Probing navigation strategies of honeybees – landmark experiments and simulations

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Abstract. In this study we probed the content of the spatial memory of honeybees in two landmark manipulation experiments accompanied by computer modelling. While the results of the first experiments are in line with an image-like representation of places, the findings of the second experiment suggest that bees also memorize the depth structure of a scene, most probably inferred from optic flow. This is supported by the fact that bees actively control their visual input.

1 Introduction

Honeybees are able to navigate in a dynamic and complex environment up to several kilometers away from their hive. To effectively collect food for their colony, they have to learn the spatial locations and return repeatedly to these places. It has been shown that insects use both odometry and landmark cues for navigation, e.g. [1–3]. In particular for flying insects, vision provides a very rich source of information. However, other modalities like scent and proprioception play an important role as well. Also, the magnetic field of the earth may be sensed by honeybees [4]. What cues are exactly extracted and memorized from their sensory input and how different cues are combined is far from clear.

In the study described in this paper, we probed the content of the spatial memory of honeybees in two landmark manipulation experiments accompanied by computer modelling. We compared the experimental results with predictions from the "snapshot model" by Cartwright and Collett [5], which is, probably due to its inherent simplicity, one of the most influential models of insect homing, i.e. the return to places visited before. This model, that is supported by experimental findings, suggests that honeybees memorize a "snapshot", a retino-topic, image-like representation of the goal-location. By comparing the currently perceived visual input with the snapshot, they then can find their way back later. Several robotic implementations have proven that a snapshot-based homing is indeed feasible, at least in static scenes, e.g. [6–10]. In [11] it was shown that image differences increase smoothly with distance from a reference position in natural environments and thus could be used by insects for homing.

2 Experimental setup and computer simulation

An indoor setup is used for the experiments that allows to control the cues available for the insects more easily.[1] The flight arena, see Fig. 1 a, has an diameter of 195 cm and consists of a cylindrical wall of 50 cm height and a flat floor, both covered with a low-pass filtered random texture. Three cylindrical landmarks were placed at 10 cm, 20 cm and 40 cm distance to the feeder with an angle of 120° between them. The feeder was a perspex cylinder (height 10 cm, diameter 1 cm) covered by a thin circular perspex plate (diameter 4 cm) on which drops of sugar solution were provided.

During testing, bees were marked individually with small dots of paint and approach flights were recorded at 125 fps with a maximum recording time of about 30 s. Additionally, flight durations were measured with a stop watch. Semi-automatic tracking of bees in the recorded stereo-video-sequences allows to estimate the 3D-flight path and the horizontal orientation (yaw) of the body. In order to minimize the influence of odometry, the landmark array was shifted during training but was always at a specified position during test flights (since the cameras did not cover the full arena). The arena and the feeder was cleaned regularly to avoid scent cues possibly deposited by honeybees. We analyzed flight duration and the spatial search distribution of bees during flights.

From a 3D computer model of the flight arena, images were rendered with the open source graphics engine "OGRE"[2]. Since bees, like most flying insects, have a very wide field of view, we used – similar to the approach described in [14] – six virtual cameras covering the whole view sphere, see Fig. 1 b. Mainly in order to make the images better recognizable for humans, the six camera images were re-mapped to panoramic images $I(u, v)$ of 1°/pixel angular resolution in azimuth and elevation (Fig. 1 c,d).[3] Note that this mapping simplifies azimuthal rotation of images and allows to use standard image processing tools, but causes significant distortions of the view sphere for very low and high elevations, i.e. for $v \approx 0$ and $v \approx 179$. In future work we will incorporate the directions of sight and the acceptance angles of individual ommatidia in our simulations.

3 Implementation and test of the snapshot model

The main question that we addressed was whether the predictions of the snapshot model were in line with the search behavior of bees. Assuming that the bees had stored a snapshot at the feeder position during their recent approach

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[1] Our experimental setup is clearly different from the environments where bees usually forage in. While this is necessary for disentangling the different navigation mechanisms, we believe that it is also important to observe animals in their natural habitat and analyze the sensory input they encounter under these conditions [12, 13].

