

Static and dynamic snapshots for goal localization in insects?

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Bees, wasps and ants navigate successfully between feeding sites and their nest, despite the small size of their brains which contain less than a million neurons. A long history of studies examining the role of visual memories in homing behavior show that insects can localize a goal by finding a close match between a memorized view at the goal location and their current view ("snapshot matching"). However, the concept of static snapshot matching might not explain all aspects of homing behavior, as honeybees are able to use landmarks that are statically camouflaged. In this case the landmarks are only detectable by relative motion cues between the landmark and the background, which the bees generate when they perform characteristic flight maneuvers close to the landmarks. The bees' navigation performance can be explained by a matching scheme based on optic flow amplitudes ("dynamic snapshot matching"). In this article, I will discuss the concept of dynamic snapshot matching in the light of previous literature.

Goal-Seeking in Insects

Insects, with their miniature brains, have evolved a simple strategy to find both their nests and profitable food sources. They approach them by "snapshot matching", i.e., finding a close match between the current view and a memorized view of the goal location (reviewed in ref. 1 and 2). How is the relevant information encoded in a snapshot? There are currently two main views: (1) Insects may extract the relevant visual features, such as the contours of prominent objects which define the goal location.³ In addition to retinal size and the position of these objects, honeybees also use color and distance cues as features to localize a food source.³⁻⁸ Currently, it is still unclear how many and what features are stored in the retinotopic snapshot. (2) A fairly new idea, which does not involve the extraction of certain features and object identification, is the "global image matching" method.⁹ This means that the insects memorize a raw panoramic image at the goal location. The image implicitly contains all important static visual features of the goal location. The insects then get

back to their goal location by moving in a way that increases the similarity of the current view with the memorized image. Recent model implementations on robotic platforms show that this method works.⁹⁻¹⁴ Even for view-based homing in natural environments, Zeil and colleagues showed that panoramic image similarities can be used.^{9,15} More recently, the behavior of ants and crickets in goal finding tasks could be explained by "global image matching".^{16,17}

Dynamic Snapshots

Within the insect navigation literature, snapshot matching is presently often pictured as a static process, which involves three steps: stopping, comparing the current view with the memorized view at the goal, and then moving to increase the similarity between the views. However, our study shows that static snapshot matching might not explain all aspects of homing behavior as honeybees are able to use landmarks that are statically camouflaged.¹⁸ Honeybees, trained to locate an inconspicuous feeder surrounded by three high contrast landmarks (Fig. 1A), were tested either with one landmark removed or with three landmarks with the same contrast and texture as the background (Fig. 1B). Removing a landmark affected the search performance of the honeybees. Surprisingly, the navigational performance was not impaired when the landmarks were camouflaged.¹⁸ In this case the landmarks could not be detected by their contrast and texture, and if the bees would had memorized a static image of the scene they would not have been able to find the goal. These landmarks only become visible when the bee moves in a characteristic way (see Fig. 1C inset).

We found that honeybees perform scanning movements in the vicinity of the landmarks.¹⁸ Through these sideways maneuvers in front of the landmarks, they become visible by relative motion. Furthermore, they employ a flight style that facilitates depth perception from motion parallax. The bees' trajectories consist of straight flight segments combined with rapid turns.^{18,19} Between turns, gaze stabilization leads to a behavioral elimination of rotational components from the optical flow pattern,^{19,20} making it easier to use the remaining translational optic flow for homing, as it contains range information. This is because images of close objects move faster across the retina than those of more distant objects. In our experiments with landmarks that had the same texture as the background this helped detection

