



Honey bees infer source location from the dances of returning foragers

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Honeybees (*Apis mellifera carnica*) communicate the direction and distance to a food source by means of a waggle dance. We ask whether bees recruited by the dance use it only as a flying instruction, with the technical form of a polar vector, or also translate it into a location vector that enables them to set courses directed toward the food source from arbitrary locations within their familiar territory. The flights of recruits captured on exiting the hive and released at distant sites were tracked by radar. The recruits performed first a straight flight in approximately the compass direction indicated by the dance. However, this “vector” portion of their flights and the ensuing tortuous “search” portion were strongly and differentially affected by the release site. Searches were biased toward the true location of the food and away from the location specified by translating the origin for the danced polar vector to the release site. We conclude that by following the dance recruits get two messages, a polar flying instruction (bearing and range from the hive) and a location vector that enables them to approach the source from anywhere in their familiar territory. The dance communication is much richer than thought so far.

Apis mellifera | waggle dance | vector communication | landmark guidance | cognitive map

Honeybees (*Apis mellifera carnica*) are the only nonhuman animals that communicate navigational information by a symbolic form of information transfer, the waggle dance, which is performed by successful returning foragers to indicate the direction and distance of the food. The dance is performed on a vertical surface inside the hive out of sight of the sun and surrounding terrain. It takes the form of a figure 8 lying on its side. Where the two loops converge, the dancing forager makes a waggle run. The angle of that run—the tilt in the 8 relative to the horizontal—is the solar bearing of the food source from the hive. The number of waggles and the duration of the waggle run are proportional to the distance of the source.

Because the sun's compass direction may change by more than 40° within an hour, the solar bearing rapidly becomes useless. In interpreting the dance, recruited foragers convert the solar bearing to a compass bearing by reference to a previously learned solar ephemeris function. The ephemeris function gives the location of the sun above the horizon panorama as a function of the time on the bee's circadian clock. It varies with both latitude and season. Thus, in conventional navigational terminology, the dance communicates the rhumb line to food from the hive (1, 2). Rhumb lines are origin-specific polar vectors. They are useless for navigation when the navigator is not at that origin. This analytic truth is the foundation of our experimental design: We displace recruits from the hive to release locations far from the hive in different compass directions, so their vector flight does not begin at the danced origin.

Dance-recruited bees also use previously acquired knowledge about the environment to navigate efficiently and adaptively between multiple locations (3–5). This knowledge consists of a memory of the outbound polar vectors between the hive and previously visited food sources, picture-like memories of the immediate surrounding of the nest and the places where food has previously been found, and memories of the sky-line profiles (panoramas). They also learn the olfactory, gustatory, and visual (color, geometric) features of the sources (6, 7). Thus, multiple features of the landscape and the properties of previously visited food sources are stored in memory.

Two questions arise from these findings: 1) Are the multiple components of navigational memory composed in their geometric relation, that is, in the form of a map constituted of location vectors? Location vectors enable the setting of a course to one location from any other location on the same map. 2) Do the memories that enable navigation within the familiar environment play a role in a recruit's interpretation of the dance? These two aspects have not been previously addressed together: The possibility that interpretation of the dance makes reference to stored terrain information has not been previously considered, let alone experimentally demonstrated.

Significance

Whether even humans form mental maps has excited controversy for a century because it bears on the level of abstraction from sensory experience at which the computations underlying behavior operate. The dance of the returned honeybee forager conveys the direction and distance of the food source from the hive—on the surface, a simple flying instruction. However, a majority of recruits captured and released far from the hive gravitated eventually toward the true location of the food source, implying that they had inferred its map location. Map locations enable the setting of a course from one location to another within the same frame of reference, even when neither location has distinguishing sensory features nor previous motivational significance.

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Here, we introduce a new method in which bees recruited to a source they have never visited are displaced far from the hive before they fly the danced vector. Thus, when they fly the danced vector, they see terrain they would not see when flying from the hive, a condition not previously tested. And, when they terminate the vector portion to begin the tortuous search phase, they are in terrain far removed from where they would be had they flown from the hive. Thus, the search phase begins hundreds of meters from where it would ordinarily begin, at a location not arrived at by flying from the hive—another condition not previously tested. To steer toward the source location during their search phase, a recruit must set a course from this unexpectedly-arrived-at location toward a not-previously-visited source location. This enables us to test the essential feature of map-based navigation: The map enables the setting of a course from any location within the mapped terrain to any other location within that terrain, whether or not they have been previously visited or arrived at by dead reckoning (aka path integration) from a known location. Path integration yields a representation of the navigator's current location relative to its starting location by summing successive displacement vectors or, if the process is conceptualized as continuous, then by integrating the velocity vector.

We track the flights of the displaced recruits with a harmonic radar. This technique has been successfully used to prove symbolic information transfer in the waggle dance (3). The recruits started not only at the hive entrance (the control condition) but in a catch-and-release design also at other sites within the explored area around the hive.

Results

Experimental Design and Flight Trajectories. Recruited bees were observed while they attended dancers that advertised for an artificial feeder at a location within the hive's foraging territory (denoted by F, see Fig. 1). When the recruit appeared at the hive entrance, a radar transponder was glued to her thorax. After release (either at the hive or at a distant release site) her flight trajectory was followed by harmonic radar with radar fixes every 3 s. Recruits had never found food at F (including natural food, see *Materials and Methods*). Therefore, they did not have vectors pointing toward F—neither from the hive nor from surrounding landmarks. Nor did they have source-location-associated horizon profiles to steer them toward it from elsewhere in their foraging territory.

