The Significance of Landmarks for Path Integration in Homing Honeybee Foragers

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During their complex foraging trails, central place foragers often integrate distances traveled and angles turned to update continuously their estimation of home direction. This system, called path integration, allows them to head directly home even from an unfamiliar site [1]. Path integration has been particularly well studied in ants [2]. Honeybees, *Apis mellifera* L., forced to deviate from straight lines between hive and a feeder by means of obstacles, indicate the actual compass direction of the target in their dances [3]. Thus, honeybees convey the results of path integration in their dance communication, but is it continually employed during flight? Our results indicate that path integration is weighted heavily when bees explore novel territory. On familiar ground, however, compass-guided flight vector instructions activated in a sequential fashion take precedence over the path integration system.

In order to demonstrate path integration of foraging bees during long-distance orientation, the animals must fly "voluntarily" to a site that fulfils two simple prerequisites. (1) No landmarks visible from this point must indicate the direction of the hive, nor may the hive be directly visible. (2) The bees must have reached this point by a route that is *not* the straight line connecting the hive and the point in question. If animals manage to steer a direct course towards the hive from a place that meets these conditions, they must have estimated it from the length of path segments, and angles between these segments, flown prior to arrival at the particular site.

To ensure condition (1), we established one Langstroth hive box containing a populous colony of European honeybees

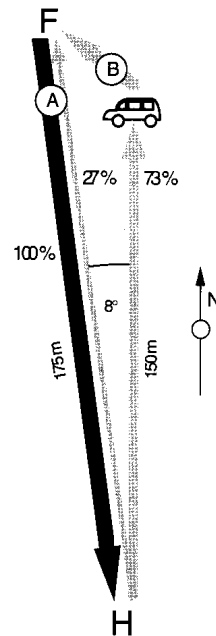* *Present address:* Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA

Fig. 1. Training setup and estimated flight paths taken by the bees during training. Bees were trained to forage for sucrose solution at a feeder F (placed on a blue cardboard 12×20 cm), 175 m north (352° if 0° is the magnetic north) of the hive H. A landmark (*car symbol*) was placed on the east side of the flight path, at an angle of 8° off the feeder direction. To test whether bees steered a direct course between H and F, or whether they deviated from this straight line to fly directly past the landmark, we placed blue cardboards at two locations (A and B) 20 m before F. Bees would frequently inspect the blue cardboards on their flights between H and F, find that there was no feeder, and then fly on to their respective destinations. An observer in each position recorded whether such bees flew towards the hive or towards the feeder. Out of 61 observed feeder-bound bees, 45 were counted in position B, and 16 in position A; 100% of the 18 observed hive-bound bees were recorded in A. The *width of the arrows* corresponds to these proportions. The flight paths taken by most feeder-bound bees deviate from a direct line between hive and feeder, whereas those of the hive-bound bees did not

in a nearly featureless and flat Chihuahuan desert dry lake bed (Willcox Playa, 120 km east of Tucson, Arizona, USA). Local landmarks were not available at all within a radius of >1 km, and horizontal marks (the Dos Cabezas and Chiricahua mountain ranges) were so far away (>20 km) that they supplied no directional information in addition to the sun compass, i.e., they could not be used for the estimation of the direction to a local target such as the hive. Bees were trained to forage for sucrose solution at an unscented feeder on a blue cardboard 175 m north of their hive (Fig. 1). All bees arriving at this feeder were marked with white paint, to ensure that we could tell experienced bees from novices during tests. The only landmark within the setup was an automobile, whose compass bearing was 8° to the right from the hive-feeder direction, and which stood at 150 m from the hive. The car measured 480 cm in length and 115 cm in height (0.7° high and 1.8° long from the hive). The hive (70 cm height, 40 cm width) covered a visual angle of <0.3° from the feeder position. Since these angles are far below the minimum detectable target of a worker bee [4], we assume that bees could not detect the hive from the feeding site, nor any other place 175 m distant from the hive. We also infer that the landmark was not visible from the hive.

