

## Dominance of Celestial Cues over Landmarks Disproves Map-Like Orientation in Honey Bees

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A recent model of landmark orientation by the bee assumes that the memory of the landmarks is arranged in a kind of a mental map. Our experiments disprove this assumption and show that the sun compass dominates the orientation without any indication of mental operations within a map-like representation of landmarks or of compass vectors and distances.

Any goal within the flight range of the bee is characterized by direction and distance from the hive. These two parameters are also the basic informations transmitted in bee dances. The direction has to be calculated by using an individually acquired sun compass, whereas the distance is estimated by the amount of energy invested during the flight [1]. Local and distant landmarks are used for supplementary control of these orientation mechanisms. Bees reconstruct a compass direction from landmarks when the sun is not visible [2]. The bee's flight is of course susceptible to wind influences; the bee must, therefore, be able to use landmarks for course corrections and to reset the memorized goal distance. Together with the automatism of path integration [3, 4] no other mechanism appears necessary to explain long distance orientation in the honey bee or other insects [5]. (For short distance orientation bees rely on sequences of memories of closer landmarks as shown by Opfinger [6], Collett and Kelber [7].) Recently, it has been proposed by Gould [8] that landmarks might not only be used for course control mechanisms, but that bees are able to perform navigational calculations within a mental representation of the landmarks. They should thus be capable of orienting according to an internal mental map. The map might result from a composition of the experienced landmarks en-route into a map-like memory, or a composition of the vectors and distances into a vector map centered around the hive. Evidence for the existence of such a "mental" map is taken from displacement experiments which were

interpreted to indicate internal operations within a map-like memory. Bees were found to fly new and previously untravelled routes after being displaced within the experienced landscape. Indeed, if bees would have established a map of landmarks or a map of vectors and distances, the assumed mental operations would guide them to fly short-cuts after displacements and thus expose them to unexperienced compass directions and landmark arrangements. Gould's interpretation in favour of a "mental map" in bees has been contradicted on logical grounds [9] and on the basis of additional experiments [5, 10, 11]. The weakness of all experiments published so far on this subject is that the actual experience of the individual bee within the landscape was not known prior to the displacement experiments. There were always good reasons to believe that the bees were well experienced and thus knew the landmarks surrounding the hive, but actual proof did not exist on the basis of the individual animal. The paper by Dyer [11] reports well designed experiments taking this factor into account, but the bees were trained over relative short distances (160 m) and thus orientation according to local landmarks rather than long distance orientation might have been tested. Here we report an experiment in which individually marked bees were used in training and displacement experiments whose knowledge of the landscape were exactly known. To ensure far distance orientation bees were trained over more than 400 m.

A small colony of approximately 4000 bees was set up in an observation hive early in September in an area which provided no natural food sources (North of Hessen, close to the town of Amöneburg near Marburg). Half of the bees were individually marked with number tags. Shortly after setting up

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the colony in the area, in which the bees had no previous experience, a group of bees was trained along a partial circle around the hive at a distance of 470 m (see Fig. 1a). During the training along the indicated path each visit of a bee at the feeder was monitored. Training along the partial circle was completed after two days, and displacement experiments started on the third day. The particular area was chosen for the experiments, because it provided a prominent landmark, a mountain to

the left side when the bees flew towards the final feeding station F, and an open area with a flat horizon to the right side (see Fig. 1a, 2). After arriving at the feeder F newly recruited bees were also incorporated into the training group and full protocols of visitation were established. Thus, two groups of bees were visiting F, those which had experienced the landscape between the hive and the moving feeder along the partial circle ("experienced bees") and those which knew only the flight

