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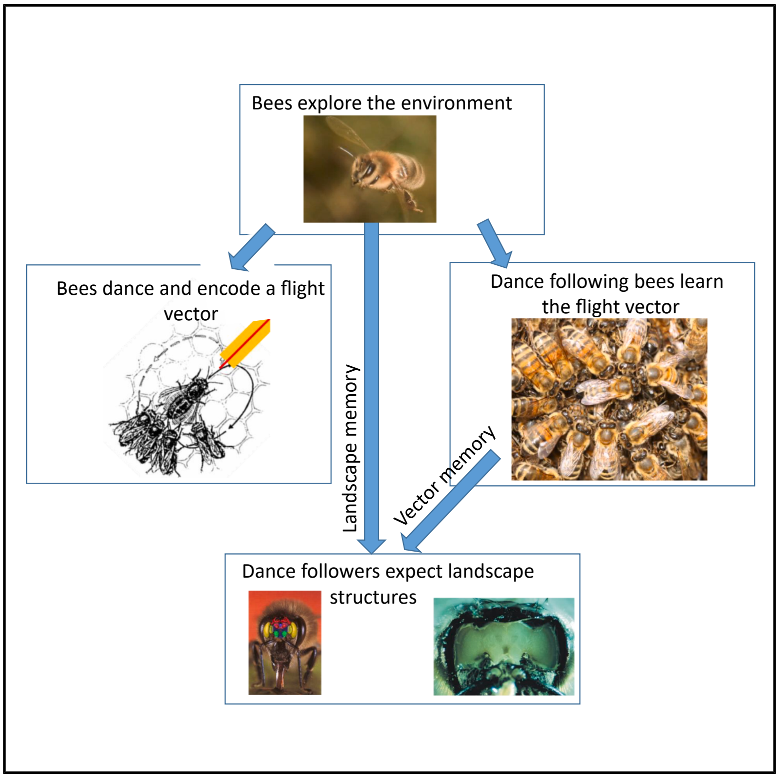
Waggle-dance-recruited honeybees expect landscape structures

Graphical abstract



Highlights

- Dance-recruited bees expect landscape features based on the dance vector information
- Recruits adjust flights at different release sites to match with the expected landscape
- The expected elongated ground structures seen by the dancer guide their flights

Authors

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In brief

Wang et al. show that honeybee dance followers derive from the dancer's vector information the specific memory of the explored environment. These dance-recruited bees expect salient landscape structures that the dancer experienced. This expectation is not based on spontaneous or otherwise learned behavior.

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Waggle-dance-recruited honeybees expect landscape structures

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SUMMARY

Honeybee foragers explore the environment before they start foraging, following dances, or performing dances. Foragers are therefore familiar with the landscape surrounding the hive during their foraging career. Here, we ask whether dance-recruited honeybees expect the landscape features that the dancer experienced during its outbound foraging flights. If this were the case, the dance-recruited honeybees would behave differently according to whether the landscape features they experienced during their outbound flight matched the expected features. In our experiments, the dance followers (recruits) had explored the environment around the hive, and the dancers flew along an elongated ground structure (a gravel road) running approximately northward from the hive in the outbound condition. The flights of the recruits were recorded by harmonic radar. The recruits were released not only at the hive but also at two remote sites within the explored area, where they faced either a similar north-running gravel road or even grassland. We found that the recruits released from the remote sites performed flights more similar to those of the hive-released bees when they experienced a similar elongated ground structure. This behavior did not result from a spontaneous or learned tendency to follow elongated ground structures as documented by control experiments. We conclude that dance-recruited honeybees expect the salient landscape structures that the dancer experienced, although the dance message includes only vector information.

INTRODUCTION

The waggle dance of honeybees (*Apis mellifera*) is a remarkable form of symbolic communication that encodes the outbound flight vector from the colony to a valuable resource such as food, resin, water, or a potential new nest site.[1] This vector, which comprises both distance and direction, has long been considered the sole navigational guide for bees recruited by the dance.[2,3] However, emerging evidence suggests that this view on the communication process may be incomplete, and the landscape memory of the dance-following bees (hereafter recruits) needs to be included. For instance, recruits have been observed to fly shortcuts between a learned location and a dance-indicated site,[4] and they search for the dance-indicated location even when starting from sites other than the hive.[5] Dancers embed their message into the landscape and make it dependent on the view of the landscape.[6] These behaviors raise the intriguing possibility that recruits anticipate specific landscape features during their outbound flights and use memories of these features to locate the dance-indicated site.[7] Such findings challenge the traditional notion that waggle-dance communication is only based on encoding and decoding vector-based information. Rather, we hypothesize that recruits may integrate the information from symbolic communication with their spatial memory of the environment developed during exploratory orientation flights and foraging flights, leading to an expectation of landscape features the dancer had experienced during its foraging flights.

Honeybees engage in extensive exploration of their surroundings before initiating dance-following and foraging activities.[8–11] Foragers can return home directly from known locations or via intermediate sites that they have previously experienced.[12,13] This ability to integrate spatial memories with current navigational tasks raises the question of whether recruits might also associate the symbolically communicated vector with specific landscape features. If so, recruits would be able to retrieve memories related to the dance-indicated outbound flight vector before physically performing the flight to the target location.

Here, we investigate whether recruits expect to encounter salient landmarks that were experienced by the dancer as guiding structures leading them to the feeding site. Our experimental design ensured that the recruits were experienced foragers but had not previously visited the area of the artificial feeder to which the dancers were trained. To address our question, we employed harmonic radar tracking, a powerful tool for recording the detailed flight trajectories of individual bees.[14] Recruits

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were released not only at the hive entrance but also at two other sites within the test area. The layout of the test area was carefully chosen and designed to expose the recruits either to a salient landscape feature—a south-north-running gravel road—that resembled the conditions experienced by the dancer, or to a contrasting environment of even grassland. These landscape features allowed us to examine whether recruits adjust their outbound flights (vector flights and search flights) in accordance with the presence of landscape features that were salient to the dancer. Furthermore, we reanalyzed data that serve as controls, allowing us to reject the possibility that the recruits choose to fly along extended ground structures like paths or roads spontaneously or learned as a landmark at the hive.

The flights of recruits can be divided into three phases: vector component, search component, and homing flight.[5] We hypothesize that the vector component is more dominated by the information from the waggle dance but will differ from vector flights starting at the hive if recruits notice the mismatch between the expected and real starting location. The search flight is expected to include information from exploratory learning of the recruits and should depend on whether the landscape experienced after release at a remote release site is more or less different from the landscape the dancer had experienced. Homing flights occur either immediately after release (rarely) or at any time during vector flight and search flight. They will not be further considered because all recruits returned home along straight and fast flights clearly different from search flights or homing flights.