[2] `www.ogre3d.org`

[3] This is still higher than the visual resolution of the bee's compound eye which has been behaviorally estimated to be in the range of $2° - 4°$ [15].
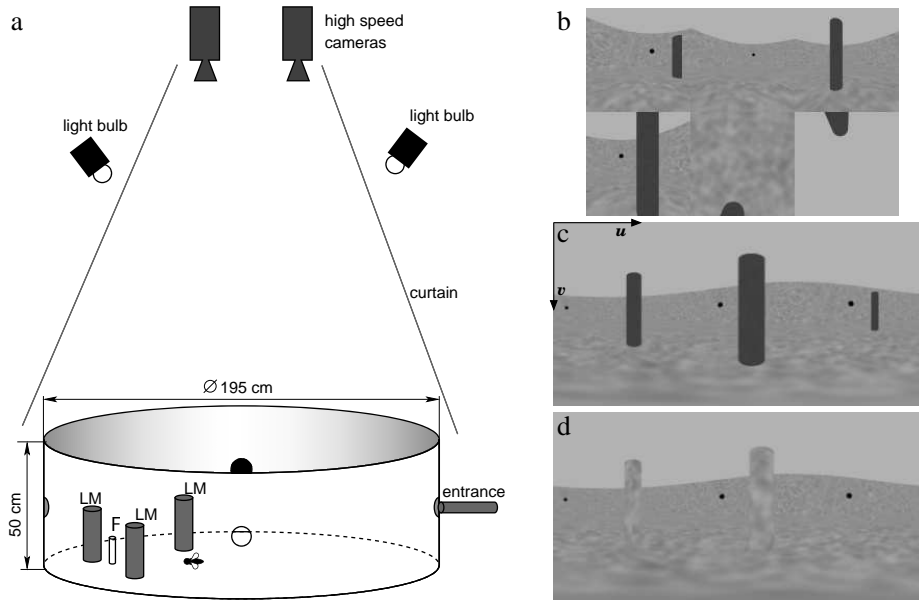
Fig. 1. a) The experimental setup: Bees enter the arena through a tube, while being filmed by three high-speed cameras; two of them are mounted on the ceiling, each covering a region of approximately $1\,\mathrm{m}^2$ on the arena floor, the third camera (not shown) with a wide-angle lens is mounted horizontally viewing the arena through a circular hole in the wall. The perspex feeder (F) is made of perspex and surrounded by three landmarks (LM) of $5\,\mathrm{cm}$ diameter and $25\,\mathrm{cm}$ height. b) Simulating the visual input: The scene is rendered using six perspective cameras with $95°$ field of view and their optic axis oriented along the normals of a cube. c) Equi-rectangularly re-mapped "panoramic image" $I(u,v)$ of the scene with uniform landmarks (view point at the feeder), resolution is $1°$/pixel, i.e. $u = 0, 1, \ldots, 359$, $v = 0, 1, \ldots, 179$. d) Scene with randomly textured landmarks.

or departure they should look for the feeder primarily at positions where the similarity between currently perceived visual input and the snapshot is high.

We started our analysis by calculating pixel-wise image distances between the panoramic image at the feeder $I^{\mathrm{h}}(u,v)$ and all images $I^{xy}(u,v)$ in the arena that lie on a grid with element size of $5\,\mathrm{cm}$,

$$D(x,y) = \min_{s=[0,360]} \sum_{u,v} w(v)(I^{xy}(\mathrm{mod}(u+s,360),v) - I^{\mathrm{h}}(u,v))^2 \ , \qquad (1)$$

$$w(v) = \sin(\pi(v+0.5)/180) \ . \qquad\qquad\qquad (2)$$

The 'min'-operation in Eq. (1) computes the best match over all orientations (in pixel steps) between the image at position x, y and the snapshot image, assuming that bees do not prefer a certain yaw angle[4]. The "sum-of-squared-

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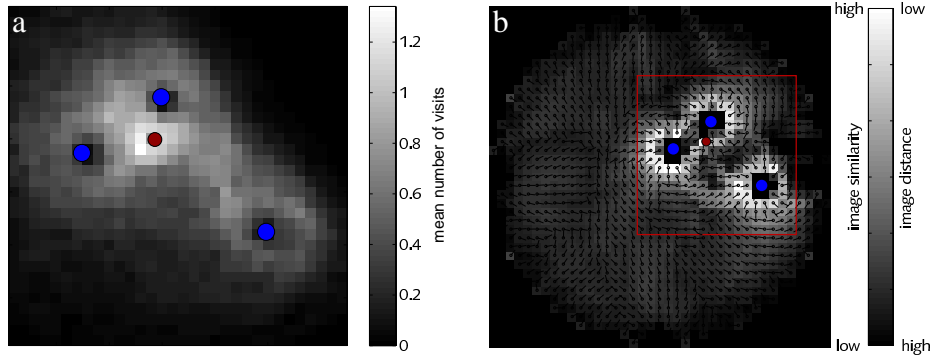[4] Pitch and roll angle are assumed to be held constant.