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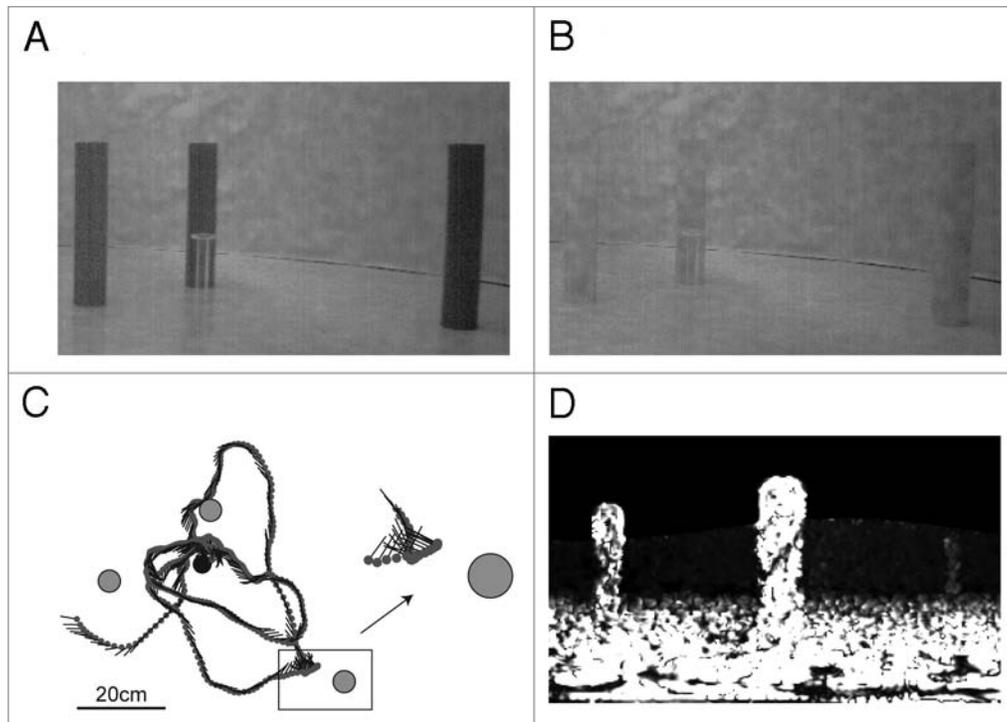


Figure 1. In our study honeybees were trained to visit a perspex feeder surrounded by three landmarks (diameter of 5 cm, height of 25 cm) placed at different distances (10, 20, 40 cm) from the feeder in a circular flight arena (diameter of 195 cm; height of 50 cm).¹⁸ (A) During training the landmarks were covered with a homogeneous texture providing luminance contrast to the background. (B) After being trained with three homogenous textured landmarks, honeybees were tested individually with landmarks that had the same random dot texture as the background of the arena. (C) The top view shows an example flight trajectory of a honeybee. Approach flights to the feeder (black circle) surrounded by three landmarks (grey circles) were recorded with three high-speed cameras at 125 fps. The position of the bee is indicated by grey circles at each 32 ms interval; straight lines indicate the orientation of the long axis of the bee. The inset shows a sideways-directed flight manoeuvre of a honeybee close to the landmark (two times magnified; Reproduced from ref. 18). (D) shows an optic flow snapshot calculated at the feeder position. White indicates high optic flow amplitudes. The landmarks “pop out” of the background although they have the same texture as the background (B). From a 3D model of the arena, panoramic images were rendered at 1°/pixel resolution. Optic flow fields were generated by simulated translations of 2 mm in the flight arena, obtaining four images at $(x \pm 1 \text{ mm}, y)$, $(x, y \pm 1 \text{ mm})$. The optic flow for these movements was computed using a modified version of the Lucas-Kanade algorithm. To generate flow amplitudes independent of the direction of motion, flow fields for the two steps (in x and y) were squared and summed.¹⁸ The optic flow snapshot implicitly contains information about the depth structure of the scene, as closer objects move faster and create a higher optic flow amplitude. This can be seen by comparing the near landmark in the centre of the picture to the middle far (left) and the far (right) landmark.

and possibly also estimation of the distance to landmarks as they ‘pop out’ when the animals move in front of them. In other behavioral tasks, motion parallax is used as a cue, e.g., for shape discrimination or distance estimation.^{21,22}

But what does a snapshot look like, and what information is stored? By means of model simulations, we made a first attempt to answer this question. Global image matching cannot explain the search behavior with statically camouflaged landmarks. Taking the honeybees movement into account, we simulated the motion pattern on the bees’ eyes during pure translational movements at the goal location (Fig. 1D). By memorizing this optic flow snapshot and comparing it with the optic flow fields at other locations in the flight arena, the honeybees could navigate even with camouflaged landmarks.¹⁸ Our study emphasises that snapshot matching should be considered a dynamic rather than a purely static process. Taking into account how the insects interact with their environment helped us to identify possible mechanisms of navigation.

Contents and Extent of Retinotopic Snapshots

Neither a static nor a dynamic snapshot can explain all the results obtained from navigation experiments. When trained with different colored landmarks, honeybees use also color cues.⁴ Perhaps a snapshot consists of landmark boundaries, which can be detected by luminance, color or motion contrast. You might also think of a combination of optic flow and texture information in an extended snapshot scheme.