Our results revealed distinct patterns of vector flights and search flights depending on the landscape context. Search flights along the gravel road diverged less from those starting at the hive, whereas flights over grassland showed greater variability dominated by more localized searching. Since an innate preference for following elongated ground structures can be ruled out as well as a search for such a learned structure at the hive, we conclude that recruited honeybees develop expectations about the landscape features they will encounter during their outbound flights based on the symbolic vector information conveyed in the waggle dance. These findings provide new insights into the cognitive processes underlying honeybee symbolic communication and navigation.

RESULTS

A small group of bees (5–8) was trained to F1r, the real feeder to the north of the hive (Figures 1A and S1). These bees (dancers) flew along a south-north-running gravel road (P1 in Figure 1). Recruits that had followed dances performed by the dancers were released either at the hive (HR) or at R1 or R2 (Figure 1). Three examples of flight trajectories are shown in Figures 1A–1C. The tests consisted of recruited honeybees released either at R1 or R2 (Figures 1B and 1C, respectively). As expected, hive-released (HR) recruits flew along this salient elongated ground structure and searched around the area of the dance-indicated location rather precisely, but no recruit landed at the feeder, and neither R1 nor R2 released recruits since no odor was applied and the feeder was just a plastic jar without a color mark. R1 was located on a rather similar, approximately south-north-running gravel road (P3), and R2 was situated at the southern edge of a large and level area of grassland (R1-released recruit, Figure 1B; R2-released recruit, Figure 1C). Also visible are the straight vector components from the release sites to the first turn of >60° (from release site to blue bar, very short in Figure 1C), the tortuous search flight (between the blue bar and the red bar), and the transition to the straight homing flight (from the red bar to the hive HR).

Vector flights

Our hypothesis about the key role of the landscape memory in recruits besides the communicated vector was examined by analyzing the flight performance first during the vector flight and then during the search flight. Vector flights are expected to be dominated by the information transmitted by the waggle dance and less influenced by the landscape structure.[5]

We first asked whether a vector flight is performed and then whether the flight characteristics (length, speed, and straightness) differ. The probability of a vector flight being performed depends on the release site. All HR bees performed a vector flight (21 out of 21), 79% (19 out of 24) of the R1-released bees, and 57% (12 out of 21) of the R2-released bees. These proportions are significantly different (chi-squared calculation: HR vs. R1 vs. R2: $\chi^2 = 12.35$, $df = 2$, $p = 0.002$). The major differences were found between the HR and R2 groups (HR vs. R2: $p = 0.008$), whereas there was no statistically significant difference between HR and R1 or between R1 and R2 (pairwise comparison: HR vs. R1: $p = 0.244$; R1 vs. R2: $p = 0.613$). It thus appears that the probability of a vector flight being performed does not differ between HR- and R1-released recruits but does differ between HR- and R2-released recruits. Even though there was no statistically significant difference between the recruits released at R1 and R2, far fewer recruits performed vector flights when released at R2, supporting the conclusion that the landscape around R1 may appear to the recruits less different from the landscape around the hive and experienced by the recruits starting at the hive (and the flights of the dancers on the way to the feeder). Note that the distance between R1 and R2 is only 185 m, so the panoramas seen at R1 and R2 should not differ greatly, suggesting that close landmarks are important.

Length, speed, and straightness of vector flights were compared across the three groups (HR-, R1-, and R2-released bees). No significant differences were found for the length, speed, and straightness of vector flight (Kruskal-Wallis test: $p > 0.05$). The flight trajectory is not strictly straight but varies within the range of 0°–60°, the latter being the angle at which, per definition, the search flight starts. Straightness was calculated by dividing the trajectory actually flown by the straight line between the beginning and end of the vector flight. HR recruits performed significantly more straight flights than R1 and R2 released recruits (Watson-William's test: $F_{2,\ 1,797} = 21.1003$, $p < 0.001$, Figure S2). There are significant differences among the three groups. Pairwise comparisons showed no difference between R1 and R2 ($F_{1,\ 1,228} = 0.0201$, $p = 0.8873$), but both R1 and R2 are different from HR (HR vs. R1: $F_{1,\ 1,243} = 38.8643$, $p < 0.001$; HR vs. R2: $F_{1,\ 1,123} = 35.2185$, $p < 0.001$; see Data S1).

Next, we quantified the density distributions of radar fixes during the vector flight (heatmaps of vector flights; Figures 2A–2C) by counting the number of fixes in concentric rings of increasing diameter around the release sites (see STAR Methods). No significant differences were found between the proportions of fixes

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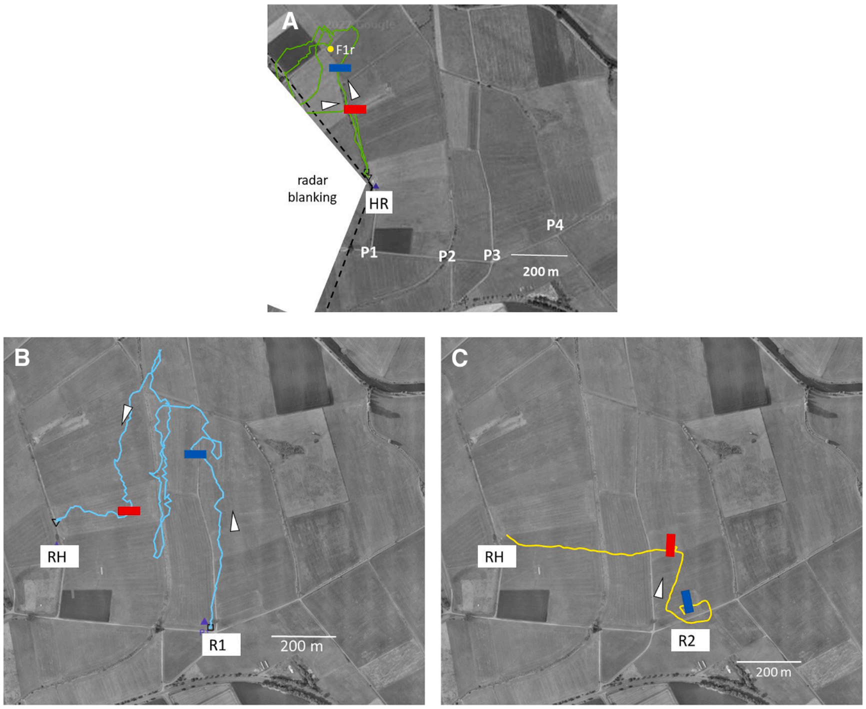

Figure 1. Three examples of recruits' flight trajectories released from different sites

(A) Example of recruit's flight trajectory released at the hive (HR, green line).

(B) Example of recruit's flight trajectory released at the release site 1 (R1, blue line).

(C) Example of recruit's flight trajectory released at the release site 2 (R2, yellow line).