Fig. 2. Search distribution of bees (a) and calculated image similarity map (b). The three landmarks are marked by blue dots, the red dot shows the position of the feeder. The small oriented lines in the image similarity map illustrate the optimal angular shift for each position (parameter s in Eq. (1)). The red box highlights the region in the arena for which search densities were calculated. This region was monitored by one of the cameras mounted above the arena. honeybees, on average, did not search extensively in other parts of the arena. The search distribution shown in (a) was calculated from 173 flights.

differences" distance function is chosen quite arbitrarily and could be replaced by similar measures, e.g. by pixel-wise cross-correlation. $w(v)$, defined in Eq. (2), is a weighting factor that compensates for the distortions of the view sphere due to the equi-rectangular mapping. All images were rendered at a constant height of $z = 11\,\mathrm{cm}$ above the arena floor.

4 Results

In the following sections, spatial search distributions and 2D image similarity maps $D(x, y)$, Eq. (1), will be compared qualitatively. For a quantitative comparison, a bee-like agent has to be simulated for which one would have to specify, for example, how image similarity controls flight behavior, whether and by what means the agent can escape from local minima, etc. This will be addressed in future work.

4.1 Experiment 1: Changing landmark configuration

In the first experiment, bees were trained with three uniformly textured landmarks (see Fig. 1 c for a rendered panoramic image). Bees were then tested individually in twelve search flights according to the following procedure: After three test flights with three landmarks, a randomly chosen landmark was removed before the next test. This sequence (of four flights) was repeated two times but with different landmarks removed.

The search distribution of bees and the corresponding image similarity map for the configuration with three landmarks is shown in Fig. 2. As expected the search distribution and the similarity map have a peak close to the feeder position, i.e. the global maximum of search distribution and image similarities (corresponding to the global minimum of image distances). The fact that they also both show distinct circular patterns around the landmarks may lead to the conclusion that an agent guided by image similarity could indeed exhibit the search behavior of honeybees, in agreement with the snapshot model. This is corroborated by the qualitative correspondence of search distribution and image similarity maps for configurations with landmarks removed. Removal of different landmarks restricts high search densities as well as high image similarities to regions around the remaining landmarks.

4.2   Experiment 2: Changing landmark texture

In the second experiment, bees were again trained with three uniformly textured landmarks. Bees were then tested individually five times with the same landmarks before replacing them with randomly textured landmarks (see Fig. 1 d for a rendered panoramic image). Subsequently, bees performed again five test flights.

Most surprisingly, the search distributions for the differently textured landmarks do not vary considerably (Fig. 3 a,b). Also, average flight duration was not significantly different in both situations (data not shown).

However, image similarity maps do not reflect these results. The similarity map for the arena with randomly textured landmarks shows local minima scattered over the whole arena, suggesting that search behavior guided by image similarity cannot explain the flight distribution of honeybees under these circumstances.[5]

4.3   Snapshots of flow amplitudes

So far, we considered snapshots containing static images of the surround scene at the feeder. However, bees will experience visual input during flight that also varies according to the depth structure of the scene. Therefore, it is likely that they use this information for their spatial representation. To test this hypothesis, we extended the image based approach to flow amplitudes. Flow fields, $\boldsymbol{f}(u,v) = (\delta u(u,v), \delta v(u,v))^\top$, were computed using a slightly modified version of the well-known Lucas-Kanade algorithm [16, 17]. To generate flow amplitudes that are independent from the direction of motion, flow fields for translation in x and y were calculated and their square amplitudes added,

$$F^{xy}(u,v) = \|\boldsymbol{f}_{\delta x}^{xy}(u,v)\|^2 + \|\boldsymbol{f}_{\delta y}^{xy}(u,v)\|^2 \ . \tag{3}$$