The selection and weighting of static or dynamic information might vary among different species and depend on the kind of locomotion the insect performs. Walking insects (e.g., ants) can more easily stay motionless relative to their surroundings (an advantage for static image matching) whereas flying insects (e.g., bees) can fly sideways (an advantage if using motion parallax information). There might also exist species-dependent differences in whether the insect memorizes a snapshot of the full field of view and whether all regions of the visual field are

weighted equally. Ants store a snapshot while fixating a landmark with their frontal field of view, which extends at least 120° into the periphery.²³ When trained with several landmarks surrounding the nest or food source, they focus on their frontal field of view and employ a sequential matching strategy of single landmarks.^{24,25} If the landmark array is enlarged without changing the size of the landmarks, the ants do not search where the retinal position of the landmarks fits but where the retinal size of a single landmark fits.²⁵⁻²⁷ In contrast, bees tested under similar conditions seem to match the retinal positions of all landmarks, if there is a conflict with the retinal size of the landmarks.³ But although the snapshot is centred on one landmark in ants, it was concluded that they identify landmarks with the aid of the background pattern, indicating that the panorama is somehow included in their representation and might help to enhance the reliability of the snapshot recall.²⁷ An experiment, in which different species are tested with the same behavioral task, might provide insights into the relevance and weighting of different navigational mechanisms and the contents and size of snapshot memories.

A Single Snapshot? Where and When?

Despite a series of studies on snapshot matching in insects, there remain some crucial questions to be answered. Today, it is still unclear how many snapshots the insects memorize and where they take these snapshots. It might be that there is no universal answer to these questions. How snapshots are used for navigation probably depends on the species, and even on the task or the learning state of the insect. Nevertheless, differences can teach us something about the underlying navigational mechanisms and their constraints. Although agents can navigate successfully to a goal location with the aid of one snapshot close to the goal, e.g.¹² there is evidence that ants, for example, memorize several snapshots and use them for returning to the goal location.^{28,29} The current idea is that snapshots are taken during learning walks in ants and during learning flights in bees and wasps.³⁰⁻³³ These learning phases have a common feature: when leaving the nest or a newly discovered food source, the insects turn back and perform distinct maneuvers. The learning walks of ants include stopping phases, in which they fixate nearby landmarks (wood ants²⁴) or the goal itself (Namibian desert ants³³) and approach the target for a short time. The acquisition of memories is thought to take place during these clear-cut events of the learning walks. Wasps and honeybees are thought to memorize snapshots while fixating the goal at the end of arcs (inspection points), when they turn back and look at the feeder during their learning flights.³⁰ Assuming that honeybees

would indeed memorize an optic flow snapshot, it could take place during the translatory phases of flight when they face their goal.¹⁹

These straight segments of the learning flights provide them with spatial information, e.g., the distance to the landmarks, which fits to the long standing interpretation that learning flights help the insects to identify close landmarks and learn their spatial relationship.^{31,32,34-36} If insects memorize snapshots during these learning maneuvers, they should follow a somewhat similar trajectory in their next return to the goal. But instead the similarity of viewing directions and flight paths between learning and return flights seems to differ between species and is less striking in honeybees.^{30,32,37,38} On the other hand, the insects might replicate some of the relevant movement sequences without following the same paths. The motion dynamics of learning and return flights are similar in bees¹⁹ and wasps (Boeddeker personal communication). The functional connection between learning walks or flights and returns still has to be understood. Analysing the detailed movements of the insects during navigation should give further insights. In a recent study, Lent and colleagues analyzed the movements of ants during the return to a goal in detail.³⁹ These wood ants perform saccadic-like body turns to match the learned visual features. The turns depend on the difference between the desired and current retinal positions of a visual feature, and they are also used to correct errors after the ants have drifted off the route. Although this provides us with an idea how snapshots are used to guide the ants' path it is yet unclear, how this connects to their learning walks. Do insects memorize all possible snapshots during their learning maneuvers? How are these snapshots used to structure the return? Learning maneuvers only occur in the early phase of foraging and even the return paths change over time.^{6,40} It might well be that several snapshots are somehow integrated into one spatial representation of the goal environment over time, allowing the insect to return reliably but at the same time to navigate flexibly to the goal location. I suggest tackling these questions using comparative studies and by analysing the insects' behavior in detail (e.g. ref. 38, 39, 41, reviewed in ref. 42). Identifying differences in the navigational strategies depending on the species, the task, the complexity of the visual environment, and the learning state of the insect, will help us understand the relevance and the constraints of the underlying navigational mechanisms.

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