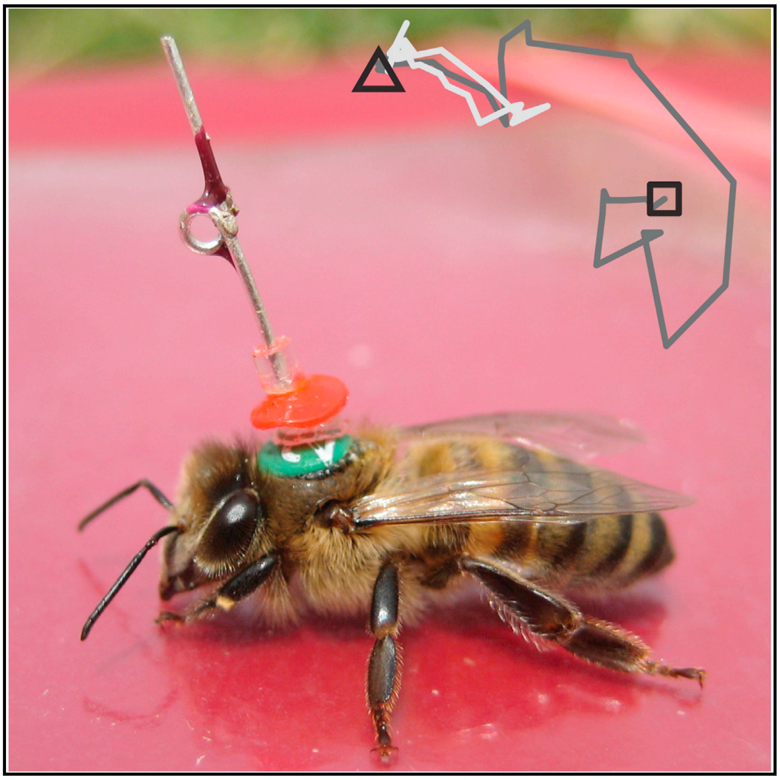
Current Biology

Report

Honeybees Learn Landscape Features during Exploratory Orientation Flights

Graphical Abstract



Authors

Jacqueline Degen, Andreas Kirbach,
Lutz Reiter, ..., Gisela Manz,
Uwe Greggers, Randolf Menzel

Correspondence

jacquelinefdegen@gmail.com

In Brief

Degen et al. used a special radar system to track bees in flight. They displaced bees after a single orientation flight into either the explored or the unexplored area. Homing flights were faster and straighter if bees were released within the explored area. The authors conclude that bees used the ground structure for homeward guidance.

Highlights

- Bees need one orientation flight for successful homing after a displacement
- During the first orientation flight, features of the hive are learned
- One long-range orientation flight leads to learning of landscape features
- The learned landscape features can be used for effective homing

Degen et al., 2016, Current Biology *26*, 2800–2804
October 24, 2016 © 2016 Elsevier Ltd.
http://dx.doi.org/10.1016/j.cub.2016.08.013

Current Biology
Report

Honeybees Learn Landscape Features during Exploratory Orientation Flights

Jacqueline Degen,[1,3,*] Andreas Kirbach,[1] Lutz Reiter,[2] Konstantin Lehmann,[1] Philipp Norton,[1] Mona Storms,[1] Miriam Koblofsky,[1] Sarah Winter,[1] Petya B. Georgieva,[1] Hai Nguyen,[2] Hayfe Chamkhi,[1] Hanno Meyer,[1] Pawan K. Singh,[1] Gisela Manz,[1] Uwe Greggers,[1] and Randolf Menzel[1]
[1]Institut für Biologie, Freie Universität Berlin, Königin-Luise-Straße 28/30, 14195 Berlin, Germany
[2]Institut für Informatik, Freie Universität Berlin, Takustraße 9, 14195 Berlin, Germany
[3]Lead Contact
*Correspondence: jacquelinefdegen@gmail.com
http://dx.doi.org/10.1016/j.cub.2016.08.013