As expected from previous research (3), both hive-released recruits and displaced recruits first performed a straight flight in roughly the direction indicated by the dance after departing from the release site (vector flight). This was followed by a tortuous search (the search phase) prior to returning to the hive (Fig. 1 *B* and *C* and *SI Appendix*, Fig. S1). The transitions from the vector flight to the search and from the search to the homing flight were identified by a sudden turn between two consecutive radar fixes of $>60^\circ$ after a long straight flight from the release site or immediately preceding a straight return flight (*Materials and Methods*). Recruits were released not only at the hive entrance but also at five other locations (Fig. 1 *A* and *C*; R1, R2, R5, R6, and R7). Homing flights are not considered further here because all recruits returned successfully home along direct flights at the end of the search phase. By design, the danced location had no features indicative of food; for which reason, most recruits released at the hive (the control group) failed to find it.

Release-Site-Dependent Perturbations of the Vector Flights.

We parameterized the outbound vector by i) the compass bearing of the line from the first (f_1) to the terminal fix (f_t) in the vector fix sequence, ii) the length of this line, iii) the speed with which the outbound vector was completed [$\text{length}/(t(f_t) - t(f_1))$], and iv) its straightness [$\text{length}/(\text{sum over interfix segment lengths})$]. Releases from sites other than the hive substantially altered these parameters (Fig. 2). They also greatly altered the locations relative to F and vF where the outbound vectors terminated (Fig. 3). The patterns of alteration differed dramatically depending on the release site, hence, on the terrain the recruit observed during the vector flight (Fig. 3). Therefore, these perturbations cannot be attributed to any factor that would be the same for any displaced release site, such as a failure to observe an expected horizon profile when flying the danced vector. Control recruits from another far distant hive released at R2 and R5 mostly flew around in the immediate vicinity of the release site and then disappeared (Fig. 4, *Bottom* two panels). Their "outbound" vector flights were few and short. In short, we find that whether the vector flight occurs and its parameters when it does occur depend strongly on the terrain over which it is made.

The site-dependent disruptions of the outbound vector flights and their dependence on familiarity with the test area imply that a recruit's construal of the dance gives her access to information about what she should and should not see while flying the danced

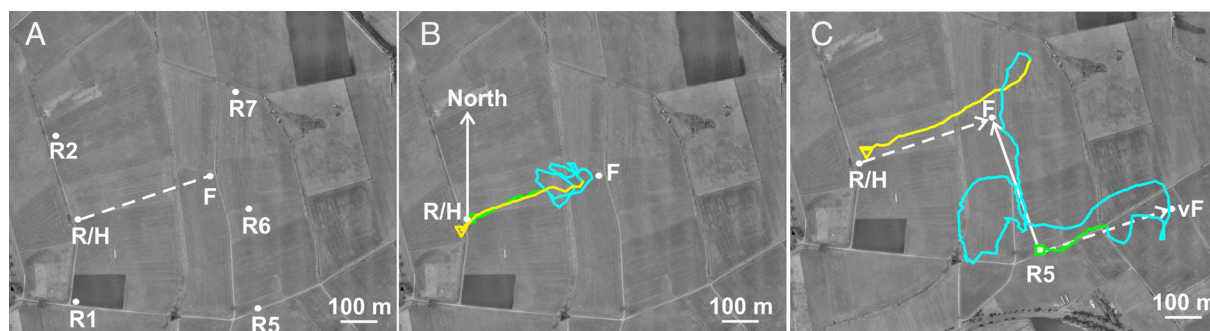


Fig. 1. Experimental design and flight trajectories. (A) Experimental area. R/H: radar and hive location; F: the feeder for the dancing bees; release sites: R/H (hive release), R1, R2, R5, R6, and R7. The dashed line gives the polar vector (rhumb line) to F communicated by the dancer (range: 384 m, compass bearing: 60°). (B) Flight trajectory of a recruit released at the hive. The green square marks the beginning of the flight and the yellow triangle the end of the flight. (C) Flight trajectory of a recruit released at R5. Notice the initial vector flight (green) toward the virtual feeder location, vF, the search flight (blue) composed of the return flight to the release site a circle to the northwest of the release site, a direct flight toward and over the real feeder F, and the homing flight (yellow). The dashed arrows mark the rhumb lines toward F from R/H and from R5 to vF. The solid arrow from R5 to F marks the shortcut from the release site to the true source.

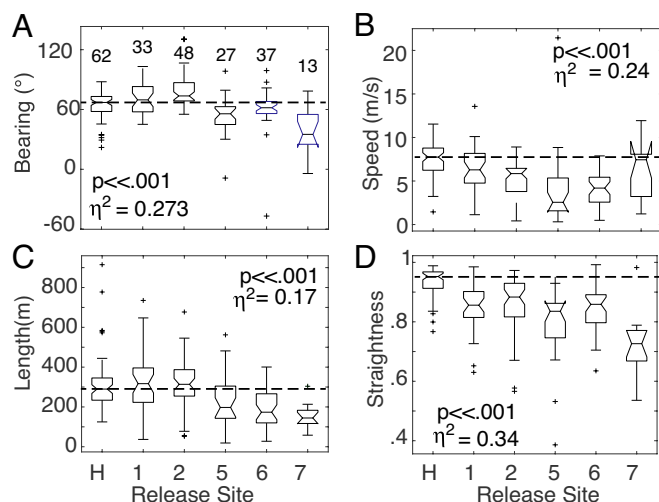


Fig. 2. Effects of release site on parameters of the outbound vector flights (box plots from one-way Matlab™ ANOVAs). Boxes indicate the quartiles of the distributions; whiskers indicate the limits of the data not taken to be outliers; pluses denote outliers. Dashed horizontal lines are at medians for hive-released bees. $p = p$ returned by one-way ANOVA. η^2 = effect size (fraction of the variance accounted for by the variation in release site). Numbers above the boxes are the n's. (A) As expected from prior work (3), displaced recruits flew in roughly the same direction as the hive released bees (dashed line), but with systematic release-site dependent deviations. (B) Regardless of release site, displaced recruits flew more slowly. (C) Recruits released east of F aborted (shortened) their vector flights. (D) Regardless of release site, displaced recruits flew more crooked vectors (for plots of the vector fixes see *SI Appendix, Fig. S1*).

vector. That in turn implies that the dance communicates more than a simple flying instruction.

