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Target-directed Orientation in Displaced Honeybees

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Abstract

Under sunny weather conditions, displaced honeybees (Apis mellifera) usually fly into the celestial compass direction and thus may be misled from their goal, or they are disoriented. Under cloudy conditions, they may determine the celestial compass direction from prominent landmarks. They may also fly directly toward their goal from a release site. In two experiments, we investigated the orientation of displaced bees when a landmark (target) was close to the goal under different weather conditions. It is shown that in sunny conditions, the celestial compass will override target orientation under most conditions. Under 100% cloud cover, the celestial compass direction retrieved from landmarks modulates target-oriented behavior but is not by itself a primary orientation factor. The bees will fly toward a previously encountered landmark that signals the target, and in case of several similar landmarks which are visible to the bees, they will choose the one in the direction nearest the celestial compass direction. The results indicate that honeybee orientation is the result of a set of context-specific interdependent orientation mechanisms.

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Introduction

Insects use celestial and familiar landmark cues to orientate themselves in space. Celestial cues, i.e. the sun’s azimuth as well as the polarization pattern in the sky, provide the insect with the celestial compass (VON FRISCH 1967). Prominent landmarks, e.g. a forest edge or an array of several large landmarks, are learned relative to the celestial compass and act as an orientation back-up system on cloudy days (VON FRISCH 1967; DYER & GOULD 1981; MENZEL 1989). In sunny weather, bees displaced from the hive or a feeding station in most cases fly into the celestial compass direction after release, i.e. on a course parallel to their original course from starting point to goal (VON FRISCH & LINDAUER 1954; VON FRISCH 1967; MENZEL 1989; WEHNER & MENZEL 1990; WEHNER 1991). Under a completely

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cloud-covered sky, they are disoriented after a release in unfamiliar territory (Menzel 1989; Chittka et al. 1992), whereas they are orientated in the celestial compass direction when released in familiar territory under such conditions (Menzel 1989; Wehner & Menzel 1990; Dyer et al. 1993). However, under certain conditions, bees use landmarks to direct their flight after displacement independently of the celestial compass direction, and thus may be led on a direct course toward the intended goal (hive or feeding place) (Menzel 1989; Dyer 1989; 1991; Dyer et al. 1993). Such a behaviour has been interpreted as an indication for map-based orientation (Gould 1986), but simpler orientation mechanisms provide a more likely explanation (Dyer & Seeley 1989; Wehner & Menzel 1990; Dyer 1991; Dyer et al. 1993). One possibility is that landmarks close to the hive or feeding place may be used as targets and are directly approached from a distance even if they appear at a novel visual angle relative to the celestial compass direction at a release site.

We set out to assess the conditions under which target-directed orientation occurs. The problem to be solved was to estimate how effective target-directed orientation would be in the context of other parameters governing orientation. Results from displacement experiments conducted by Dyer (1991) and Dyer et al. (1993) may be interpreted to indicate that bees need to have a direct view of the landmarks in the goal’s close vicinity to be able to fly toward the goal. It has been shown in other experiments that orientation in a direction indicated by landmarks varies with their apparent size or conspicuousness (von Frisch & Lindauer 1954) and the bees’ prior flight experience (Lewtschenko 1959, cited in Wehner 1981, p. 464). The degree to which bees will be orientated in the celestial compass direction after release varies with the accessibility of celestial cues, and thus with weather conditions.

We have focused our attention on the bees’ orientation under different weather conditions and with respect to different landmarks close to the goal. We displaced bees under both a sunny and a 100% overcast sky. In the first experiment, the target close to the hive was a stack of tree trunks on the ground not visible from far away, and the bees were displaced under sunny conditions. Here, we tested whether the bees would fly toward this target landmark or into the celestial compass direction when released very close to the hive. In the second experiment, bees were displaced under 100% overcast conditions in an area containing two large landmarks. One of these was positioned next to the hive and acted as the target landmark, while the other, at some distance from the hive, resembled the target landmark. In this experiment, we tested whether the bees would fly toward either of the landmarks or into the celestial compass direction, which they might reconstruct from the landmarks surrounding the experimental area.

Methods

Honeybees were trained to fly toward artificial feeders by first placing the feeder in front of the hive until forager bees had settled on it, and subsequently moving it in small steps to the ultimate position. After the feeding station had been thus established, the bees were allowed to forage from it for at least 2 d before the experiments started. The sucrose concentration in the feeders varied between
2 m and 0.3 m, adjusted to keep the number of bees at the feeder at any one time fairly constant. During this time, bees were individually numbered at the hive by gluing small numbered tags onto their thoraces.