SUMMARY

Exploration is an elementary and fundamental form of learning about the structure of the world [1–3]. Little is known about what exactly is learned when an animal seeks to become familiar with the environment. Navigating animals explore the environment for safe return to an important place (e.g., a nest site) and to travel between places [4]. Flying central-place foragers like honeybees (*Apis mellifera*) extend their exploration into distances from which the features of the nest cannot be directly perceived [5–10]. Bees perform short-range and long-range orientations flights. Short-range flights are performed in the immediate surroundings of the hive and occur more frequently under unfavorable weather conditions, whereas long-range flights lead the bees into different sectors of the surrounding environment [11]. Applying harmonic radar technology for flight tracking, we address the question of whether bees learn landscape features during their first short-range or long-range orientation flight. The homing flights of single bees were compared after they were displaced to areas explored or not explored during the orientation flight. Bees learn the landscape features during the first orientation flight since they returned faster and along straighter flights from explored areas as compared to unexplored areas. We excluded a range of possible factors that might have guided bees back to the hive based on egocentric navigation strategies (path integration, beacon orientation, and pattern matching of the skyline). We conclude that bees localize themselves according to learned ground structures and their spatial relations to the hive.

RESULTS AND DISCUSSION

Bees perform two forms of exploratory orientation flights: (1) short-range orientation flights that concentrate on the exploration of the hive's immediate surroundings and (2) long-range orientation flights that usually lead into one narrow sector of the landscape because the outbound and inbound components of the flight are quite close to each other [11]. Furthermore, consecutive long-range orientation flights are directed toward sectors of the environment that overlap only partly or not at all, resulting in effective exploration of novel sectors around the hive. These behavioral strategies suggest the formation of a memory that stores the relations of environmental features for effective homing.

Bees Are Lost When Displaced before Their First Orientation Flight

Fourteen bees were displaced under good weather conditions to locations in various directions around the hive before they had performed their very first orientation flight (Figure S1B). Although all bees performed flights after the displacement, none returned to the hive entrance. The distances of the release sites from the hive ranged from 65 to 253 m, and the displaced bees were between 5 and 33 days old. The flight durations until bees were lost by the radar tracking system ranged from 8.6 to 243.2 min (mean ± SD: 60.8 ± 62.7 min) and the flight lengths from 317 to 13,082.5 m (mean ± SD: 3,008.2 ± 3,273.5 m).

Our experimental procedure did not affect the motivation of the bees to perform a flight, and they had enough energy to search intensively for the hive. The failure of these bees to return to the hive did not depend on their age or the displacement distance. These results confirm the findings of Buttel-Reepen [12] but are somehow in conflict with the results of Becker [6] since she found that inexperienced bees were able to return to the hive after a displacement of less than 100 m, with older bees being more successful than younger ones. She concluded that bees were able to find their way back to the hive by odor cues. However, in our experiments two bees came close to the hive (less than 50 m) and another two even crossed the position of the hive without interrupting their flights, indicating that the odor of the hive did not guide the bee back into the hive. Furthermore, their searching behavior differed from bees performing their first exploratory orientation flight. The latter flew along a rather narrow single segment with a tendency to follow extended ground structures, whereas inexperienced bees searched in widely distributed curving flights, ignoring ground structures (Figure S2A).

Homing Behavior Is Rather Successful after One Short-Range Orientation Flight

Short-range orientation flights bring bees no further than 30 m away from the hive and lack any clear direction. Bees were