While our methods guaranteed that a displaced recruit had not previously found food at the danced location, they did not rule out the possibility that at least some recruits had visited some landmark in the general vicinity of the food source and then flown directly back to the hive from that landmark, storing in memory the displacement vector between the hypothesized landmark and the hive. One could amend the just-a-flying-instruction interpretation of what the dance communicates by postulating that displacement vectors prime the recall from memory of the characteristics of the landmarks with which they are associated. This hypothesis does not, however, explain the release-site specificity of the perturbations in the vector flights. Regardless of where displaced recruits were released, they failed to see the horizon panorama they would have seen had they not been displaced and they failed to see the terrain between the hive and the food source. The perturbations of the vector flights depended strongly not only on what the displaced recruits did not see but also on what they did see, which implies that they had expectations about what they would see.

Search Phase Statistics. There is an extensive experimental and theoretical literature indicating that searches efficiently survey terrain centered on an initial estimate of the location of a sought-for goal (e.g., the nest, for a homing ant) (8, 9). If all a recruit gets from the dance is a flying instruction, then the searches of the displaced recruits should look like those of the hive-released control group but centered on the terminus of the H→F vector when the origin of this polar vector has been translated to the release site. We call these termini the virtual food locations (vF).

The Fig. 4 plots the search-phase fixes from the bees in eight groups (six released in their foraging territory and the two control groups composed of recruits unfamiliar with the foraging territory—see *Materials and Methods*). Although the fixes of the control group surround F (*Upper Left* panel in Fig. 4), the fixes of the

recruits released to the east of F fall almost entirely to the west of vF. Thus, the flying-instruction-only hypothesis fails at the group level; the distributions of search fixes from displaced recruits dramatically depart from the spatial relation to the vF that is expected given the relation of the control-group fixes to F. See also *SI Appendix, Fig. S2*, which plots the centroids of the search fixes.

As may be seen in the publicly available movies of the individual search-fix sequences (*OSF*), the rhumb-line-only hypothesis also fails at the within-group level and the within-search level.

Within-Group Failure: Different recruits released at the same site make very different searches (see *Movies*).

Within-Search Failure: In different phases of her search, a recruit often directs it to different locations (F, vF, and the release site, RS, see *SI Appendix, Figs. S3–6* and *Movies*). Thus, the assumption that a search has a single center is often false; the early phase of a search may be directed to vF, a later phase back to RS, and a still later phase (or phases) to F (see for example, Fig. 1C).

The simplest test of the hypothesis that recruits direct their search as much toward the true location of the food as to its virtual location is to compare their closest approaches to the two putative goals. To do that, we subtracted for each search the closest approach to the food, denoted CA_F , from the closest approach to vF, denoted CA_{vF} . When a recruit approached the true location, F, more closely than the virtual location, vF, the sign of $CA_F - CA_{vF}$ is negative. The absolute value of the difference, $|CA_F - CA_{vF}|$, tells us how much closer. Substantial fractions of the recruits in groups R1, R2, R5, R6, and R7 got closer to F than to vF (Fig. 5A)—17%, 28%, 45%, 69%, and 94%, respectively. In the groups released at R6 and R7, 24% and 38% of the bees got more than 200 m closer to F than to vF. Importantly, a majority of the closest approaches to F made by displaced recruits fell within the range of closest approaches made by recruits released at the hive (Fig. 5B). Thus, bees released in different compass directions and hundreds of meters away from the hive more often than not approached the true location of the food as closely as did many of the control bees released at the hive. The tendency to approach F more closely than vF during their searches was particularly marked in the recruits released east of F, even though their vector flights carried them toward vF and away from F.

The large difference in Figure 4 between the eastward orientation of the searches by recruits released west of the hive and the westward orientation of those released to the east of F is readily understood when one realizes that the terrain seen by recruits flying from H, R1, and R2 confirmed that they were flying in the general direction of F (because F lay within a compass sector of 45° to the east of those three release sites); whereas the terrain seen by recruits flying east toward vF from R5, R6, and R7 implied that they were flying away from F (because F was west of those three release sites, hence behind the recruits flying eastward from them). This explanation, however, assumes that the displaced recruits had inferred the longitude (relative to the hive) of the danced source and that they were also able to estimate their longitude (again, relative to the hive) at some point after they had aborted their vector flight and begun their search. Recruits that could only follow the flying instruction conveyed by the dance without reference to remembered geometric information could not determine their longitude relative to the hive and to F. They could only find a familiar landmark and use its associated home-vector to fly back to the hive or toward a location where they had previously found food. Thus, a melding of landmark-associated home vectors and vectors based on current dead reckoning (10) would not steer displaced recruits toward F.

