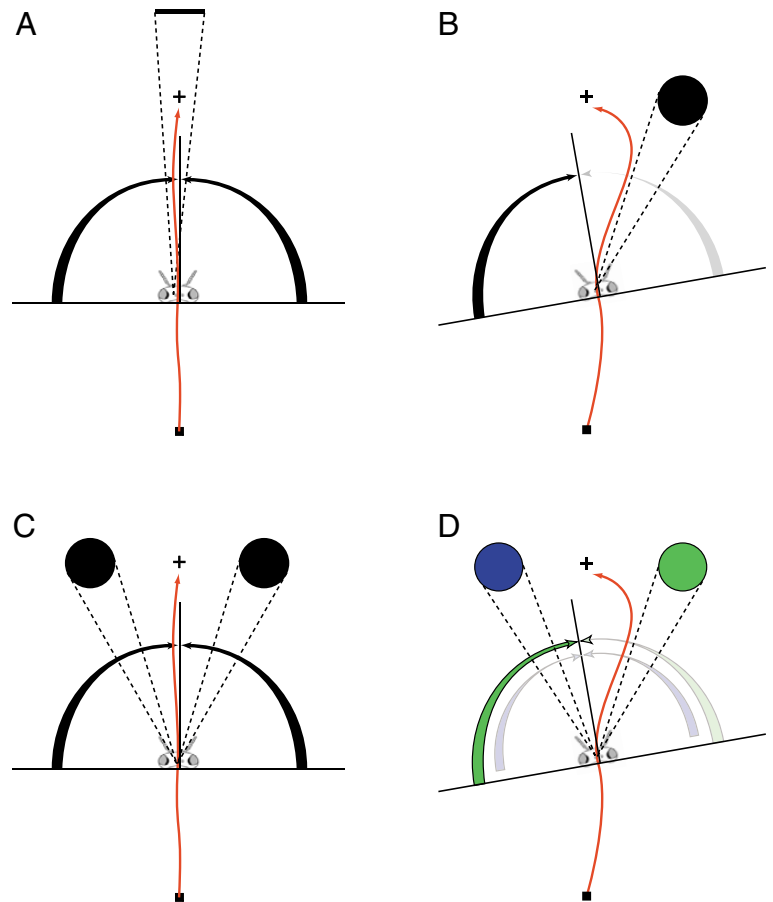


Fig. 9. Visuo-motor guidance model. (A) Frontal landmark, symmetric response. (B) Lateral landmark, biased response. (C) Two black cylinders, symmetric response. (D) Cylinders of different color, biased response to green cylinder. Red arrows indicate hypothetical approach paths from the entry (black square) to the food hole (cross). Curved arrows indicate the strength with which landmarks are 'pushed out' of each hemisphere by compensatory turning reactions. For example, in D, the thick green arrow indicates a strong (anti-clockwise) turning response for right-to-left movement of the green cylinder. For details, see text.

other cylinder. Our experiments therefore suggest that the bees form visuo-motor associations only with respect to one out of several distinguishable landmarks. It remains to be tested whether our model applies likewise in a different set of circumstances, such as when there is a richer or more natural visual surround.

### Relevance for natural foraging behavior

For the benefit of experimental control, we performed our experiments under extremely restrictive sensory conditions. Hence, the question arises as to whether our results are likely to represent naturally occurring visuo-motor responses under more complex environmental conditions. Honey bees have indeed been reported to use prominent single landmarks in the field as beacons (von Frisch, 1967; Collett and Baron, 1994; Chittka et al., 1995). Compelling similarities exist between our data and previous analyses performed

in ants. Wood ants traveling between a learned food site and the nest use prominent landmarks as beacons for a direct approach (Nicholson et al., 1999; Collett and Collett, 2002). Biased detours (Collett et al., 1992) and idiosyncratic foraging paths (Wehner, 2003; Kohler and Wehner, 2005) are described for desert ants. In summary, the flexible combination of basic navigational strategies could represent a widespread feature at least in central place foraging insects.

### *Putative role of image matching*

Goal-approaching honey bees appear not to apply image matching in the form originally proposed by Cartwright and Collett (1983). The strongest evidence against the use of a 'snapshot' memory comes from the experiments in which we trained bees with a pair of black (Fig. 7) or colored (Fig. 8) cylinders and tested them with one cylinder removed. The bees fixated the remaining landmark with the frontal retina (Fig. 7C,D) and not at the positions predicted from a snapshot strategy. Furthermore, an image-matching strategy would predict a direct goal approach in the case of the symmetric array of colored cylinders (fig. 3a in Möller, 2001), but the bees instead relied on a single cylinder for an indirect approach of the goal (Fig. 8D).

It is interesting to ask if the behavior we observed in our experiments is consistent with recent modeling approaches. Unfortunately, most simulations were performed with landmark configurations consisting of at least three landmarks (Franz et al., 1998; Nicholson et al., 1999; Möller, 2000; Lambrinos et al., 2000). One study did, however, apply a variant form of the 'snapshot' model ('partial image matching model'; fig. 7a in Möller, 2001) by using a symmetrically paired landmark configuration, comparable to the one used in the present account (Fig. 7). As this model at any particular time matches a single landmark, the resulting path toward the goal is curved rather than direct, and hence is reminiscent of beacon navigation. However, in the presence of two black cylinders, the bees' approach paths were generally oriented toward the food hole rather than toward one of the landmarks.

Although snapshot matching can provide a viable navigation strategy, as demonstrated in numerous numeric (e.g. Cartwright and Collett, 1983; Nicholson et al., 1999; Möller, 2001) and robotic simulations (e.g. Franz et al., 1998; Möller, 2000; Lambrinos et al., 2000), its feasibility for free-flight control remains to be demonstrated. In particular, it is questionable whether an image-matching mechanism could meet the exceedingly high demands of visuo-motor flight control in terms of robustness and speed (e.g. 30 ms in mate-chasing houseflies; Land and Collett, 1974). Whereas snapshot memories are evidently important in a large number of visual tasks (reviewed by Menzel et al., 1996; Collett and Collett, 2002, 2004; Wehner, 2003), the flight paths of honey bees approaching their goal seem to be based on simple visuo-motor control strategies that provide flexibility, robustness and speed.

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