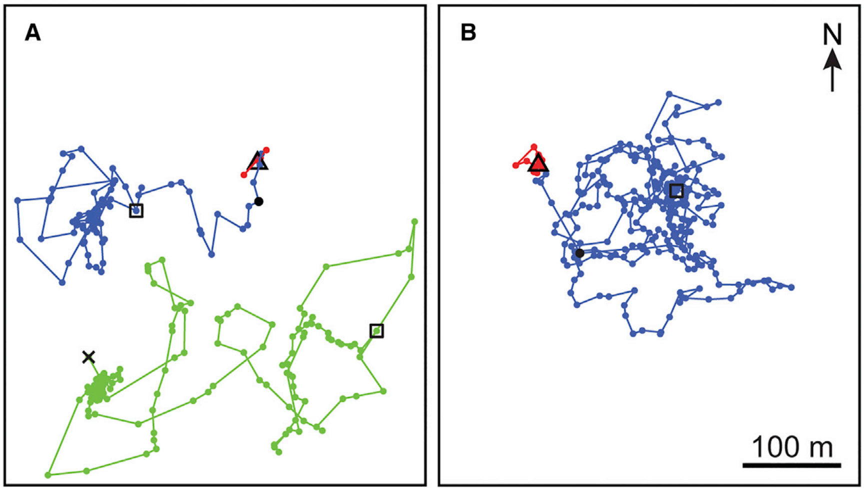


Figure 1. Representative Flight Trajectories of Bees Displaced after One Short-Range Orientation Flight

The flight trajectories of the short-range orientation flights are shown in red. The squares mark the release sites, and the dots on flight paths are the positions given by radar (usually every 3 s). Black dots mark the homing points, the locations at which the bee performed straight homing flights. The position of the hive is marked by the triangle.

(A) Flight trajectories of a bee that was displaced into two different directions. The bee did not return to the hive from the second release site (green flight trajectory). The cross marks the location where the bee dropped to ground.

(B) Flight trajectories of a bee that was displaced only once.

See also Figures S1 and S3.

displaced once or twice to various locations in different directions around the hive (Figures S1C and S1D). All bees performed flights (flight examples: Figure 1), and only two out of 13 flights (15.4%) did not end at the hive (flight example: Figure 1A, green flight trajectory), indicating that the experience gained during the short-range orientation flight was sufficient for rather successful homing. All successful homing flights had a relatively low level of straightness, reflecting that the bees needed to search before they returned to the hive, and the flight durations varied considerably (Figure 2A). This variation could not be explained by variance in the displacement distance, the age of the bees, or the prevailing weather conditions (Table S1). Furthermore, the use of odor cues emanating from the hive was excluded as an influencing factor (Table S2).

The locations at which the bees performed straight homing flights (homing points) also varied considerably, with distances to the hive that ranged from 34.1 to 98.6 m (mean ± SD: 65.5 ± 22.8 m). This suggests that the recognition area established during an orientation flight is likely to be larger than the calculated catchment area of the hive (radius 60 m). However, the distance of the homing point to the hive might also depend on the pattern of the short-range orientation flight. Although these flights lack a clear direction, all flights had one, two, or three radar signals that were at least several meters away from the hive. We determined the compass directions of these radar signals and measured the minimum angle to the compass direction of the homing point. Only two out of 11 homing points had a high angular deviation to the orientation flight, and these were within the calculated catchment area of the hive (Figure 2B). Six homing points were located outside of the calculated visual catchment area of the hive. All of these latter homing points had a direction close to one of the radar signals not located directly at the hive (Figure 2B; see flight example Figure 1B), which indicates that a short-range orientation flight might not extend the recognition area in all directions. The homing flight patterns of the bees were influenced by extended landmarks on the ground because bees directed segments of their flights according to parallel mowing tracks that structured one part of the experimental field (Figures S2B and S2C). This indicates that these extended landmarks were learned during the short-range orientation flight and used for a successful return to the hive.