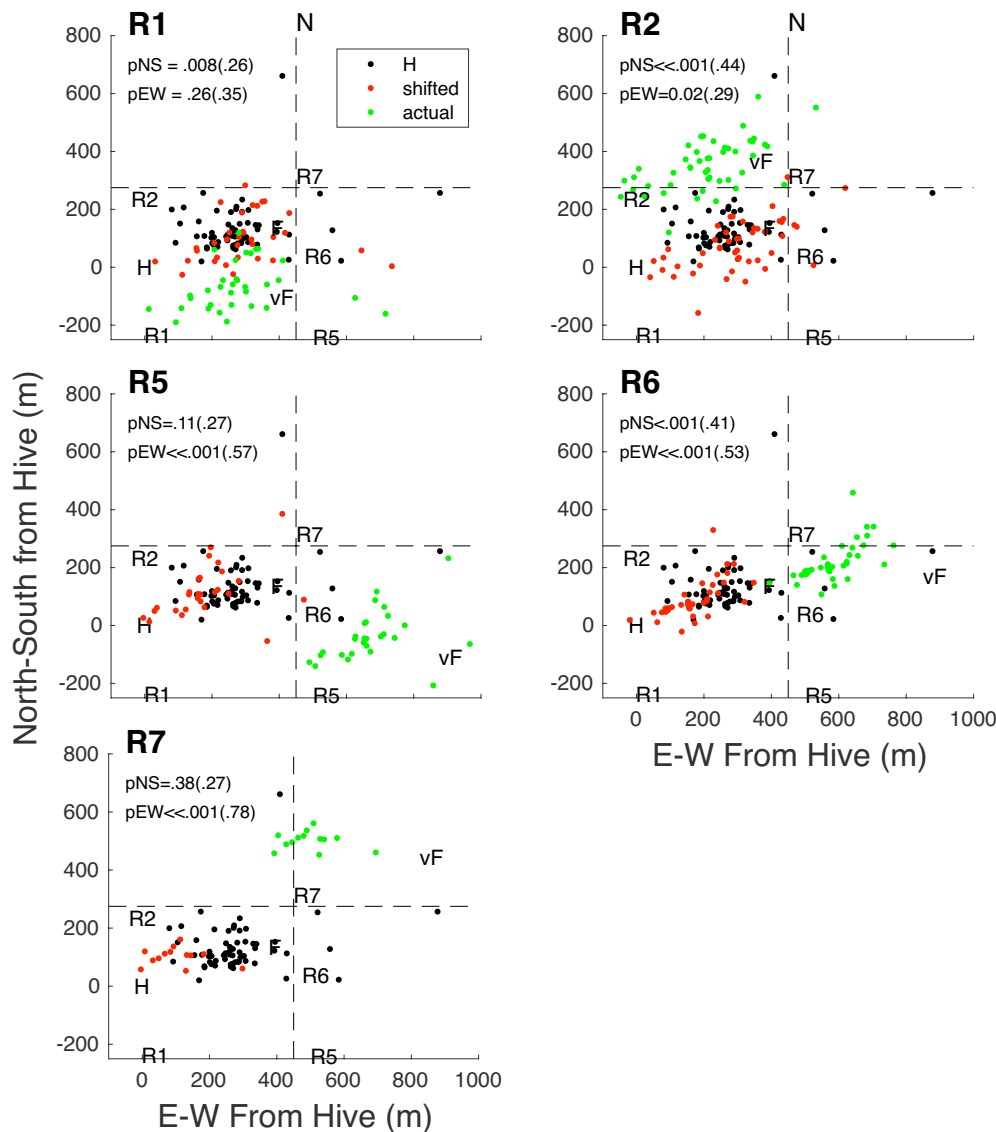


Fig. 3. Endpoints of the vector flights from the different release sites shown in relation to the feeder F and the virtual feeder vF. The black dots (repeated in each panel) give the vector endpoints of recruits released at the hive (H). The green dots are the vector endpoints of the recruits released at the particular release site. The red dots are those same terminations but displaced by the difference between the hive location and the location of the release site so that their distribution may be visually compared to the black dots. The p values are from Kolmogorov-Smirnov 2-sample tests comparing the latitudinal distribution (north-south coordinates) of the red dots to the latitudinal distribution of the black dots (pNS) and likewise for the longitudinal distributions (pEW). Note that the pattern of the differences in vector terminations depends very strongly on the release site.

Search Flights of Displaced Recruits Often Have Multiple Goals.

As is evident from the movies made from the search fixes (OSF), F was rarely the only goal toward which portions of a search were directed. The movies show that some recruits in each group made a run toward the food, some toward the vF, and some to the RS. They also show that many recruits searched systematically toward more than one target in different phases of their search (see for example, Fig. 1C). To capture this aspect of the data, we devised a measure of the strength with which multi-fix segments of a search gravitate to a target location (Fig. 6).

With reference to Fig. 6, the efficiency with which the course segment defined by two successive fixes moves the bee closer to g is $\cos(b_e)r_i$. The overall progress toward g may be measured by the ratio between the initial distance to the goal (d_i) and the distance as of the fix that terminates the segment (d_j). G_{j-1} is the sum of the products of these two measures of goal progression: $G_{j-1} = \sum_{i=1}^{j-1} (d_i/d_j)r_i \cos b_e$, where j ranges from 2 to the total number of fixes.

The gravitation analysis was first applied to the search flights of hive-released recruits and affirms that the searches of hive-released recruits usually gravitate toward F (SI Appendix, Fig. S3).

The Fig. 7 shows search fixes from displaced bees and the corresponding plots of gravitations toward F (red curves), vF (blue curves), and RS (cyan curves). Because the range of G is huge (note the differences in y axis ranges in SI Appendix, Fig. S3), the G_g 's have been logged—after converting their negative elements to the reciprocals of their absolute values. The reciprocals of the absolute values of the negative elements are invariably <1 ; thus, their logarithms are negative. Only the positive values of G_g indicate the strengths and durations of the runs toward the different targets.

The G measure enables us to parse fix sequences into runs directed at the different plausible targets (F, vF, and RS). A sequence of fixes was scored as a gravitation toward one of these goals when the G score was >50 over the fixes in that segment and greater than the G scores for the two alternative goals. (For overall G statistics, see SI Appendix, Figs. S3–S6).