In both experiments, bees were caught at the feeder after they had fed to satiation just prior to their departure for the hive. They were individually placed in small glass containers which were immediately put into a dark cushioned container and transported to one of the release sites within 10 min.

Bees were repeatedly displaced in both experiments. They were released and their vanishing bearings were recorded with a compass. Repeated displacements did not affect the distribution of vanishing bearings. All directions and the vanishing bearings were measured as angles relative to north in a clockwise direction (0°/360° = north). The experiments were performed in late Aug. and early Sep.

First Experiment: Competition between the Celestial Compass and Target Landmarks

The first experiment was conducted in Seewiesen, South Germany, close to the Max Planck Institut für Verhaltensphysiologie. A small experimental hive (approximately 2000 individuals) was set up in the area 2 d prior to the beginning of the experiments; thus, the bees had only these 2 d to acquaint themselves with the area. There were no obvious landmarks close to the hive other than a stack of tree trunks, about 1.2 m high. The experimental area was surrounded by patches of forest. The feeding station S/E was located 475 m away from the hive to the north-east (30°), and thus the celestial compass direction from the feeding station to the hive was 210°. Between hive and feeding station was a small hill, so that it was impossible to see the hive from the feeding station and vice versa. However, once they had passed the hill on their way to the hive, the bees could see the hive and the stack of trunks next to it. The hive's entrance was to the south-west, so that bees leaving the hive for the feeding station and those returning to the hive from the feeding station had to fly around the hive and the stack of trunks. All bees shuttling back and forth between hive and feeding station flew a west-bound curve to depart and arrive at the hive. Bees were displaced to four different release sites (S/R1–S/R4, where S stands for Seewiesen). From all release sites, the hive and stack of tree trunks were easily visible. Seen from the hive, S/R1 was at 10° (70 m distant from the hive), S/R2 was at 260° (50 m distant from the hive), S/R3 was at 225° (40 m), and S/R4 was at 180° (30 m). The layout is depicted in Fig. 1, left side. Weather was variable, but cloud cover never exceeded 80%.

Thus, the bees had two options after their release: fly toward the hive or the stack of trunks next to it, or fly in the celestial compass direction.

Second Experiment: Competition between Large Target Landmarks under a Fully Overcast Sky

The second experiment was conducted in a narrow valley in the north of Italy (Ahr Valley, near Bruneck, South Tyrol). A hive native to the area was used, and thus the foragers were familiar with the area. The peaks of the surrounding mountains were 1000 m above the valley ground which ran south-west–north-east. Both the eastern and western slopes of the valley were covered by forest.

The bees were trained to fly in two groups, one to a feeding station situated on the densely forested western valley edge approximately 300 m to the north-east of the hive (called northern feeding station, compass direction to the hive: 215°), and the other one to a feeding station approximately 330 m to the south-west (called southern feeding station, compass direction to the hive: 51°). The compass direction from the northern feeding station to the hive was thus 215°, while it was 51° for bees displaced from the southern feeding station. Both feeding stations and the hive were on the western edge of the valley. A white house (called landmark 1) stood directly near the hive, 5 m distant from it. We released the bees in a meadow on the valley floor. In this meadow, a small white village church was located (called landmark 2), while several other buildings surrounded the valley. Both landmarks were quite symmetric in appearance and looked similar from all sides. Landmark 1 was easily visible from the southern feeding station. From the northern feeding station, the direct view of landmark 1 was blocked by a group of trees projecting from the forest growing on the western slope, but bees saw landmark 1 during the last 70 m of their regular flights from the northern feeding station to the hive. Landmark 2 was visible from both feeding stations. Therefore landmark 1, the white house, was seen by the bees before they saw the hive itself on their return trips from the feeders, as
the fairly inconspicuous hive was surrounded by several low bushes. During training, weather was fair, and cloud cover never exceeded approximately 70%.

Bees of both groups were displaced to two release sites. The first release site, called 1/R1 (where 1 stands for Italy), was located approximately 300 m away from the hive at 150°; the second release site, called 1/R2, was approximately 250 m away from the hive at 100°. From 1/R1, landmark 1 was 220 m away at 330°. It was 200 m away from 1/R2, at 280°. Landmark 2 was approximately 200 m away from 1/R1 at 20°, while it was 50 m away from 1/R2 at 10°. From both release sites, landmarks 1 and 2 were visible. During these displacements, the sky was completely occluded by clouds (100% cloud cover, the celestial compass could not be seen through the clouds), and the horizon profile changed frequently with the height of the cloud cover. Bees were observed to fly at approximately 9–12 m height during their normal foraging bouts as well as during their orientation flights after a release.
To determine the bees' orientation under a sunny sky in this area, we displaced bees from both feeding stations to S/R1 under a blue sky (25-75% cloud cover) when the weather was fair. The experimental layout is depicted in Fig. 2, left side.