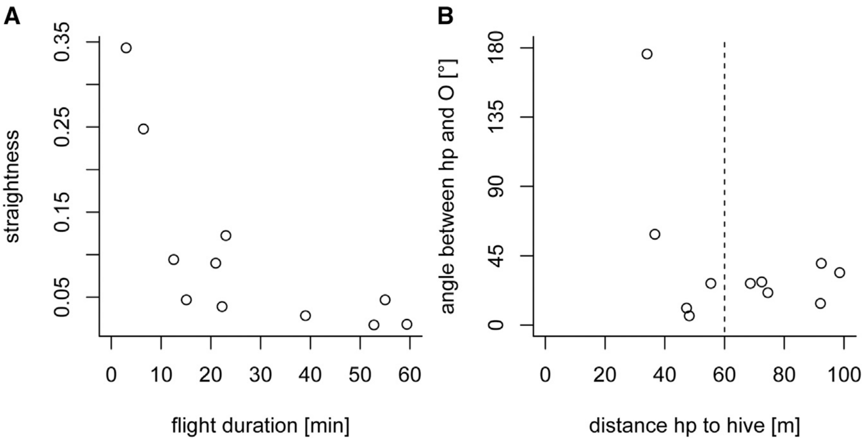


Figure 2. Homing Performance and Locations of Homing Points of Bees Displaced after One Short-Range Orientation Flight

(A) Homing performance determined by the time bees needed to return from a release site to the hive and the straightness of the whole flight, where a value of 1 would indicate a straight flight back to the hive.

(B) The locations of homing points (hp) determined by their distance to the hive and their angle to the orientation flight (O). The calculated visual catchment area of the hive is indicated by the dashed line.

See also Figures S1 and S2 and Tables S1 and S2.

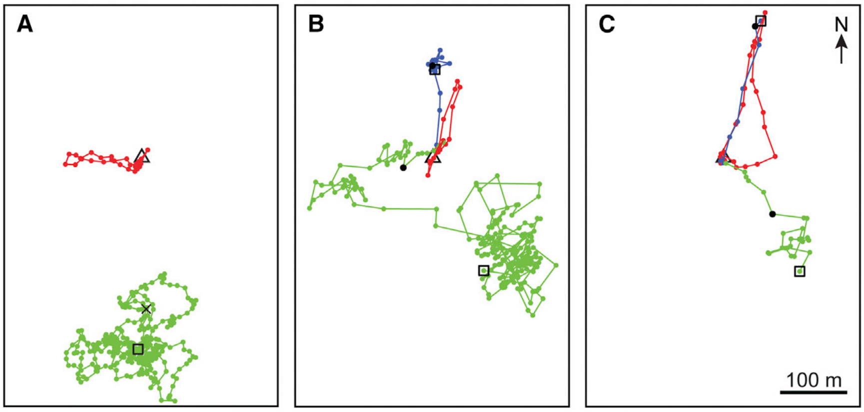


Figure 3. Representative Flight Trajectories of Bees Displaced after One Long-Range Orientation Flight

The flight trajectories of the long-range orientation flights are shown in red, those after displacement to an explored area in blue, and those after displacement to an unexplored area in green. The squares mark the release sites, and the dots on flight paths are the positions given by radar (usually every 3 s). Black dots mark the homing points, the locations at which the bee performed straight homing flights. The position of the hive is marked by the triangle.

(A) This bee did not return to the hive after displacement to an unexplored area. The cross marks the location where the bee dropped to ground.

(B and C) Flight examples of bees that returned to the hive from the respective release site.

See also Figures S1 and S3.

Homing Behavior Is Successful after One Long-Range Orientation Flight

A total of 33 bees were displaced once or twice after one long-range orientation flight in a similar or different direction relative to the direction of the orientation flight, as defined by the compass direction of the track point furthest away from the hive (flight examples: Figure 3). Ten out of 50 recorded flights (20%) did not end at the hive (Figure S1E; flight example: Figure 3A, green flight trajectory), and seven of these unsuccessful flights were recorded under unfavorable weather conditions (temperature <20°C and/or wind speed >20 km/h and/or no sun at all). Only 12 out of 50 flights (24%) were recorded under such weather conditions. The ten unsuccessful flights occurred after displacements in various directions and distances as related to the respective orientation flight. The age of these bees ranged from 7 to 31 days and did not differ significantly from the age of bees that returned successfully to the hive (t test: $t_{49} = 0.363$, $p = 0.718$).