The white arrowheads indicate the flight direction. The blue bar marks the transition from the initial vector flight to the search flight, and the red bar marks the transition from the search flight to the straight homing flight. The background shows an aerial view of the test area with the respective locations of the hive and radar (HR), the feeder for the dancers (real feeder F1r in A), and the release sites R1 and R2. P1–P4 mark the four gravel roads running approximately south to north. The scale bar gives the dimension of 200 m. The broken lines and the white sector in (A) show the radar scanning range with its blanking range in the west. The recruit left the scanning area twice and subsequently returned. A small river can be seen in the northeast corner.

F1r, Feeder 1 real site; F1v, Feeder 1 virtual site; F1vR1, Feeder 1 release site 1; F1vR2, Feeder 1 release site 2; EEN, east-east north; SN, south-north, RH, Radar and hive site.

in HR- and R1-released recruits (Z = 0.740, $p = 0.739$), but highly significant differences emerged between R2-released recruits and both other groups (between HR and R2: $Z = 6.354$, $p < 0.001$; between R1 and R2: $Z = 5.909$, $p < 0.001$; Figure S3; see Data S1). These differences can be traced to two effects. (1) Initially, the higher proportion of fixes results from the lack or the shortness of the vector flights (up to a radius of 180 m). (2) At greater distances from R2 (<200 m), the recruits showed a higher probability of switching to directed flights toward natural food sources close to the creek in the north (see also the heatmaps for the search flights in Figure 3). Unfortunately, we were not able to track these flights with our radar system because the natural food sources were out of range of the radar (see Figure 1).

In summary, significantly fewer recruits performed vector flights when released at R1 and R2 as compared with release at the hive. These recruits performed almost similar vector flights in length, speed, and straightness (these flight parameters are not significantly different between R1 and R2 released recruits), indicating that they recognize already during the vector flight that they are not at the hive. Although there was no significant difference between R1 and R2 released recruits in flight direction, the R1 and R2 released recruits' flights deviated in variance of bearing as compared with HR recruits. These findings support the conclusion that R1 and R2 released recruits (1) did not just perform according to the dance transmitted vector information, (2) recognized that they were not at the hive, and (3) performed partly differently depending on whether they were released at an elongated ground structure that resembled that available at the hive. The guiding effect of P3 could reflect an innate tendency to follow an elongated ground structure or an attempt to follow a salient landscape feature the dancer had experienced. This question will be studied by examining the search flights and by control experiments.

Search flights

The search period starts at the end of the vector flight and ends at the start of the homing flight (Figure 1; STAR Methods). Figure 3 shows the density distribution of radar fixes during the search period in the form of heatmaps for the three experimental groups. HR bees concentrate their search south of the dance-indicated feeder F1r, and some extend their search to regions further north than F1 and to the northeast of the feeder. We observed dances by bees other than our experimental bees that indicated a natural food source (predominantly pollen) along the south bank of a small river. It is thus likely that the recruits heading off from the hive had been foraging before at these natural food sources. Since F1r did not emit any odor and was visited by a rather small group of dancers, it is not surprising that none of the HR-released recruits landed at the feeder, corroborating earlier findings.[5] Some of the recruits released at R1 or R2 returned to the release site, as indicated by the high density around the release site, but R1-released bees searched predominantly along P3 and to a lower degree also along P2. F1v, the virtual feeder for R1-released bees, is located between P2 and P3. One R1-released bee traveled toward F1r (faint trace in Figure 3) and then back to the hive. The extensions of the searches along P2 and P3 mimic quite precisely the stretch traveled by the dancing bees along P1. This is very different in R2-released recruits. Their searches were rather close to the release site, with a slight tendency westward toward P3 and even P2. For the R2-released recruits, F1v was located on level grassland, showing a low density of search fixes, and those bees that flew further away followed P3 northward over a short distance.

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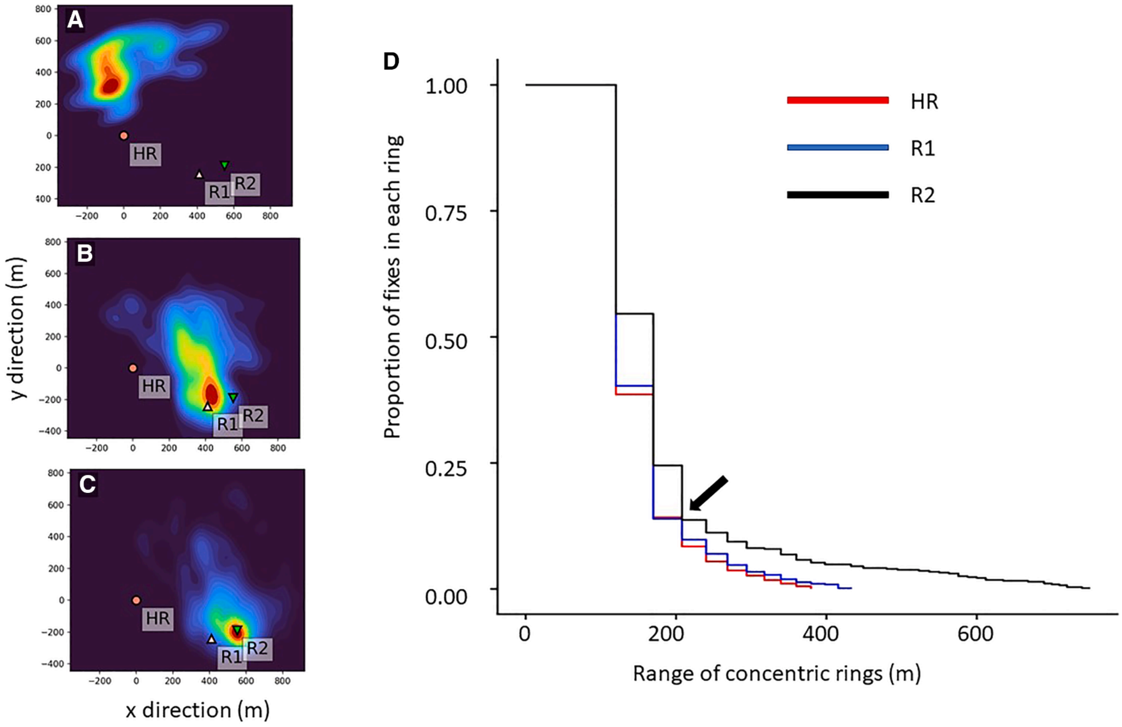

Figure 2. Heatmaps and proportions of fixes of vector flights in concentric rings around the release sites

(A–C) Density distributions of radar fixes of vector flights for hive-released recruits (A, HR), R1-released recruits (B), and R2-released recruits (C), expressed as heatmaps. The *x* and *y* axes give the dimensions of the map. The hive (HR) is depicted with a red circle, and the release sites R1 and R2 with a yellow upright (R1) or green inverted triangle (R2). The number (*N*) of recruited honeybees in the HR, R1, and R2 groups was 21, 24, and 21, respectively. See Figure 1 for the landscape background.