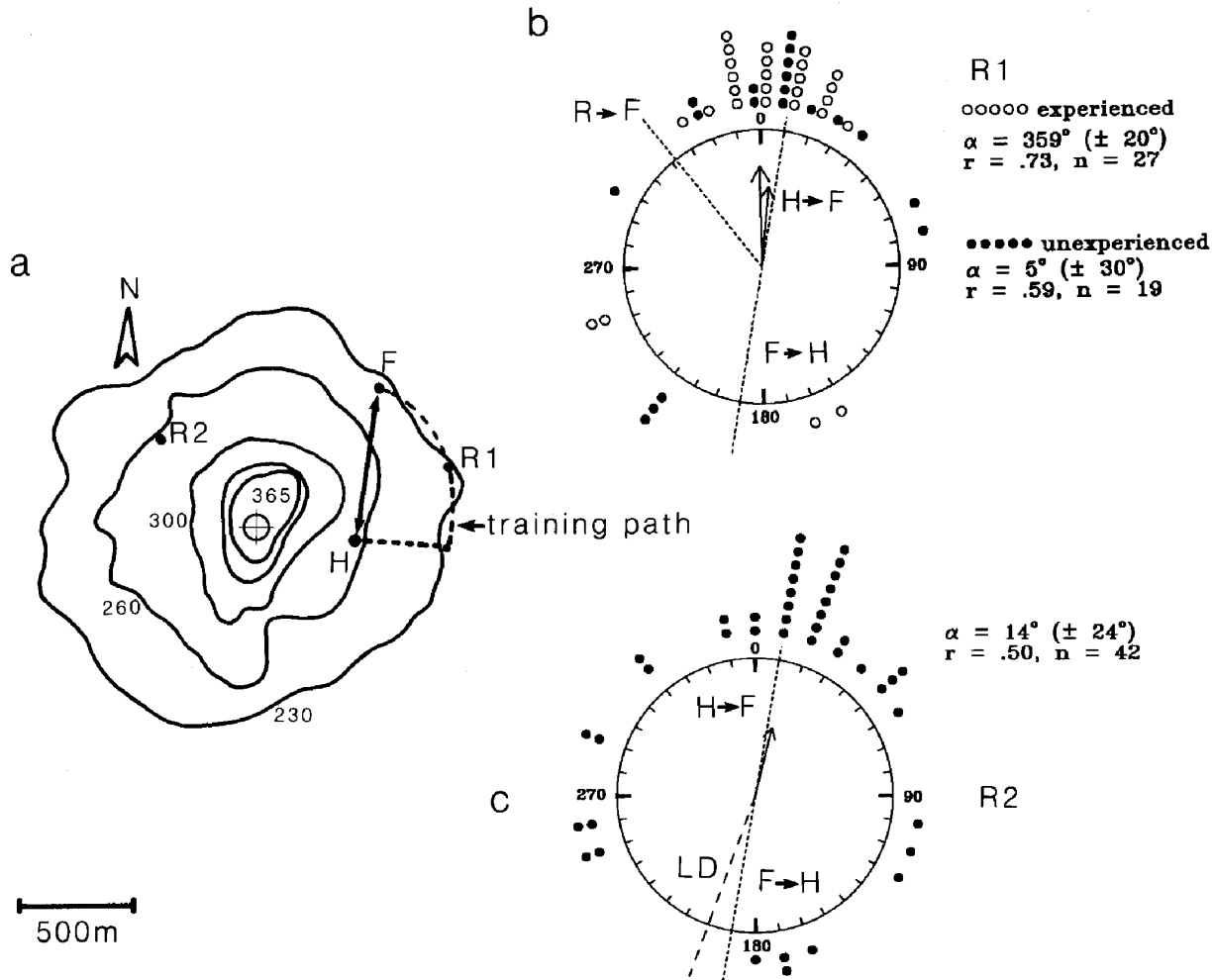


Fig. 1. a. Schematic representation of the landscape at the experimental site (Amöneburg close to Marburg/Hessen). The bees were trained from the hive H, first straight to the east and then along a halfcircular path to the final feeding station F (dotted line). R1 and R2 indicate the release sites R1 and R2. The number at the contour-lines of the mountain give meters above sea level.