Figure 4A shows the duration and straightness of all successful homing flights. In addition to fast and relatively straight flights back to the hive, flights of long duration and low straightness were also observed. Since variance in the displacement distance, the age of the bees, or the prevailing weather conditions (Table S1) and the use of odor cues from the hive could be excluded as influencing factors (Table S2), the observed variance in homing performance must be ascribed to learning during the long-range orientation flight.

We therefore analyzed the locations of homing points, where the bee directed its flight straight toward the hive, in order to classify areas explored or not explored during the orientation flight (Figure 4B). Because the visual catchment area of the hive was supposed to be up to a radius of 60 m around the hive, homing points located outside of this visual catchment area were considered to indicate the recognition of areas learned during the long-range orientation flight. Using the formula described in the Supplemental Experimental Procedures, we determined that the bees were able to return to the hive from any direction when they got closer to the hive than 72 m. Bees were also able to navigate toward the hive when they got closer than about 100 m (shortest distance) to the orientation flight trajectory. Based on this analysis of homing points (Figure 4B), we classified explored and unexplored areas. Afterward, we determined for each release site whether it was located in a previously explored or unexplored area. The homing performance of bees differed significantly between displacements to explored (n = 15; Figure S1F) and unexplored areas (n = 25; Figure S1G). Bees displaced to an explored area returned significantly faster (linear mixed-effects model [LMM]: $F_{1,38} = 9.277$, $p = 0.009$; Figure 4C) and with a significantly higher level of straightness of flights (LMM: $F_{1,38} = 16.648$, $p = 0.001$, Figure 4D) to the hive than did bees displaced to an unexplored area.

Thus, bees learned landscape structures during their long-range orientation flights that led to fast homing from the explored area. Indeed, the homing flight pattern of bees displaced to an unexplored area and of those that did not return to the hive was influenced by extended landmarks on the ground because bees directed segments of their flights according to parallel mowing tracks that structured one part of the experimental field (Figures S2D and S2F). Homing flights after a displacement to an explored area were seemingly not influenced by extended landmarks because the flight segments that were bounded by two consecutive radar signals were distributed uniformly (Figure S2E). It is nonetheless likely that the extended landmarks were used as reliable navigational cues since bees that localize themselves after a displacement might not need to fly along these structures for a fast return from the release site to the hive.

Taken together, our findings show that bees need at least one short- or long-range orientation flight to return successfully to the hive since bees displaced before their first orientation flight did not return to the hive entrance. This indicates that the visual features of the hive are learned reliably during the first orientation flight. The detailed analysis of homing behavior after a displacement suggests that bees also learn features of the immediate surroundings of the hive during both, short- and long-range orientation flights because they performed straight flights home at locations where the hive itself was not visible. The displacements of bees after their first long-range orientation flight revealed that bees displaced in an explored direction returned faster and with a higher flight straightness to the hive than did bees displaced in an unexplored direction. Since we excluded a range of other possible influencing factors (path integration, beacon orientation, pattern matching of the skyline, age of the bees, odor orientation, and varying weather conditions; see the Supplemental Information), we ascribe the observed differences in homing behavior to the learning of landscape features. We therefore conclude that