Thus, the bees had three options after their release: they could fly in the celestial compass direction as determined from the surrounding landmarks, or they could fly toward one of the two landmarks because they had learned to fly toward a landmark (namely, landmark 1) from the feeding stations.

Statistics

The statistical test used to determine whether the vanishing bearings of the displaced bees were randomly distributed or clustered around a particular direction (e.g., the direction from a release site toward the hive) was the V test (Batschelet 1981, p. 59). This test determines whether a distribution is significantly centered on a hypothetical direction determined prior to the experiment, or whether the distribution is random. If the animals are clearly oriented and it is to be determined whether the mean direction deviates significantly from such a predetermined hypothetical direction, the V test is not applicable. Instead, the confidence intervals for the mean angle were determined (Batschelet 1981, p. 84). In case of bimodal distributions, the broken axis approach was used to determine the mean vector lengths and angles of the two modes (Holmqvist & Sandberg 1991).

Results

First Experiment: Competition between Celestial Cues (Celestial Compass) and Target Landmarks

Bees were displaced to release sites S/R1–S/R4, close to the hive, to test whether the celestial compass would dominate over orientation toward the goal under sunny weather conditions. Seen from S/R1, the hive and the stack of trunks beside it was almost in the celestial compass direction, whereas from S/R2–S/R4, hive and stack were seen in novel directions. As the bees were motivated to fly toward the hive and the stack of trunks, and also motivated to fly in the celestial compass direction, there were now two possible directions for them to take: the celestial compass direction from the feeding station to the hive, or directly toward the hive. At S/R1, they could either determine from their landmark memory that they were almost on the normal flight path between feeding station and hive and thus approach the hive, then turn around it and alight at the entrance, or they could fly past the hive, following the entire length of the vector connecting the feeding station and the hive.

At S/R1, no vanishing bearings were recorded because all bees (n = 13) flew into the celestial compass direction — following the last part of their usual journey — and then turned around to enter the hive. The approximate flight path is shown in Fig. 1, left side.

At S/R2, the mean vanishing bearing of bees released there is 193° (r = 0.92, n = 25, Fig. 1: A), and that of bees released at S/R3 is 202° (r = 0.97, n = 5, Fig. 1: B). These mean directions are not significantly different from the celestial compass direction (p < 0.0001, V test). Two bees from S/R2 and one from S/R3 flew directly toward the hive. The vanishing bearing distribution from bees released at S/R4 is bimodal (mean angles of the two modes: 3.9° and 223.4°, r = 0.86, n = 32, Fig. 1: C and C'). Here, one mode is not significantly different from the direction toward the hive (p < 0.0001, V test), while the other is not significantly different from the celestial compass direction (p < 0.0001, V test).
Thus, almost all bees displaced in Seewiesen were orientated in the celestial compass direction. At S/R4, which was closest to the hive, about half of them were orientated in the direction of the hive, and the other half were orientated in the celestial compass direction. At the other release sites, S/R1, S/R2 and S/R3, only three bees flew toward the hive. Under sunny conditions, therefore, bees are orientated in the celestial compass direction after displacement from a feeding station, and orientation toward a target is the exception, even when the bees are released close to the target. This result corroborates earlier findings that bees displaced under sunny conditions are orientated in the celestial compass direction (MENZEL et al. 1990; WENNER & MENZEL 1990; WENNER et al. 1990).

Second Experiment: Competition between Large Target Landmarks under a Fully Overcast Sky

This experiment was performed at an experimental site where a fully overcast sky could be expected. We chose a narrow valley surrounded by high mountains, the peaks of which were hidden behind clouds most of the time.

Bees foraging at the northern as well as those foraging at the southern feeding station experienced landmark 1 regularly on their flights from the feeding stations to the hive. The critical experiments were performed such that at either release site, the angle toward landmark 1 was different from the celestial compass direction for bees displaced from either feeding station. The direction toward landmark 2 was close to the celestial compass direction for bees displaced from the southern feeding station and almost opposite the celestial compass direction for bees displaced from the northern feeding station. Therefore, landmark 1 was seen at an angle quite different from the angle toward landmark 2. The potential influence of landmark 2 was further varied by releasing the bees closer (I/R2) or farther (I/R1) from landmark 2. We now tested whether bees displaced under 100% cloud cover would fly toward landmark 1 or 2, or in the celestial compass direction as determined from the surrounding landmarks.