(D) Proportions of fixes of vector flights in concentric rings around the release sites. HR (red line), R1 (blue line), and R2 (black line). The black arrow marks the transition from short or non-occurring vector flights to directed long-range flights.

The number of trajectories and fixes analyzed are as follows: HR: 21, 570; R1: 27, 675; and R2: 21, 555. Statistics: chi-squared test (HR vs. R1 vs. R2, $\chi^2 = 50.913$, $df = 2$, $p < 0.001$). Pairwise comparison: no statistical differences between HR and R1 on their vector flight ($Z = 0.740$, $p = 0.7398$), great differences between HR and R2 ($Z = 6.354$, $p < 0.001$) and between R1 and R2 ($Z = 5.909$, $p < 0.001$).

See also Figures S2 and S3 and Data S1.

Several analyses were performed to quantify the differences in search flights between these three groups of bees (Figure 4; see Data S1). The total lengths of the search flights are significantly higher for R2-released bees, but no statistical differences appeared between HR and R1 or R1 and R2 (Kruskal-Wallis test: $\chi^2 = 10.437$, $df = 2$, $p = 0.005$; HR vs. R2, $p = 0.002$; Figure 4A), and no differences were found for the speed of search flights among the three groups ($p > 0.05$; Figure 4B). Most importantly, the search flights of the R1-released recruits were much more elongated in the direction of the dance-indicated location when the recruits were flying along the salient ground structures P3 (and P2), which ran in a rather similar direction as P1, the elongated structure experienced by the HR recruits and the dancers. So, the flight straightness was different among these three groups (Kruskal-Wallis test: $\chi^2 = 12.093$, $df = 2$, $p = 0.002$; Figure 4C). Specifically, both HR and R1 showed significant differences from R2 (HR vs. R2: $p = 0.004$; R1 vs. R2: $p = 0.003$), but no significant differences between HR and R1 ($p = 0.841$). Taken together, the three characteristics of the search flights are most different in the R2-released bees from those of the HR bees and are also partly different from those of the R1-released bees, indicating a significantly different search strategy in R2-released recruits.

Next, we applied the same analyses as for vector flights to quantify the spatial distribution of fixes as visualized in heatmaps (Figures 3 and 5). These quantifications document significant differences (Figure 5; $\chi^2 = 83.816$, $df = 2$, $p < 0.001$). The R1-released recruits performed the most elongated searches, leading to significant differences in the proportion of longest distances (HR vs. R1, $Z = 7.797$, $p < 0.001$; R1 vs. R2, $Z = -7.583$, $p < 0.001$). Significant differences were also found between HR- and R2-released recruits (HR vs. R2, $Z = 2.946$, $p = 0.009$; Figure S4). The shorter distances of the search flights undertaken by recruits from the release sites HR and R2 result from the fact that neither group of recruits searched along an elongated ground structure, but the causes of this are different. HR-released recruits search around F1r, and R2-released recruits around the release site (see Figure 3).

Control experiments

Are elongated ground structures chosen innately or spontaneously?

We first want to emphasize that recruits had no specific experience with an elongated ground structure leading to a food source. Their knowledge about the landscape came from exploratory orientation flights and potentially from foraging flights

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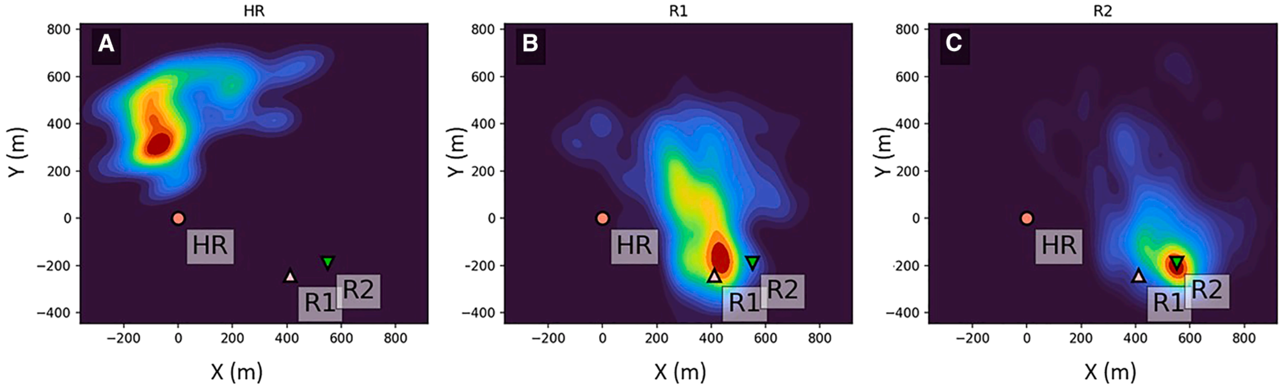

Figure 3. Heat maps of fixes of search flight released from three different sites

(A) Density of search flight fixes of bees released at HR.

(B) Density of search flight fixes of bees released at R1.

(C) Density of search flight fixes of bees released at R2.

The red dot gives the location of the hive (HR). The yellow upright triangle marks release site R1, and the green downward-pointing triangle R2. The number of recruits released at the hive, R1, and R2 was 21, 24, and 21, respectively. The *x* and *y* axes give geographical coordinates centered on HR ($x = 0$, $y = 0$) in m. North is straight upward. See Figure 1 for the landscape background.

See also Data S1.

either in the village to the west, the landscape structure being drastically different from the experimental area east of the hive, and/or small flower patches along the creek in the north. These latter patches attracted very few foragers, as indicated by the rare dances reporting them.

The question of attraction to path following by recruits, either innately or spontaneously, was addressed here by the comparison between R1 and R2 released recruits and in several already published experiments and tested with (1) foreign recruits, (2) trained foragers, and (3) young bees performing exploratory orientation flights. We have reevaluated and summarized these already published data and present the result here.

Foreign recruits

Wang et al. trained dancers in a different area than the experimental bees in the test area, and the recruits had explored the foreign area[5] (Figures 6A and 6B; Data S2). The hive in the foreign area was located 4,400 m southeast of the test area behind a hill (50.793190° N, 8.926897° E; Figure 6B). Both the ground structures and the skyline differed substantially from the conditions in the test area. The feeder for the dancers in the foreign area appeared at the same direction and distance as the feeder F2 for the experimental dancers (angle of 69°, distance of 373 m). The recruits were caught at the hive exit in the same way as in the main experiment, stored in a catching device, and transported within 20 min to one of two release sites (R2 and R5) in the test area, equipped with a transponder, and radar tracked. Release site R2 was a site north of the hive at path P1, and release site R5 was the same as R1 in the experiments reported here. The full flights are plotted as heatmaps. As one can see from the heatmaps of R2 and R5 released recruits (Figures 6D and 6E), they performed no vector flights, and their total flights were narrow without any tendency to follow a road, neither in the direction of path P1 (at R2) nor in the direction of the road at R5 (R2 or R5: distance: Wilcoxon test: $W = 703$, $p < 0.001$; angle: Watson-Wheeler test: $W = 23.419$, $df = 2$, $p < 0.001$; Rayleigh test, R2 vs. R5: 0.7354 vs. 0.8876). These results strongly support the conclusions that (1) recruits recognized immediately the mismatch between the expected release site and the experienced location and (2) did not use elongated ground structures as guides for their flight. These data are, therefore, particularly relevant to reject the possibility that recruits follow elongated ground structures innately or spontaneously because recruits were tested and the tests addressed the question of path following of recruits directly.