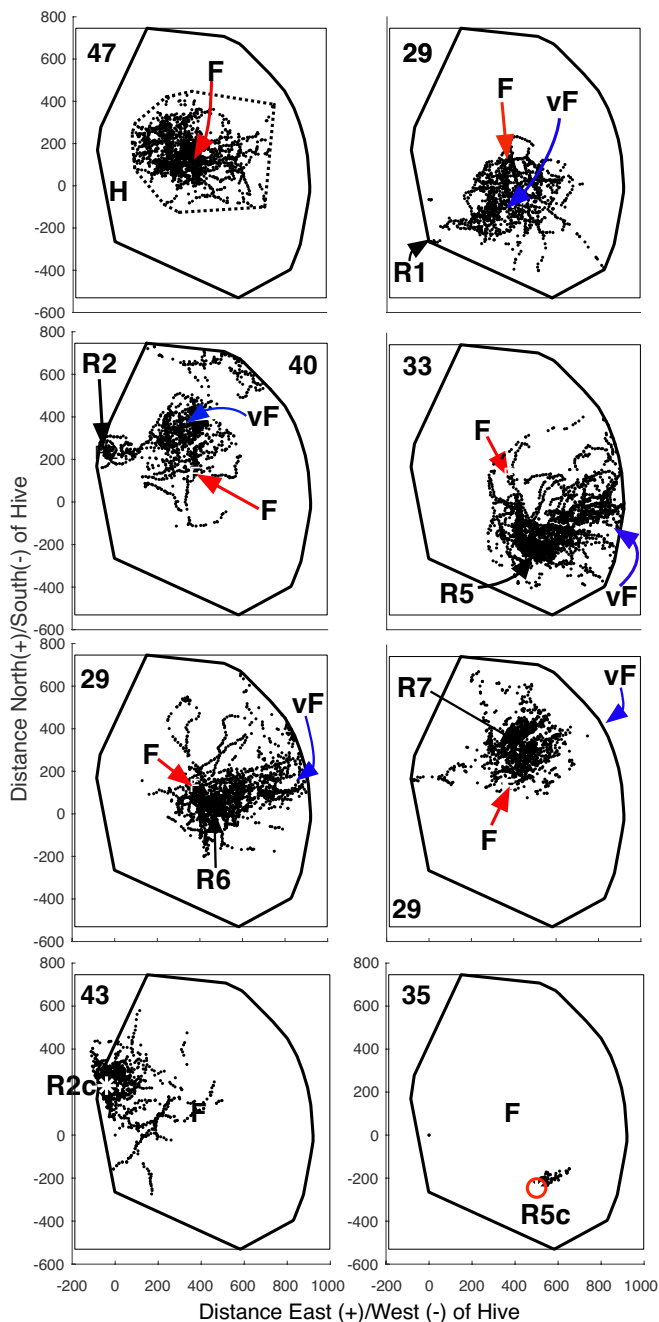


Fig. 4. Search-phase fixes for eight release groups plotted inside the convex hull of the fixes from the six groups captured at H. Release site F and vF indicated with bold letters. The bottom two panels (R2c and R5c) are the fixes from two control groups captured on exiting a distant hive; hence, unfamiliar with the territory. The number in a corner of a panel is the number of recruits in the group. The number of fixes contributed by a recruit varied from 4 to 369. The hive-release panel (Top Left) shows the convex hull of the hive-released searches (dotted outline). It is centered on F. Note that many of the fix patterns for displaced groups are not centered on the vF (for example, R5, R6, and R7).

More than half the bees in every experimental group gravitated one or more times toward the true location of the food at some point in their search (blue bars in Fig. 8). This fraction was significantly greater than the equivalent fraction for the vF and RS goal locations (red and orange bars). This fraction was 0 for one of the control groups taken from a distant hive (R5c); for the other (R2c), it was 0.38. The fraction of hive-released bees showing strong gravitation to F was 0.82. This fraction was approximated by three of the groups released at displaced sites in familiar territory (R1, R5, and R6). In short, displaced recruits released in

familiar territory were almost as likely to make at least one run toward F in the course of their search as were recruits released at the hive, while recruits unfamiliar with the release terrain rarely or never made such runs.

Discussion

At some point during the search phase, the majority of the displaced recruits set a course for the true location of the food from wherever they then found themselves. A recruit may or may not have previously flown over terrain near the inconspicuous food location, but that location had never been a goal to which it had flown from the hive or from a nearby landmark. It was an arbitrary goal location known as such only by hearsay (the observed dance). The locations from which displaced searchers set these courses were scattered all over the familiar terrain to the east of the hive. Thus, these food-directed courses were set from arbitrary locations to an arbitrary location. Because our design guaranteed that the recruits had never obtained food at the danced location and because very few of the recruits released at the hive actually found F, displaced recruits could not have navigated toward F on the basis of some beacon-like