b. Angular distribution of the vanishing points of experienced (open circles) and unexperienced bees (closed circles) at the release site R1. The dotted lines give the angular bearings for the directions: from the hive towards the feeding station (H → F), from the feeding station to

the left side when the bees flew towards the final feeding station F, and an open area with a flat horizon to the right side (see Fig. 1a, 2). After arriving at the feeder F newly recruited bees were also incorporated into the training group and full protocols of visitation were established. Thus, two groups of bees were visiting F, those which had experienced the landscape between the hive and the moving feeder along the partial circle ("experienced bees") and those which knew only the flight

c. Angular distribution of vanishing points for bees released at release site R2. Same symbols as in b. The dashed line (LD) gives the direction relative to the mountain (compare with Fig. 2).

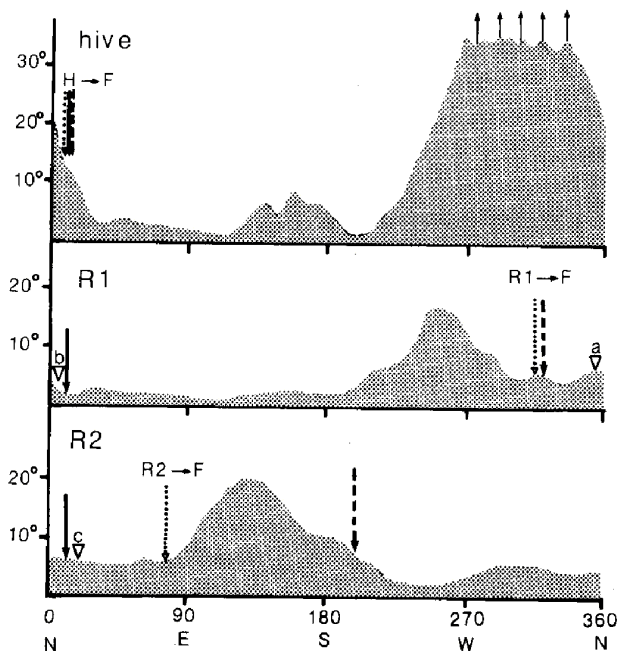


Fig. 2. Horizontal profile as seen from the hive and the release sites R1 and R2. The dotted arrows (.....▶) mark the shortest directions towards the feeding station ("map direction") from the hive (H → F), and from the release sites (R1 → F, R2 → F). The solid arrows (→) give the compass direction from the hive to the feeding station (10° east of north). The dashed arrows (---▶) show the approximate directions relative to the prominent landmark (70° to the right of the mountain peak, dashed line LD in Fig. 1 c). The open triangles (▽) mark the average directions of the vanishing points for the three experimental groups; ▽ a: experienced bees released at R1, ▽ b: unexperienced bees released at R1, ▽ c: bees released at R2. The thin arrows pointing upwards in the first graph (hive) indicate that the mountain profile continues upwards (to 65° visual angle for the peak).

path between the hive and F ("unexperienced bees"). The unexperienced bees might have left the hive before being recruited to the feeder F, but they have not been trained to any food source in this area and should thus have only a knowledge of the landmarks in the immediate surrounding of the hive. This was also verified by observing the dances of bees in the hive.

**Displacement and flight path:** The bees were caught at the hive entrance when they were heading out for F. Each bee was transported separately to the release site (R1 or R2) in the dark and released individually. The initial orientation of the released bee was monitored by determining the vanishing point. Generally bees circle around the

new release site for a few seconds spiraling higher and higher up in the air and then make a sharp turn to fly along a straight line out of sight (vanishing point). The direction of the vanishing point was determined with a simple circular pointer. The experimenter did not know to which group a particular bee belonged. Since the area surrounding the release sites was open and flat, bees departed from the circling mode to the straight line at a relatively low height (less than 4 m) and were easy to follow. If a bee was lost within a distance of less than 15 m, no flight direction was recorded. Bees were not repeatedly released, since earlier experiments showed [10] that they gradually learn new flight directions during multiple releases. Circular statistics [12] are used to evaluate the data. The mean angle of the distribution of vanishing bearings is the "center of mass" of the data on a polar histogram. The degree of variance of the data is given by  $r$  ( $r = 1$  for identical orientation of all bees,  $r = 0$  for random orientation). A mean angle is considered significantly different from a predicted angle if the prediction lies outside the 95% confidence interval of the mean.