Recruits in the same test area

The experimental design of the experiments by Wang et al. included a control experiment relevant for our experiments.[5] Figure 6A shows that recruits had followed dancers for F2 at the south-north-stretching path P3. The feeder was reached after flying over even grassland. The recruits were released at R5 or R6. R5 was located directly at the intersection of the EEN- and SN-stretching paths. R6 lied at an SN-stretching road, a direction close to similar to path1 at the hive. R5-released recruits searched in two directions: the dance-communicated direction and the direction toward the feeder F2 (Figures 6F and 6G; see Data S3). R6-released recruits, however, searched around the release site and not along P3. These results exclude the possibility that R6-released recruits search for the hive along P3. The rather narrow search of R6-released recruits may result from the close location to F2, since flying according to the dance information would bring them further away from F2. The statistical results showed no significant differences between R5 and R6 in flight distances ($p = 0.56$) and average flight speed ($p = 0.6$), but as expected, their flights were more tortuous at R5 than at R6 (straightness: $p = 0.014$).

Trained foragers

Menzel et al. found that foragers follow elongated ground structures only if they have been specifically trained to them.[15] Several training/test conditions were explored, using both the locations of the hive or a feeder for guiding the search flights. None of these conditions can be compared with the experimental design used here because recruits were not tested.

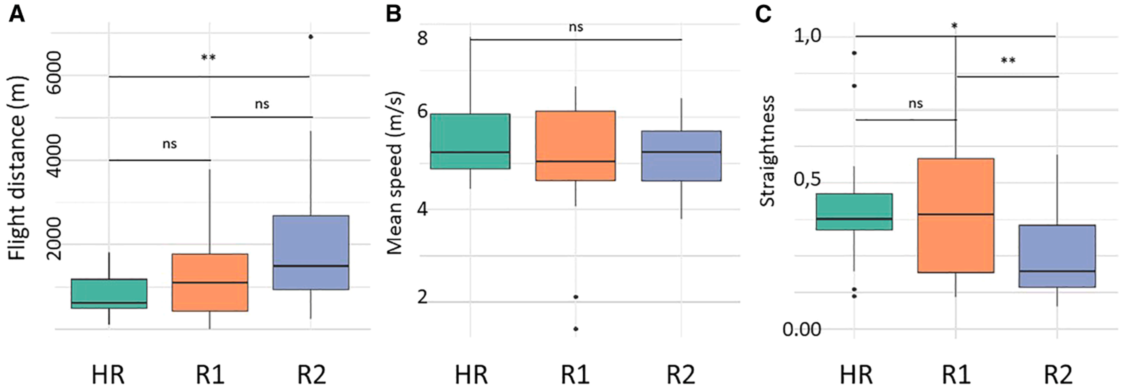

Figure 4. Comparison of three characteristics of the search flight fixes of the three groups

(A) The length of the search flights.

(B) The average speed of the search flights.

(C) The straightness of the search flights. The bee numbers of each group are HR: 20; R1: 31; and R2: 34.

Stars and ns give the significance level for the Kruskal-Wallis test followed by Dunn's test to compare the differences between HR/R1, HR/R2, and R1/R2. Significance levels: ns, no significant differences, $*p < 0.05$, $**p \leq 0.01$, $***p \leq 0.001$.

See also Data S1.

Young bees performing exploratory orientation flights

Degen et al. reported a tendency to follow elongated structures in orientation flights.[11] The test/training conditions were different in several important aspects. Importantly, the elongated ground structures appeared in a pattern of multiple parallel lines, and the tested bees explored the environment in multiple orientation flights. We documented that bees learn landscape features during orientation flights.[16]

Taken together, we can reject the possibility that recruits tested here are innately or spontaneously guided by elongated ground structures. We can also exclude the possibility that they searched for the hive before they flew straight back to it after completing their search.

DISCUSSION

Any process of communication raises the fundamental question of whether the received message is integrated into the knowledge of the receiver, and if so, how. The reproduction of the message by the receiver depends on innate and possibly learned decoding mechanisms, which the receiver computes together with the signals that it receives from the sender. Recruits starting at the hive perform intriguingly precise searches at the dance-indicated location[7,15] that are more focused than expected from the variance of the dance.[17] To unravel the decoding processes, one needs to inquire about the question, as we have done here, of whether a recruit recalls stored spatial information while decoding the information in the dance. Indeed, recruits control their search flights not only in relation to the egocentric vector information (flight instructions regarding the vector of the outbound flight) but also according to the memory that they have acquired during exploratory orientation flights[5] (see Menzel[7]). The latter is reflected in novel shortcuts within a reference system that stores spatial relations, a paradigmatic test condition in research on animal navigation.[18] Thus, the decoded dance message is embedded in and retrieved from a map-like spatial memory. Such a conceptual frame raises the question of whether recruited honeybees expect landmark features that the dancer has experienced and about which the recruit is informed by its exploratory orientation (and possibly foraging) flights.

Several essential requirements must be met in the design of the experiments to rule out more elementary explanations. (1) The landscape feature experienced by the dancer (here: the north-running gravel road) must be a salient landscape structure that is not innately chosen and has not been learned by the recruit during foraging flights before dance-following. (2) The landscape selected for the tests should allow for generalization of the selected landscape feature at a different geographical location (generalization and transfer). (3) The data collected about the recruits' flight behavior should not be susceptible to biased interpretations and must be highly informative. (4) Since the hive was located at a gravel road, one needs to exclude the possibility that recruits are motivated to directly spot the hive rather than applying the dance information. (5) Control experiments are required to exclude also the possibility that the selected landscape feature experienced by the dancer is innately or spontaneously chosen by the recruit.