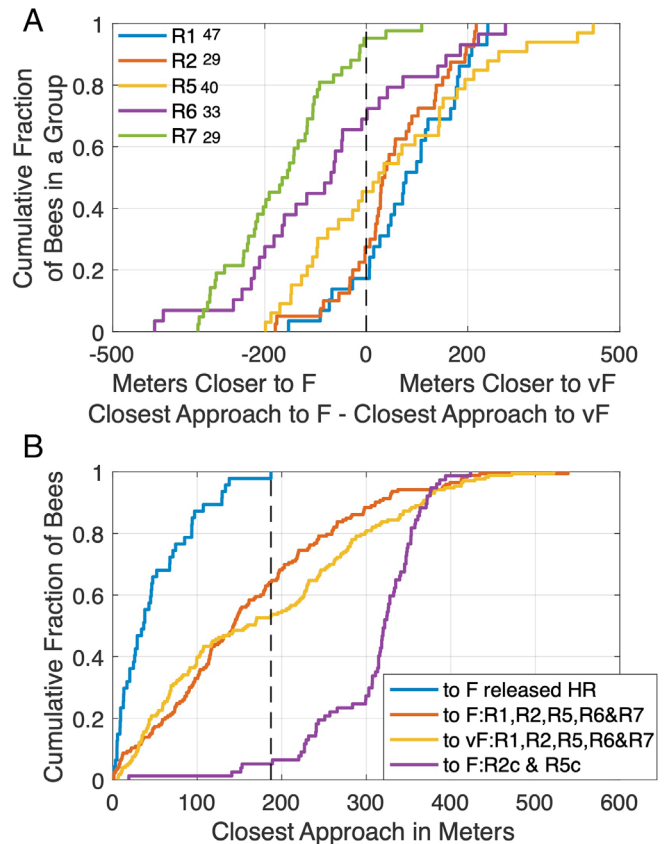


Fig. 5. Cumulative distributions (CDFs) of the closest approaches to F and to vF. (A) CDFs of the bee-by-bee difference between a recruit's closest approach to F and her closest approach to vF; one CDF for each displaced release group. Each step in a CDF is from a different bee. The fraction on the y axis at the top of a step is the fraction of the differences less than or equal to the value on the x axis. The portion of a CDF to the left of the vertical dashed line at 0 is the proportion of bees in a release group that came closer to F than to vF. (The number of bees in a group is in the legend.) (B) The CDFs of the closest approaches to F in hive-released recruits (HR, blue), to F in displaced recruits released in familiar territory (yellow), and by control recruits from a far distant hive released at the same sites (R2 and R5) as two of the groups from the local hive (purple). The proportions of the yellow, red, and purple plots to the left of the vertical dashed line are the proportions of recruits whose closest approach to F was within the range of the closest approaches of hive-released recruits (the control group).

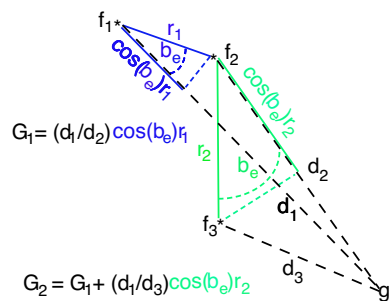


Fig. 6. The quantities in the computation of G , the tendency to gravitate toward a target location, g ; b_e is the bearing error of a fix-fix segment (the angular distance of the bearing of the line between the two fixes from the bearing of g from the first of the two fixes); r_i is the fix-fix distance; $d_{j=i+1}$ is the distance to g .

property of F . In the animated fix-by-fix sequences (**OSF**), one sees recruits approach F from diverse and distant locations in every compass direction. Because the bees were displaced for hundreds of meters away from the hive and because they then often flew a vector flight that carried them even further from it, our design succeeds in showing that displaced the bee's search satisfies the operational

definition of a map: It is a representation of the spatial relations between mapped objects and horizon profiles that enables a navigator to set a course toward any location within the map's frame of reference from any other location within that frame of reference (11, Chap. 5). Our results require a richer interpretation of what the dance of a returning forager communicates to its followers than the one that has been almost universally embraced in the 50+ years since von Frisch's Nobel-prize-winning discovery. They require a still richer conception of the computational and representational power of an insect brain.

Those without practical experience of open field (marine or back country) navigation may wonder why if recruits had a map, they did not make straight for F . Those with practical experience of backcountry navigation made without modern instruments and charts will know that errors in courses set toward goals known only by hearsay may be large for three reasons: 1) Errors in landmark recognition: Dead reckoning plays an important role in landmark recognition; the estimate of one's current position strongly informs one's judgment/interpretation of what one is looking at. The displacement of the recruits destroyed this source of information, making it much harder to use what they saw when released and thereafter to correctly recognize the landmarks

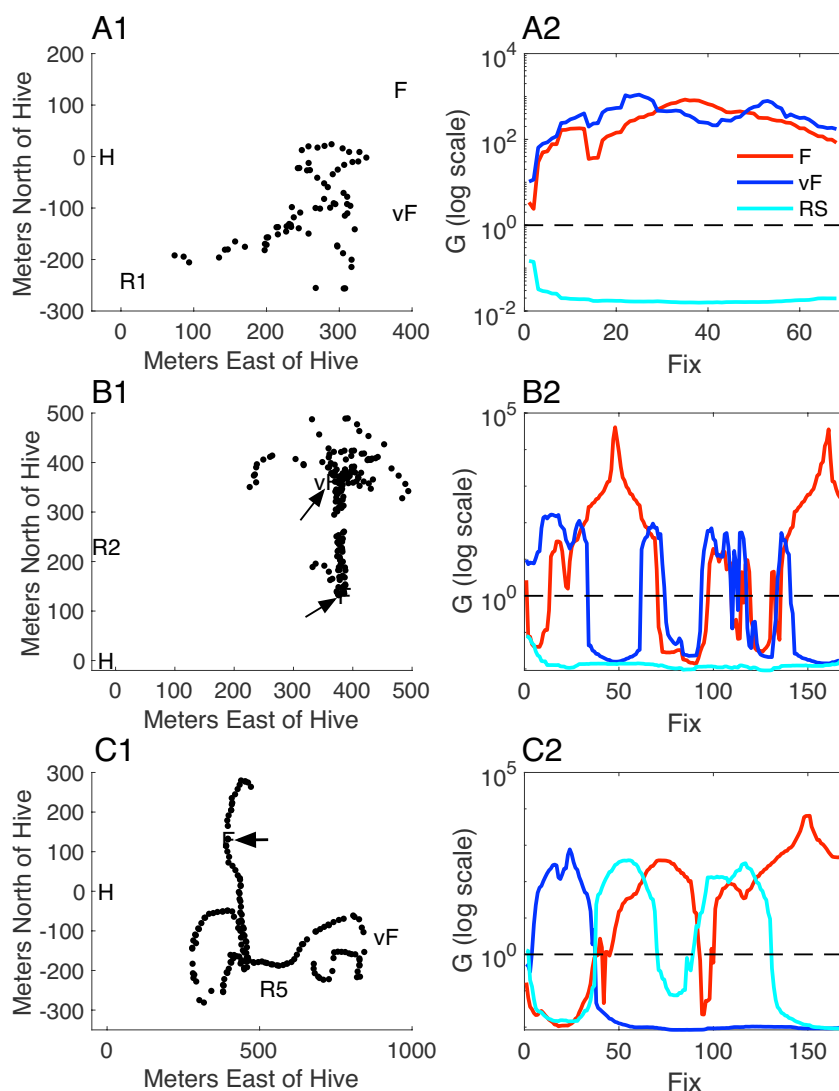


Fig. 7. Three illustrative search-fix sequences (panels on *Left*) and the fix-by-fix plots of G_F (red), G_{vF} (blue) and G_{RS} (cyan) in the panels on the right. These gravitations are plotted as a function of the successive fixes in the search sequence, starting with the second fix. (A) Released at R1. (B) Released at R2. Arrows indicate F and vF , which are mostly obscured by fix marks. The recruit flew twice directly from vF to F . (C) Released at R5. Arrow indicates F . The recruit went first to vF , then back to NW of R5, then due north toward F , then back to NW of R5, then due north directly over F (see Fig. 1C for this same trajectory).