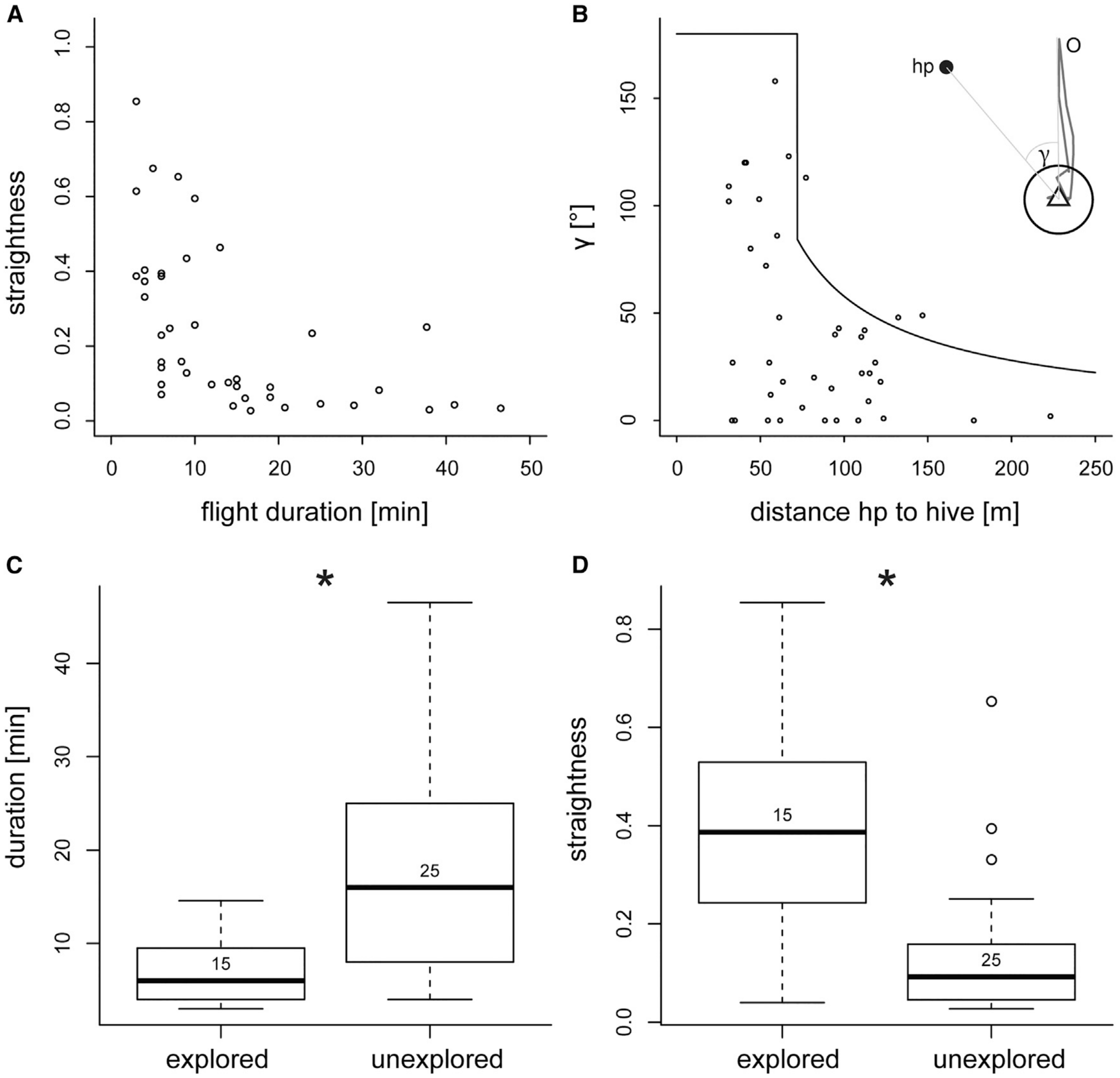


Figure 4. Homing Performance and Locations of Homing Points of Bees Displaced after One Long-Range Orientation Flight

(A) Homing performance was determined by the time bees needed to return from a release site to the hive and the straightness of the whole flight, where a value of 1 would indicate a straight flight back to the hive (n = 40).

(B) The locations of homing points (hp) were determined by their distance to the hive and their angle (γ) to the orientation flight (O; see inset). Homing points far from the respective orientation flight and rather close to the hive indicate guidance by the hive, and those far from the hive and close to the respective orientation flight are guided by the memory from the orientation flight. The curve is based on the analysis of the displayed homing points and was used to classify explored (below the curve) and unexplored (above the curve) areas.