The first requirement is addressed in our study by proving that elongated ground structures such as the north-running gravel road need to be learned and are not followed by innate behavioral routines. Menzel et al. and Bullinger et al. showed that elongated ground structures guide the flights of foragers only if they have been specifically trained to follow them.[15,19] Wang et al. found that recruits did not follow an elongated ground structure if the dancer had flown over level grassland.[5] The grassland in the test area (see aerial view in Figure 1) was frequently cut by farmers, and natural food sources were scarce and restricted to small patches along a creek to the northeast of the hive. The experiments reported here were thus carried out in a landscape that addressed requirement 2. Several almost parallel north-running gravel roads with areas of grassland between them allowed us to select the two release sites for the recruits such that they either closely resembled the condition the dancer had experienced with respect to the gravel road (R1), or they did

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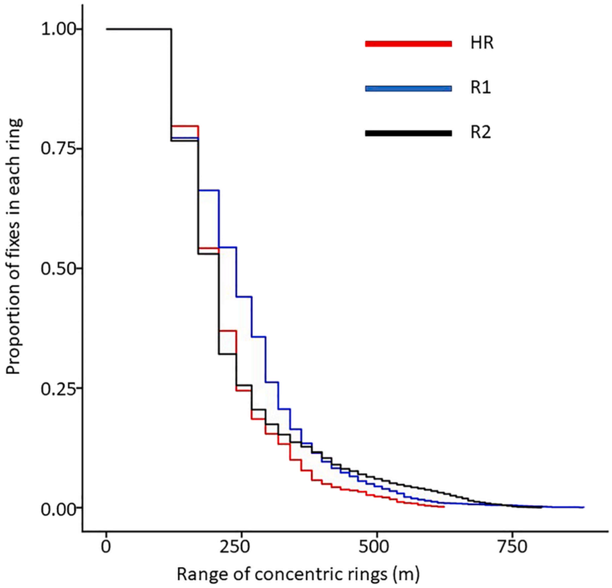

Figure 5. Proportions of fixes of search flights in concentric rings around the respective centroids: HR (red line), R1 (blue line), and R2 (black line)

The numbers of trajectories and fixes analyzed are as follows: HR: 20, 1,031; R1: 31, 2,578; and R2: 34, 4,827. Statistics: chi-squared test (HR vs. R1 vs. R2, $\chi^2 = 83.816$, $df = 2$, $p < 0.001$). R1-released recruits perform the most elongated searches, leading to significant differences in the proportions of longest distances (HR vs. R1, $Z = 7.797$, $p < 0.001$; R1 vs. R2, $Z = -7.583$, $p < 0.001$). Significant differences were also found between HR- and R2-released recruits (HR vs. R2, $Z = 2.946$, $p = 0.009$).

See also Figure S4 and Data S1.

not (R2). Requirement 3 was met by using harmonic radar to track the flights of the recruits with a high degree of temporal and spatial resolution.[13,20] Requirement 4: by far most of the recruits were not motivated to fly toward the hive when released. Those few who performed no vector flights and no search flights but rather flew straight back to the hive. These recruits were excluded from our analyses (as pointed out in the STAR Methods section). Furthermore, all experimental recruits flew toward the hive after performing vector and search flights. These homing flights were fast and straight and not guided by the paths. These homing flights were not included in the analyses presented here. Requirement 5 was addressed by specific control experiments (see control experiments). The landscape conditions made it possible to address the question of whether dance-following may incorporate the retrieval of memories of landscape characteristics on the part of the recruits. This memory stems from exploration undertaken prior to foraging and possibly from foraging experience,[11,16] the latter being less likely because of the lack of natural food sources north of the hive.

The recruits' flight trajectories were split into three phases: the initial straight and fast vector flight reflecting the vector information from the dancer, the tortuous search flight, and the straight homing flight. The probability of a vector flight being performed was found to be lower in R2-released recruits (57%) than in HR (100%) or R1-released recruits (79%). Vector flights of R1- and R2-released recruits differed significantly from HR recruits in flight length, speed, and straightness. These flight characteristics were not significantly different between R1 and R2 released bees. The dominant effects in vector flight behavior are their differences to the HR behavior, indicating that they recognized the different release site, but differences also appear between the two release sites. Overall, releasing recruits at two unexpected release sites significantly changes their vector flights, corroborating earlier findings that vector flight performance differs in accordance with differences between the area around the hive and the area around the unexpected release site.[5]

The large differences in the distributions of search flight fixes for the three release sites are well illustrated in false-color heatmaps (Figure 3). The quantitative analyses presented in Figure 5 document these differences. Overall, the R1-released recruits searched along P2 and P3 and got much closer to their virtual feeder location F1vR1 than the R2-released recruits got to their virtual feeder F1vR2 (Figure 4). Correspondingly, the distances from the search flight fixes to the release site are significantly shorter for the R2-released recruits. Several additional observations support the conclusion that the R1-released recruits expect the dance-indicated feeder at P2 and/or P3 at the distance indicated by the dance: (1) the switch from P3 to P2 and the flight of one R1-released recruit toward the real feeder F1r additionally indicate that the real feeder is expected to lie west of the paths P3 and P2. (2) If the R2-released recruits fly further away from the release site, they switch over to P3 and fly along this path. Note that there is a path P4 to the east of the grassland over which the R2 recruits searched (see aerial view in Figure 1), but this path is not chosen (Figure 3).

The differences in search characteristics between R1 and R2 released recruits support the conclusion that flights along paths P2 and P3 in R1 released recruits result from the exposure to these south-north-stretching paths at R1. However, it might well be possible that recruits (as well as naive or trained bees) might prefer to fly along elongated ground structures, a behavior that will not be seen in R2 released recruits because there is no such structure close by. We controlled for this possibility in earlier studies and included these controls with additional analyses here. The most informative data come from an experiment carried out by Wang et al., which trained dancers in a foreign area in a similar way as here.[5] The recruits had explored the foreign area that lacked elongated ground structures close to those in the test area (Figures 6A and 6B). The recruits were transferred into the test area and released at two release sites, one being identical to the one used here (R1 here was the same location as R5 for the foreign recruits). The other release site for the foreign recruits was a novel release site (R2) located on the same gravel road as the hive. The full flights of the foreign recruits were analyzed because no vector flights were seen. No hints were found that they followed the paths in the test area (Figures 6D and 6E).

Wang et al. trained dancers to a feeder (F2; Figure 6A), which they reached after flying across even large grassland.[5] The F2 recruits were released at several release sites, two of which (R5 and R6) provide data that serve as controls for our experiments reported here. The search flights of R5-released recruits were stretched along the dance-communicated direction and path P3, the south-north-stretching path at which the feeder F2 for the dancers was located. R6 released recruits searched around the release site and not along P3.