The vanishing bearing distribution of bees displaced from the southern feeding station to I/R1 was almost axial under cloudy conditions (mean angles of the two modes: 18.6° and 189.2°, r = 0.68, n = 18, Fig. 2: A and A'). The celestial compass direction of 51° is not included in the confidence intervals of ±22° for this

Fig. 2: The experimental area for the second experiment, conducted in St. Johann, Italian Alps. The hive, the feeding stations (northern and southern feeding stations), the release sites (I/R1 and I/R2), and the two landmarks (landmark 1 and landmark 2) are shown at left. The mean angles of the vanishing bearing distributions of bees displaced from the northern and southern feeding stations to the release sites are indicated by black arrows. Letters at the tips of these arrows correspond to vanishing bearing distributions shown at right. Here, white crossed arrows indicate the celestial compass direction, white arrowheads indicate the direction toward landmarks 1 or 2, and black arrows indicate the mean vectors of the vanishing bearings. For bees displaced from the southern feeding station to I/R1 or I/R2, the black arrows show the mean angles of the two modes (A and A' for bees displaced from the southern feeding station to I/R1, B and B' for bees displaced from the southern feeding station to I/R2). In a separate box are shown the vanishing bearing distributions for the two control groups, bees from the southern and northern feeding stations released at I/R1 under sunny conditions.
distribution. Most bees displaced from the southern feeding station to I/R1 were orientated toward or away from landmark 2 (p < 0.0001, V test for both modes), while two of them flew in approximately the direction of landmark 1.

The vanishing bearing distribution of bees displaced from the southern feeding station to I/R2, the release site closer to landmark 2, was bimodal (means of the two modes: 14.4° and 302.4°, r = 0.69, n = 40, Fig. 2: B and B'). We found that one-half of the bees displaced from the southern feeding station were orientated toward landmark 1 (p < 0.0001, V test), while the other half were orientated toward landmark 2 (p < 0.0001, V test). The celestial compass direction of 51° is not included in the confidence intervals of ±17° for this distribution.

The vanishing bearings of bees displaced from the northern feeding station to I/R2 were fairly broadly distributed around the direction of landmark 1 (mean vanishing bearing 276.2°, r = 0.78, n = 16, p < 0.0001, V test, Fig. 2: C). The direction of landmark 2 (10°) is not within the confidence interval of this distribution (±22°), nor is the celestial compass direction of 215°.

We then tested the orientation of bees displaced under sunny conditions. Vanishing bearings from bees which were displaced from both the southern and the northern feeding stations to I/R1 were centred on the celestial compass direction (from the southern feeding station: mean vanishing bearing 37°, r = 0.93, n = 10, p < 0.05, V test, Fig. 2: box; from the northern feeding station: mean vanishing bearing 230°, r = 0.91, n = 13, p < 0.05, V test, Fig. 2: box). The directions of landmarks 1 and 2 are outside the confidence intervals of the vanishing bearing distributions for bees displaced from the southern feeding station (confidence interval ±13°) and for those displaced from the northern feeding station (confidence interval ±12°).

The distributions of vanishing bearings in the second experiment indicate that in the absence of celestial cues, the bees fly toward the visible targets, and not in the celestial compass direction as reconstructed from surrounding landmarks. Under sunny conditions, however, bees are orientated in the celestial compass direction, similar to bees displaced in the first experiment.

Discussion

In the first experiment (Seewiesen), most bees displaced from the feeding station close to the hive flew in the celestial compass direction, directly perceived from celestial cues, even though the hive and the stack of tree trunks next to it was close by and perfectly visible to them. One may argue that these bees flew in the celestial compass direction rather than straight to the hive because of the little experience they had with the area. However, the bees were displaced very close to the hive, to an area which bees can learn after only a few excursions from the hive (Von Frisch 1967).

Bees that were displaced to S/R1 first flew parallel to the original flight path and, when they reached the 'catchment area' of the hive (Cartwright & Collett 1987), turned around the hive to fly to its entrance. If they had navigated strictly by their path-integration memory, which contains a vector equaling the vector
from feeding station to hive, they should have flown past the hive. However, navigation according to the path-integration memory was terminated when the bees came close to the hive, and the bees flew toward its entrance. Also, some bees displaced to S/R2, S/R3, or S/R4 flew directly toward the hive, ignoring the information retrieved from celestial cues. These results are in line with CHITTKA & GEIGER’s (1995) and CHITTKA et al. (1995), who showed that previously encountered landmarks strongly influence the bees estimate of distance to the goal, even if the landmarks are encountered at unfamiliar locations.