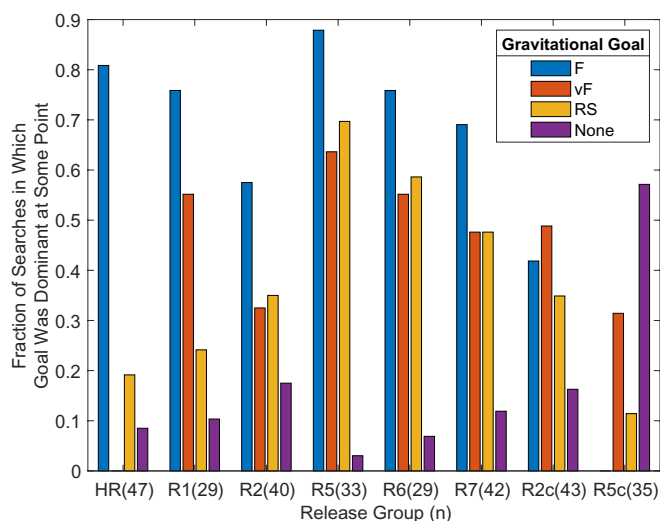


Fig. 8. The fraction of the searches in each release group that included at least one strong gravitation ($G \geq 50$) toward the goal indicated by the color of the bar (blue for F, red for vF, orange for RS). Purple bars give fraction whose search had no dominant segments. The numbers in parentheses are the n's. χ^2 tests for differences in the F:vF (blue: red) proportions and F:RS (blue: yellow) proportions across groups R1, R2, R5, R6, and R7 yield p 's $< .0001$. R2c and R5c give the results for the two control groups. A blue bar is absent from R5c because the fraction directed to F = 0; red bar is absent from H, because vF $\equiv$ F.

they observed. 2) Map errors: When the coordinates assigned to landmarks are based on dead reckoning, the resulting maps generally contain large errors. The impressive errors in the 1507 *Waldseemüller map* are an example. It was the state of the map-maker's art in the days when estimates of both latitude and (most particularly) longitude were often based on dead reckoning. Erroneous landmark recognitions together with incorrect locations for correctly recognized landmarks make for large errors in the estimates of the location from which a course is set. 3) Goal location errors: Errors in the dances observed and in the computations that translate sensory input from the dance into a compass bearing and a distance from the hive may produce large errors in the location coordinates assigned to the food source by a recruit. The existence of large goal-location errors in some recruits is implied by the fact that slightly more than 20% of the hive-released recruits did not come within 100 m of the source (blue distribution in Fig. 5B) and by the further fact that almost 20% of the hive-released recruits never set a course clearly directed toward the food source (left-most blue bar in Fig. 8). Setting a course requires subtracting the current location coordinates from the goal coordinates; large errors in subtrahends and minuends produce large errors in the resulting displacement vector, hence in the polar course vector. In such cases, the goal is never reached.

Our results may be understood on the hypothesis that the bee brain, like the vertebrate brain, constructs a Euclidean cognitive map of the terrain in which the animal forages. A Euclidean map is a vector space on whose vectors distances and directions are defined (that is, computable from the location vectors) and Euclid's parallel postulate holds. For simplicity and economy of representation and computation, the basis vectors are commonly taken to be orthogonal. Navigational computations—vector addition and subtraction, vector inversion, Cartesian-to-polar, and polar-to-Cartesian conversion—operate on the vectors in this space or on vectors computed from them. Among the location vectors in this space is one that marks the animal's current location; it is updated by path integration (dead reckoning). Thus, the undisplaced navigator generally knows approximately where it is on its map.

Location vectors also give access to terrain views and to goal-properties that may prove useful in the future, such as the color, odor and shape of the flowers the foraging bee has visited (6, 7, 11, Chaps. 14 and 15). In mammals, nonspatial information accessed by way of location vectors is represented in other vector spaces (12, 13). Vector representations of nonspatial features (e.g., odors) are also seen in insects (14). Vector representations of diverse aspects of the experienced world appear to be neurobiologically common across disparate phyla.

In our view, these new results cannot be explained by existing concepts of insect navigation. Some forms of map-like navigation are captured by a model in which the trajectories of foraging bees are determined by the combined effects of i) remembered hive-directed polar vectors with origins at familiar landmarks and food sources, ii) hive-directed polar vectors derived from a subject's dead-reckoned location, and iii) polar vectors directed toward previously experienced food sources from landmarks surrounding them. These polar vectors are assumed to combine so that the subject moves in a manner analogous to a particle in a force field (10). The demonstration that displaced recruits can find their way toward a goal from any location within the explored area to a location known only by hearsay calls for alternative or augmented explanations that enable setting a course from any estimated current location to any estimated goal location, whether that location has or has not been a goal in previous foraging or the origin of a polar home vector. It will be interesting to see whether models of insect navigation may be developed in which the representation of the geometric relations between hive, food sources, landmarks, and horizon panoramas is not homomorphic to a Euclidean vector space.