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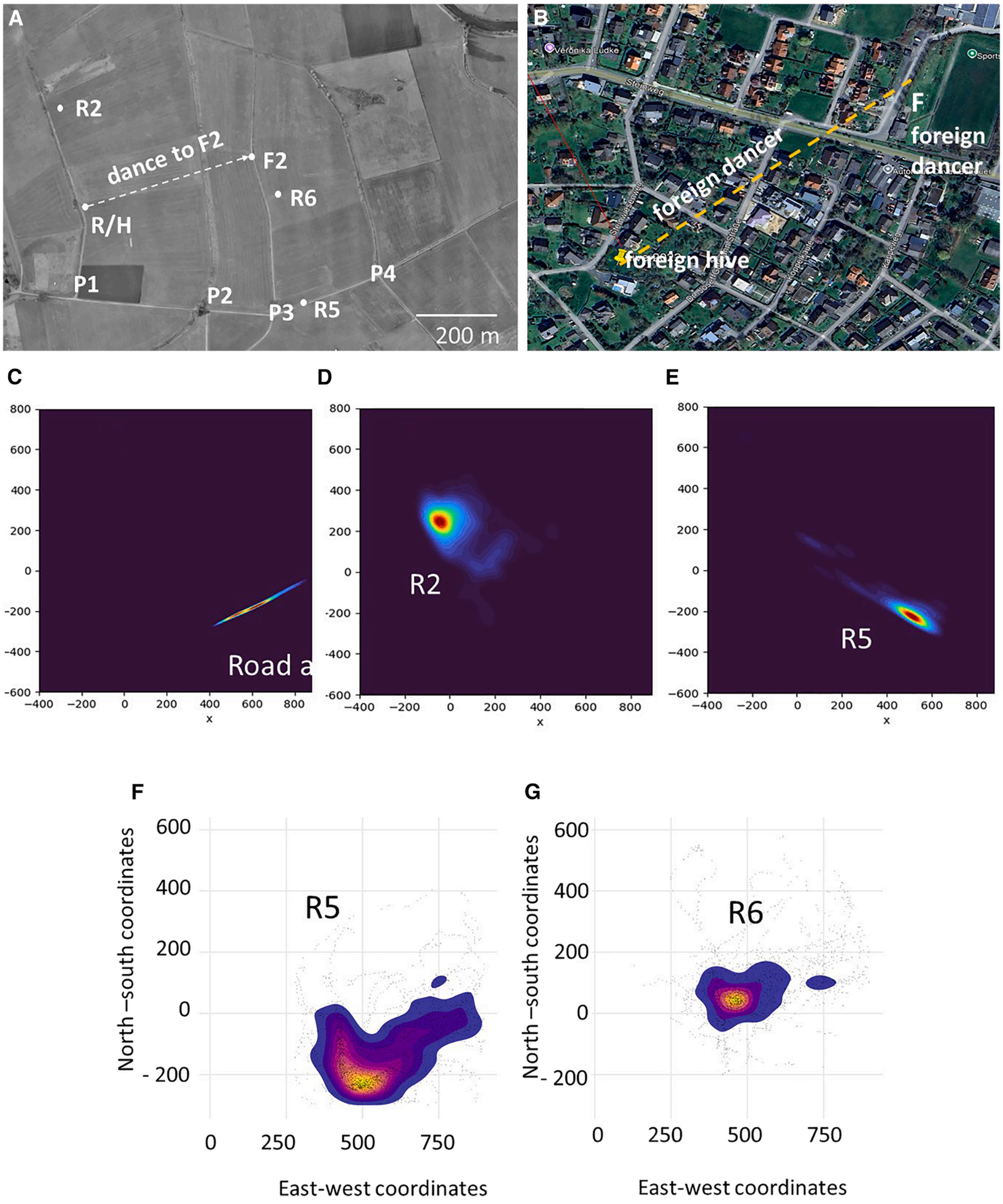

Figure 6. Design of the experiments with foreign recruits

(A) Layout of the experiments in the experimental area. RH: hive, F2: feeder of the dancers, and R5 and R6: release sites of the recruits. Notice that R5 is the same release site for the recruits in the study here and the foreign recruits. See also Data S3.

(B) Foreign area. The hive and the feeder appeared in the same direction and distance as for the recruits tested in the experimental area. The foreign recruits had explored this area as the experimental bees had in their area. The foreign recruits were tested in the experimental area.

(C) Heatmap of a radar transponder carried by an experimenter along the road at R5 as a marker for the directional stretch of the road at R5.

(D) Heatmap of the full flights of foreign recruits released at R2. Notice that R2 lies at the northwest-stretching P1 road.

(E) Heatmap of the full flights of foreign recruits released at R5. Notice that the flights are not stretched along the road. The heatmaps in (D) and (C) include both the vector and the search flight components (full flights). R2: *N* = 20, *n* = 1,421; R5: 29, *n* = 458 (*N*, number of recruits; *n*, number of radar fixes).

(F and G) Heatmaps of search flights of F2 recruits that were released at R5 (F: *N* = 33, *n* = 3,287) or at R6 (G: *N* = 29, *n* = 2,241). Notice that recruits released at R6 do not fly along P3, excluding the possibility that they search for the hive.

See also Data S2 for (C)–(F).

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Additional data are relevant in this context. Menzel et al. and Bullinger et al. found that foragers need to be specifically trained to follow elongated ground structures.[15,19] Degen et al. reported a tendency to follow elongated structures in orientation flights.[11] This effect can be tracked to learning during exploratory orientation flights and does not reflect a spontaneous or innate tendency to follow elongated ground structures.[4]

In conclusion, our experiments addressed the question of whether the vector information conveyed by the dance is integrated into a recruit's spatial representation—constructed from its own experience—and whether this integration occurs within a common frame of spatial reference shared by both the reported symbolically communicated vector and self-experienced locations. We took advantage of the layout of a landscape with almost parallel gravel roads running from south to north. The recruits performed more extended vector and search flights if they were released on a gravel road running in the same direction as the road along which the dancer had flown, as compared with a release site from which they flew over level grassland. This behavior cannot be explained by an innate or spontaneous tendency to follow a salient elongated ground structure or by previous learning of this elongated ground structure on the part of the recruits. The recruits thus develop an expectation about the landscape that they will fly over when applying the dance instruction. This expectation appears to be based on a memory retrieval process in the recruit during the communication process. In our view, the cognitive structure of the retrieved memory is most adequately conceptualized as a cognitive map, given the results from multiple experiments on navigation and on decision-making in the context of waggle-dance communication (recent reviews Menzel[7] and Jeffery et al.[18]). By revealing the interplay between symbolic communication and spatial memory, our work advances the understanding of the complexity of honeybee navigation and highlights the waggle dance as a multifaceted form of communication.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and for resources and data should be directed to and will be met by the lead contact, Randolf Menzel (menzel@neurobiologie.fu-berlin.de).

Materials availability

This study did not generate new, unique reagents.