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[5] Since the bees do several flights in the arena with randomly texture landmarks, they possibly could switch to a snapshot containing randomly textured landmarks. However, the corresponding image similarity map (not shown) again has local minima not restricted to the region defined by landmarks.
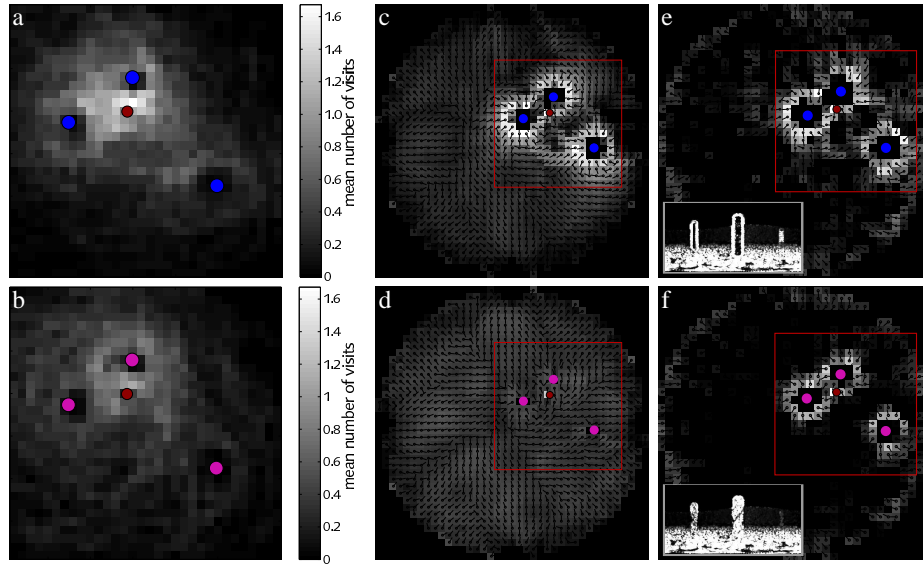
Fig. 3. Results of the landmark texture experiment and simulations: Spatial search distributions for a) three uniformly textured landmarks (45 flights in total), b) three randomly textured landmarks (45 flights in total). c,d) Corresponding image similarity maps assuming snapshot images with three uniformly textured landmarks. e,f) Similarity maps for optic flow amplitudes described in section 4.3, insets show examples of computed flow amplitudes.

For the results shown in Fig. 3 e,f, we used constant translations $\delta x = \delta y = 2\,\mathrm{mm}$, and in Eq. (1), we simply replaced images $I(u,v)$ by flow amplitudes $F(u,v)$. As expected, similarity maps for flow amplitude are highly consistent in both situations, and also in line with the search distributions. These findings suggests that honeybees may use – possibly in addition to an image-like representation – snapshots containing the 3D structure of the scene.

Future work will have to show whether similar results can be obtained with visual input reconstructed from single flights using biologically plausible motion detectors, see e.g. [18–20], which are known to respond not just to image motion but also to image contrast and frequency content in a non-linear fashion. We will also investigate further whether one can find post-processing operations for the static images that can give similarity maps consistent with the search distributions in both situations.

5   Outlook: Active vision for enhanced depth perception?

Search behavior guided by flow amplitudes, as suggested in the previous section, has to rely on flow fields generated by translation since they depend on the 3D structure of a scene, while flow fields from rotation are independent of distances
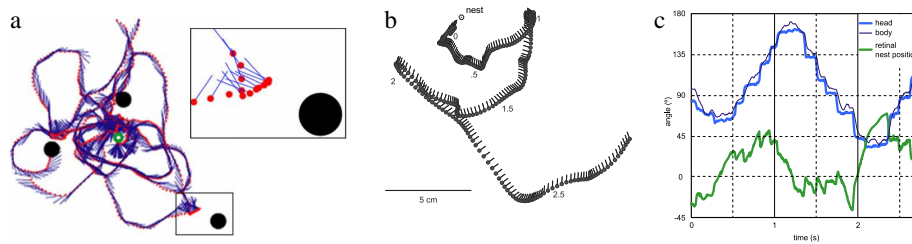
Fig. 4. Active control of optic flow: a) Flight trajectory of a honeybee during approach to feeder (red dots: body position, blue lines: body orientation). Inset shows side-ward motion while facing a landmark. b) Trajectory (dots) and head orientation (forward pointing lines) of a ground-nesting wasp during departure from nest. c) Head orientation (thick blue curve) and body axis orientation (thin curve) during departure, note the pronounced step-like changes in head orientation that are hardly visible in the body orientation curve; the thick green curve shows the azimuth of the retinal nest position (b,c adapted from [12]).

to objects. Analysis of body axis orientation of honeybees during approach flights reveals sequences in which side-ward translational motion dominates, see Fig. 4 a for an example. This actively controlled behavior reduces rotational flow and is very likely to simplify perception of the depth structure. In future experiments with close-up video recordings, we expect to find further support for this hypothesis: It has been shown in other insects, e.g. flies [21, 22] and wasps [12], that head orientation is kept almost perfectly constant during such maneuvers generating a purely translational flow field (see Fig. 4 b,c).

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