When displaced under a blue sky in the second experiment (Italian Alps), all bees displaced from either feeding station to I/R1 flew in the celestial compass direction, disregarding both landmarks 1 and 2. These bees were well acquainted with the area. Both results show that regardless of the level of experience with the area, most bees displaced under a sunny sky fly in the celestial compass direction and not toward any target landmarks. In most other displacement experiments (WEHNER & MENZEL 1990), bees displaced from their feeding stations were also orientated in the celestial compass direction after their release. Thus, the directly seen celestial compass dominates over target-directed orientation. However, DYER (1991) and DYER et al. (1993) found that some bees displaced from the hive into familiar territory under a sunny sky fly toward the food source and not in the celestial compass direction. As our results from the first experiments indicate that some of our bees did so as well, any studies concerning the interaction or competition between target-directed and compass orientation need to take into account more thoroughly the experience which an individual bee has had with these orientational cues. In particular, it needs to be investigated whether well-experienced bees indeed weight target cues more strongly than less experienced bees.

After displacement under a 100% overcast sky, nearly all bees in the second experiment approached one of the landmarks (landmarks 1 or 2), and they were never orientated in the celestial compass direction. Which of the two landmarks they approached depended on the amount of divergence between the celestial compass direction and the direction toward landmarks 1 or 2 from the release site. Bees displaced to I/R1 from the southern feeding station flew toward or away from landmark 2. From I/R1, the direction toward this landmark is closer to their celestial compass direction than the direction toward landmark 1. Bees displaced from the northern feeding station to I/R2, which is located near landmark 2, were orientated toward landmark 1, and not toward landmark 2 which appears almost opposite to their celestial compass direction. Thus, they flew toward landmark 1 because the direction of this landmark is closer to the celestial compass direction than that of landmark 2. We conclude, therefore, that bees fly toward the landmark that is closer to the celestial compass direction as seen from the release site.

These results also indicate that the celestial compass direction was indeed retrieved from the surrounding landmarks, presumably the mountains surrounding the valley, or and the valley’s edges. Otherwise, the bees should not have been orientated toward the landmark closer to the celestial compass direction. The features used for celestial compass reconstruction could not have been simply the
horizon profile, as that was highly variant due to the constantly changing height of the cloud cover.

When bees were displaced from the southern feeding station to I/R2, half of the bees displaced there from the southern feeding station flew toward landmark 2, while the other half were orientated toward landmark 1. Here, landmark 2's features are obviously (to human observers) different from those of landmark 1. The similarity in features between the two targets therefore also modulates orientation toward either landmark. This finding indicates that the worse the match between the seen image of the landmark (here: landmark 2) and the previously stored image (image of landmark 1), the higher the probability becomes that the bees will not approach that target even if it is closer to the celestial compass direction.

Four bees displaced from the southern feeding station to I/R1 flew directly away from landmark 2 (mean vanishing bearing 189.2°). This may indicate a change in the motivational state of these bees, possibly caused by the novel situation to which they were exposed after their displacement. These bees may have been motivated to fly away from the hive and the landmark near it, and in the direction which they would take on their way toward the feeding station from the hive. Similar axial distributions indicating a change in some of the bees' motivational state have been observed several times (e.g. Dyer et al. 1993).

In no case did our experiments yield any necessity to assume that bees store the geometric relations between objects in a cognitive map in order to locate their goal (Tolman 1948; Gould 1986). Goal-directed behaviour is common in animal orientation (Fraenkel & Gunn 1961). It means simply that the bees approach a visible landmark even if the landmark is seen in a new direction relative to an allothetic orientation system like the celestial compass. Such orientation is based solely on visual cues and the retrieval of snapshot images previously stored, and on the relative strength of the celestial compass, derived from celestial cues or, if those are not available, from prominent landmarks.

Thus, honeybee orientation appears to result from a set of context-specific interdependent and hierarchically organized mechanisms. Normally, bees will orientate in the celestial compass direction. If that is not possible due to overcast weather bees will fly toward a previously encountered landmark that signals the target, aided by image matching. If several similar objects are visible to the bees, they will choose the one in the direction nearest the celestial compass direction. When the goal is signalled by a landmark under 100% cloud cover, the reconstructed celestial compass modulates such target-orientated behaviour but is not by itself a primary orientation factor.

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