In addition, our results add information to the understanding of symbolic communication by the waggle dance. The symbols used (body movements in the dark hive on a vertical comb surface) are rather simple but they allow the receiving bee to derive a representation of the goal's location. Although this has been shown for the receiving bee only in our experiments, one can safely generalize to the dancing bee, because foraging bees frequently switch between dancing and dance following. Thus, the dance message is not only a flight instruction; it is part of a navigational conversation about where food is and how to get to there.

Materials and Methods

Experimental Site, Honeybee Colony, and Experimental Design. The experiments were carried out in 2015, 2016, and 2017. The experimental site was a structured flat agricultural landscape with grass fields stretching to the east of the area scanned by a radar (located at R/H, Fig. 1, coordinates: 50°48'52.21"N, 8°52'20.43"E) with trees and bushes, pathways, and creeks close to the Großseelheim village (Germany). The whole grass area east of R/H was frequently cut by the farmers. The experiments started in early August at a time when natural food sources appeared only west of R/H in gardens of the village (marked bees from our colony were frequently seen by the garden owners) and a few small spots along the creeks. Scattered flowers of *Lapsana communis*, a yellow blooming composite providing only pollen, appeared 3 to 4 d after the last cut rather equally distributed over the whole grass area and disappeared with the next mowing soon after. No denser patches of these flowers were ever seen at the area around F.

The bee colony in an observation hive with about 3,000 bees was introduced to the area 10 to 14 d before the experiments started in order to familiarize the foragers with the area. During this period and throughout the experiments, the bees appearing at the hive entrance were marked individually with number tags. The two-digit number tags had five different colors and were glued to the thorax of the bees in four different directions relative to the body length axis allowing to mark close to 2,000 different bees (numbers sensitive to the direction of reading were excluded, e.g., 66 and 99, 69, 96). All bees used in the experiment as trained

bees (dancers) or recruited bees (recruits) were individually marked and full protocols were established. The trained bees were additionally marked with a white dot on the abdomen including the period of training from the hive to the final feeder location. No bee used as trained bee at any stage of training was used as a recruit. Dances of bees for natural food sources were observed throughout the experimental period, and no dances indicating a source to the East (the radar-scanned area) were observed, except by those trained to dance to F.

Recruits were caught at the hive entrance after they had followed a dance of an experimental dancer using a transparent marking device (a tube with a stopper) and transported to the release site in a dark box. The time interval between catch and release was close to the same for all release sites including the control experiment. Returning recruits were removed from the colony when they arrived at the hive entrance and after the radar transponder was collected. The feeding place F for the trained bees was located at a distance of 384 m and a direction of 60° east of N. The trained bees served as the dancers. The feeder was an unscented plastic container standing on a small table. Recruits rarely found the table and landed at the feeder (3 out of 47 hive released bees, none of the displaced recruits), most likely due to the unnatural conditions and the lack of odor. Bees without abdomen marker were frequently seen dancing for natural food sources in the west of the colony. Recruits were released either at the hive (R/H) or at one of the five additional release sites (R1, R2, R5, R6, and R7, Fig. 1A).

Tracking by Harmonic Radar and Segmentation of Flight Trajectories.

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 second harmonic component of the signal (18.8 GHz) was the target for the radar. The receiving unit consisted of an 18.8-GHz parabolic antenna, with a low-noise preamplifier directly coupled to a mixer (18.8-GHz oscillator) and a downstream amplifier with a 90-MHz ZF-filter. A 60-MHz ZF-signal was used for signal recognition, leading to a fixing of the bee carrying the transponder. The transponder had a weight of 10.5 mg and a length of 11 mm. 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. The frequency of radar fixes was every 3 s. 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 in a calibrated geographic map created with the software Pix4D from aerial images (15) taken with a commercial drone (DJI Inspire). In the rare cases when no fixes were received from a bee for more than 30 s, the flight trajectory was interrupted, and the last, as well as the first, fixes before and after interruption were marked.

Analyses of Flight Trajectories. Segmentation of flight trajectories: A total of 369 recruits were tested. Typically, recruits performed a sequence of three sequential flight segments: the outbound vector flight; the search flight; and the inbound homing flight (Fig. 1A). Homing flights were not further considered here because all bees returned home on fast and straight flights. Some of the recruits released at R1 or R2 initiated a straight homing flight after close exploration around the release site without performing a vector and or search flight. These

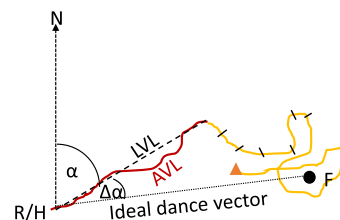


Fig. 9. Parsing of a recruit's radar fixes into an outward-bound vector, a search component, and a hive-bound vector was done by an algorithm. Magenta = vector portion; yellow = search portion; cross-ticks on search portion indicate fixes at 3-s intervals; red triangle marks beginning of hive-return vector. Bearing α : bearing of terminal vector fix in degrees clockwise from N. Length: line between release site and terminal of vector flight (dotted line). Speed: interval between start and end of vector flight and the real distance flown (AVL: accumulated distances of fix-fix segments). Straightness: proportion of LVL and AVL. F = food location.

recruits were not included in our analyses. The transitions from the rather straight vector flight to the search flight and the search flight to the homing flight were characterized by a sharp turn of $\geq 60^\circ$ with straight stretches before and after the turn with at least three fixes each (Fig. 9).

Statistics. Statistical analyses were run by scripts in R or in Matlab™. The code that implements the G computation has been uploaded [here](https://osf.io/a59rs/), along with the raw data, all of the results of our analyses, and the code that produced those results. A one-way ANOVA was used to compare vector parameter data from displaced groups to the data from the hive-released group. The proportions in Fig. 8 were compared by chi-square tests.

Data, Materials, and Software Availability. Radar fixes and Computer Code data have been deposited in Open Science Forum: https://osf.io/a59rs/files/?view_only=6da39e230c8d4072b27ab70cceb06e2 (16).

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