Data and code availability

- All data have been deposited in the supplemental information: Data S1, S2, and S3.
- All original code has been deposited: not relevant.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Z.W.: performed experiments, analyzed data, and worked on drafts. J.M.: analyzed data, wrote scripts for statistical analyses, and created figures. X. C.: organized data, worked on figures and statistics, and worked on figures and drafts. R.M.: designed, supervised, and performed the experiments and wrote drafts and the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- METHOD DETAILS
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    - ○ Radar tracking
    - ○ Analyses of flight trajectories
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
All numerical data used in this paper	The authors of this paper	See supplemental information
Experimental models: Organisms/strains		
Apis mellifera	The honeybee colonies were kindly provided by Dr. R. Büchler, Bieneninstitut Kirchhain	https://llh.hessen.de/bildung/bieneninstitut-kirchhain/
Software and algorithms		
R	R version 4.4.2	https://www.r-project.org/
RStudio	2024.09.1 Build 394	https://posit.co/downloads/
Other		
Radar transceiver	NSC 2525/7 XU	Raytheon Marine GmbH, Kiel.
Transponder	Prepared by authors of this paper	Schottky diode HSCH-5340.

EXPERIMENTAL MODELS AND SUBJECT DETAILS

The honey bee, *Apis mellifera*, was used in the experiments.

METHOD DETAILS

Experimental site, honeybee colony

The experimental site was a highly structured agricultural landscape with grass fields stretching to the east of the area scanned by harmonic radar, with trees and bushes, pathways, and creeks close to the village of Großseelheim (Germany, hive and radar location at: 50°48’50.11” N, 8°52’21.32” E). The experiments were performed in the late summer and autumn when natural food sources were scarce, with only a few patches of flowers along the narrow river to the north of the hive. The grass area dominating the landscape in which the recruits were tracked was regularly cut by the farmers and lacked any natural food sources. The bee colony was placed close to the radar near a gravel road (P1) running south to north, parallel to the east-facing edge of the village that was outside the scanning region of the radar (Figure S1). The colony was housed in an observation hive with approximately 3500 animals. Between 1500 and 2000 foragers were individually marked with number tags. Trained foragers to feeder F1r were additionally marked with a white dot on the abdomen, allowing us to identify immediately whether the respective dance was performed for the feeding site F1r (the real feeder F1, distance: 431 m, direction with respect to N 344°). A complete protocol was established at the feeder and no other than the few individually marked foragers serving as the dancers visited the feeder. The feeder was a small plastic jar standing on a photo-tripod. No odor or color marks were used. None of the HR recruits landed at the feeder corroborating that the artificial design of the feeder made it unattractive to the recruits. The dance-following bees, here referred to as recruits, were identified by their individual numbers. They have explored the landscape around the hive but did not visit the feeder for the dancers. Exploration leads to learning of the landscape features.[16] They may have foraged far out the radar scanning range but not within the radar range because no natural food sources appeared within the radar range. When one of them left the dancer after following it for several rounds and then headed for the exit, its number was announced to a person standing in front of the hive. This bee was then captured, stored in a veil in the dark for a short time, and then equipped with a radar transponder and released at the hive exit (hive-released bees) or brought in a dark box to one of two release sites within 10 min and released there. Each recruit was tested only once. All the recruits returned successfully to the hive and were removed from the colony. Only few recruits flew back straight to the hive when released and did not perform vector flights or search flights. These few bees were not included in our analyses. The dancers foraging at the feeding site continued flying to the feeding site during the experiments with the recruits. Since no odor was used at the feeder and only few dancers were foraging at the feeder it can be excluded that odor from the feeding site was detected by the recruits. A control for this conclusion comes from the tests with foreign recruits (see Control Experiments). These recruits were tested during periods in which the dancers in the test area foraged at the feeder. These control bees showed no tendency to fly to the feeder.

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Radar tracking

Tracking bees by harmonic radar was carried out as previously described.[13] We used a system with a sending unit consisting of a 9.4 GHz radar transceiver (Raytheon Marine GmbH, Kiel, NSC 2525/7 XU) combined with a parabolic antenna providing approximately 44 dBi. The transponder fixed to the thorax of the bee consisted of a dipole antenna with a low-barrier Schottky diode HSCH-5340 of centered inductivity. The harmonic component of the signal (18.8 GHz) was the target for the radar. A 60 MHz ZF-signal was used for signal recognition, leading to a fixing every 3 s of the bee carrying the transponder. The transponder weighed 10.5 mg and was 11 mm in length. We used a silver or gold wire with a diameter of 0.33 mm and a loop inductance of 1.3 nH. The range of the harmonic radar was set to 0.5 nautical miles in most experiments. The raw radar output was captured from the screen at a frequency of 1 Hz, stored as bitmap files, further analyzed offline by a custom-made program that detected and tracked radar signals (fixes) and converted circular coordinates into Cartesian coordinates, taking into account multiple calibration posts in the environment. Finally, the fixes were displayed on a calibrated geographical map.

Analyses of flight trajectories

Segmentation of flight trajectories

recruits performed flights composed of three sequential segments: the straight outbound vector flight (the rhumb line as learned from dance communication), the tortuous search flight, and the straight inbound homing flight. Homing flights were not included in our analyses here since all the recruits returned home on fast and straight flights after their search flights (see Wang et al.[5] their Figure 1B and Figure 1 A, B, C). The transitions from the vector flight to the search flight and from the search flight to the homing flight were characterized by a sharp turn of ≥60°, preceded by a straight stretch in the transition to the search flight and followed by a straight stretch in the transition to the homing flight. The vector flight was thus the initial part of the flight until the first sharp turn, and the search flight was the part between the end of the vector flight and the beginning of the homing flight. The segmentation was carried out using a custom-made algorithm. The x, y, t values of the flight fixes for the flights are given for each recruit separately in the Data S1, S2, and S3.

QUANTIFICATION AND STATISTICAL ANALYSIS

A chi-square test was applied to examine the frequency of bees perform vector flights. The flight characteristics, distance, speed and straightness, were first assessed of normality within each group using Shapiro-Wilk tests and homogeneity of variances using Levene's test. Kruskal-Wallis tests were used to compare flight characteristics among HR, R1 and R2, Dunn's tests were used as post hoc tests to compare between each two groups of HR, R1 and R2. Student t-tests were used to compare the flight distances, speed and straightness if there were only two groups, such as in our control experiments between R5 and R6. Rayleigh tests were used to determine the angular distribution of vector flight. Circular analysis was performed on radians calculated angles from each fix of the vector flight to the release site and then northward. Watson-Wheeler tests were used to determine the angle differences in vector flights between the HR, R1 and R2 groups.

Quantifications of heat maps and comparisons between heat maps of the vector and search flight fixes of recruited honeybees released at the hive, R1 and R2 were performed as follows. The distributions were compared by determining the quantity of fixes in concentric rings around the respective release site. The area in each ring was the same and was equal to the area around the release site with a radius of 120 m. These data were used to determine trends in the proportions along the rings, first applying multivariate Cox PH models separately for the dance and the recruit data. A survival analysis with a Cox regression[21] was applied to the decreasing trends in the number of dance vector endpoints and search fixes that fell in each concentric ring.