(C) Time bees needed to return from release sites located in areas explored or not explored during the long-range orientation flight to the hive.

(D) Straightness of the whole flight, where a value of 1 would indicate a straight flight back to the hive, after displacements to areas explored or not explored during the long-range orientation flight. Boxplots show the median (black line), interquartile range (box), minimum and maximum value within 1.5 times the interquartile range of the box (whiskers), and outliers (circles). The number in each boxplot gives the sample size.

Statistics were determined via a linear mixed-effects model (LMM); significant differences ($p < 0.05$) are marked by asterisks. See also Figures S1 and S2 and Tables S1 and S2.

bees learn about the further surroundings of the hive during their very first long-range orientation flight and that the learned landscape features are used for effective homing.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.08.013.

AUTHOR CONTRIBUTIONS

J.D., U.G., and R.M. contributed to conception, design, and interpretation of the experiments, and all authors contributed to the execution of the experiments. The data analysis and drafting of the article were done by J.D. and R.M.

ACKNOWLEDGMENTS

We are grateful to Professor W.D. Haass and Dipl.-Ing. B. Fischer for constructing and building the harmonic radar device and to the farmers in Klein

Lüben who gave us access to their grassland. We thank Marcus Groß for statistical advice and Tobias Degen for assistance with the programming for the data analysis. The experiments were supported by DFG grant Me 365/34-2.

Received: April 12, 2016
Revised: June 20, 2016
Accepted: August 2, 2016
Published: September 29, 2016

REFERENCES

1. Tolman, E.C. (1948). Cognitive maps in rats and men. Psychol. Rev. *55*, 189–208.
2. Birke, L.I.A., and Archer, J. (1983). Some issues and problems in the study of animal exploration. In Exploration in Animals and Humans, J. Archer, and L.I.A. Birke, eds. (Van Nostrand Reinhold), pp. 1–21.
3. Renner, M.J. (1988). Learning during exploration: the role of behavioral topography during exploration in determining subsequent adaptive behavior in the Sprague-Dawley rat (Rattus norvegicus). Int. J. Comp. Psychol. *2*, 43–55.
4. Wiener, J., Shettleworth, S., Bingman, V.P., Cheng, K., Healy, S., Jacobs, L.F., Jeffrey, K.J., Mallot, H.A., Menzel, R., and Newcombe, N.S. (2011). Animal navigation, a synthesis. In Animal Thinking: Contemporary Issues in Comparative Cognition, R. Menzel, and J. Fischer, eds. (MIT Press), pp. 51–78.
5. Lindauer, M. (1952). Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. Z. Vgl. Physiol. *34*, 299–345.
6. Becker, L. (1958). Untersuchungen über das Heimfindevermögen der Bienen. Z. Vgl. Physiol. *41*, 1–25.
7. von Frisch, K. (1967). The Dance Language and Orientation of Bees (Harvard University Press).
8. Vollbehr, J. (1975). Zur Orientierung junger Honigbienen bei ihrem 1. Orientierungsflug. Zool. Jb. Physiol *79*, 33–69.
9. Winston, M.L. (1987). The Biology of the Honey Bee (Harvard University Press).
10. Capaldi, E.A., Smith, A.D., Osborne, J.L., Fahrbach, S.E., Farris, S.M., Reynolds, D.R., Edwards, A.S., Martin, A., Robinson, G.E., Poppy, G.M., and Riley, J.R. (2000). Ontogeny of orientation flight in the honeybee revealed by harmonic radar. Nature *403*, 537–540.
11. Degen, J., Kirbach, A., Reiter, L., Lehmann, K., Norton, P., Storms, M., Koblofsky, M., Winter, S., Georgieva, P.B., Nguyen, H., et al. (2015). Exploratory behaviour of honeybees during orientation flights. Anim. Behav. *102*, 45–57.
12. Buttel-Reepen, H. (1900). Sind die Bienen Reflexmaschinen? Experimentelle Beiträge zur Biologie der Honigbiene (Arthur Georgi).