In the first series of displacement experiments (release site R1, Fig. 1 b) we ask the question whether experienced bees behave according to a map concept. Since the bees knew the release site R1 from the initial training, they should have headed towards F along a short cut if they were able to perform an internal calculation using a map like memory. In that case the bees would have had to overcome their learned compass direction of 10° right to north (flight path H → F) and steer a new direction of 38° left to north (R1 → F), (see Fig. 1 and 2). The dominant landmark (mountain) is always located left to the flight path also on the learned flight from H to F. Since we had not seen any indication of orientation according to a mental map in former experiments [5, 10], we designed the experimental conditions such that the dominant landmark might favour orientation according to a mental map.

Even under these favourable conditions the bees chose the compass direction and not the short-cut from R1 to F. The experiments shown in Fig. 1 b were carried out on sunny days. Data were collected within 4 days after the initial training along the partial circle. Unexperienced bees were released at the same time. The experienced and unexperienced

bees chose the same average vanishing bearings. This angle corresponds to the compass direction between the hive and the feeding place (H → F in Fig. 1b) and is significantly different from the short-cut to F for both groups of bees. Thus, bees head-off into the compass direction, which they would have taken when flying from the hive to the feeding place, irrespective of whether they know the release site or not. The total overlap in the vanishing directions between experienced and unexperienced bees proves, that site specific information from an earlier experience is not used for the determination of the shortest direction to the feeding place. This result excludes both possibilities of a mental map in honey bees, the vector kind of map and the cartesian arrangement of experienced landmarks.

These results suggest that the sun compass dominates far-distance orientation in bees so strongly that even prominent landmarks, such as a mountain (see Fig. 2) might be of little importance when the sun is visible. However, the orientation according to the line of the horizon could not be tested at release site R 1, because the flight directions taken according to the sun compass and the line of horizon are very close together (see arrows in Fig. 2). The landscape, where the experiments were carried out, offers the opportunity to dissociate these two orientations and to test whether prominent patterns of far-distant landmarks are used either in addition, or alternatively, to the sun compass. Fig. 2 gives the azimuthal distribution of the profile of the horizon as seen from the hive and from the two release sites, R 1 and R 2 (see also Fig. 1a). The dominant landmark is shifted by nearly 180° at R 2. Bees released at R 2 show a somewhat broader distribution of vanishing points, but on average chose the same compass direction as at R 1 (Fig. 1c). The experiments were again performed on sunny days. This result indicates that bees ori-

ent their initial flight path in an unknown area according to the sun compass. A very prominent landmark might provide additional information, but is not used under the conditions of this experiment (sunny days).

The experiments reported here were designed such that the experience of each bee within the landscape was well known prior to a translocation. This constraint made it necessary to train and test the bees within a few days late in the year when no other than the experimental food sources are available. The consequence, however, is that all the bees we used in these experiments had only short experience with the landmarks and their position relative to the colony, relative to each other and relative to the sun compass directions of the flight paths. Particularly, the bees were trained quickly along a path and thus may have made only a few flights between the hive and each of the changing positions of the moving feeder. Furthermore, they had only experience of a few days of active foraging flights with the landmarks en-route. Since they were all foragers already at the moment when the hive was moved to the new location they had, however, extensive experience with the sun compass.

Our experiments provide conclusive evidence against an internal calculation within a map-like representation of the external world and indicate the dominance of the sun compass over even prominent landmarks. This conclusion is restricted to the special conditions of the experiment, namely the short experience of each bee within the landscape and sunny weather conditions.

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