In the tests, we moved the feeder on its blue cardboard to a position 30° to the left of the training direction, while its distance to the hive remained the same (Fig. 2b, c). The vanishing bearings of bees that had landed and fed at this feeder were recorded. Bees were given a colored paint dot on the abdomen in order to avoid repeated tests with the same individuals. All bees arriving at the feeder during tests had taken part in the training, as evidenced by their white color markings. Tests took 20–30 min; between tests, the training situation was restored and bees were allowed to forage for at least 1 h. The experiments differed with respect to the position of the landmark only. In Exp. 1 (Fig. 2b) it was positioned in the same angular position relative to the feeder as during training, i.e., 8° to the right of the hive–feeder axis. In Exp. 2 (Fig. 2c) the landmark was kept at the training position, as was a blue cardboard. We presumed that if bees took the hive direction from the novel position of the feeder, they must have relied upon a
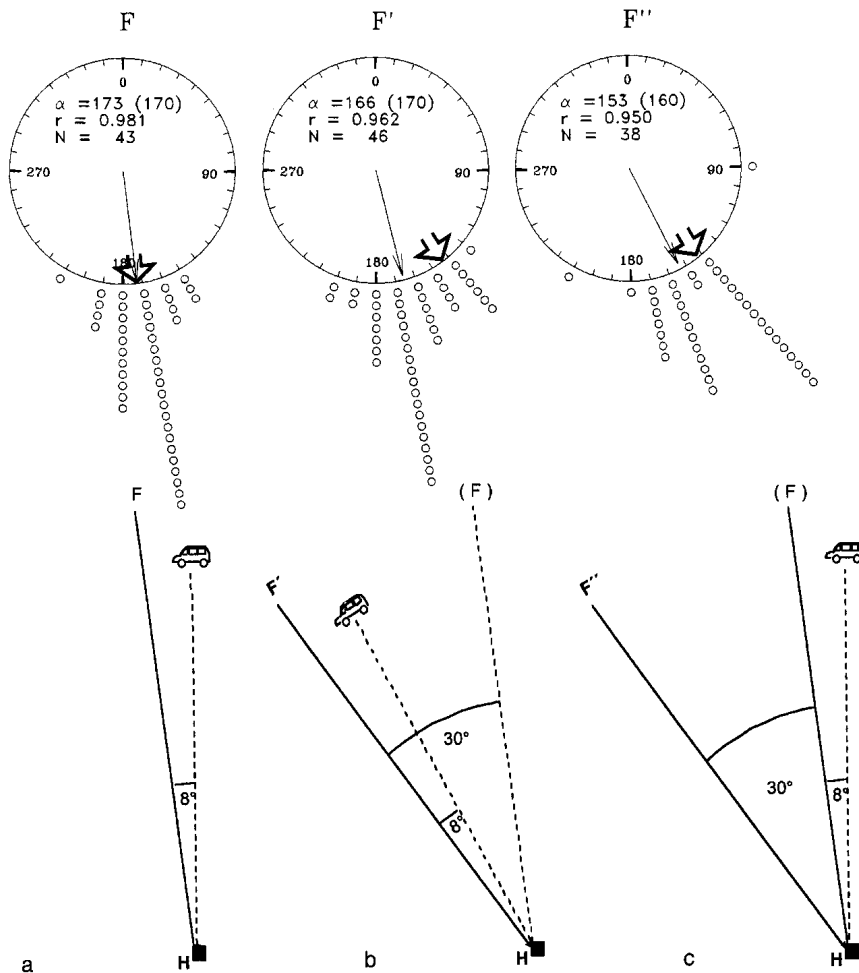
Fig. 2. Vanishing bearings of bees taken from feeders in different positions, and the respective test setups. α indicates the mean (median) angle, r is the mean vector length (as shown by *thin arrows*), N the number of observations. *Open arrows* indicate the true hive direction from the respective feeder sites. a) Distribution of vanishing points of bees during the training situation, with both the feeder and the landmark in place (control condition). b, c) Directions taken by the bees from a feeder placed 30° to the left of the training route, but at the same distance from the hive as during training. The two tests differed only with respect to the position of the landmark, as indicated by the *automobile symbol*. F marks the feeder site in the training setup, F' and F'' are the feeder positions in the tests. All three distributions are significantly different from random ($p < 0.001$; Rayleigh test, [10])

small visual angle covered by the landmark from the hive's location, it is unlikely that bees can detect it from this distance [4].

Most bees departing from the feeder during training flew exactly into the hive direction (172°, Fig. 2a), with a mean (median) of 173° (170°), confirming the observation presented in Fig. 1: homebound bees do not deviate from a straight line to incorporate the landmark into their course. The 95% confidence interval [6] extends from 171–175° and thus includes the hive direction of 172°. In Exp. 1 (Fig. 2b, both feeder and landmark displaced 30° to the left), the bees chose the same compass bearing as they did during training when starting towards the hive (mean 166°; median 170°). The direction taken is not significantly different from the hive direction during training (95% confidence interval 160–172°). The true hive direction from this novel position of the feeder (142°) does not, however, lie within these confidence limits. Obviously, bees had not applied a path integration strategy for their estimation of hive direction. They did not even make use of the landmark, whose angle relative to the hive direction would have indicated the target direction as well. In general, bees seem to pay little attention to landmarks when they are close to the start of a given flight vector [7].

In Exp. 2 (Fig. 2c, only the feeder displaced) only few bees arrived at the feeder, so that the test had to be repeated several times to test a sufficiently high number of novices. In contrast to Exp. 1, many bees had vanishing bearings exactly towards the hive (mean 153°; median 160°). The 95% confidence interval (here calculated for the median because the distribution is skewed [8]) covers 140–160° and thus includes the true hive direction of 142°. The compass direction in which the hive was from the feeder during training (172°) is excluded from the confidence limits. In this test the probability that they might have arrived at the feeder by means of a direct path is extremely low. Thus, bees must have applied a path-integration mechanism to estimate the hive direction so precisely.

It is noteworthy that the results of path integration are apparently weighted, depending only on where the landmark is positioned, since this is the only difference between Exps. 1 and 2. If bees encounter the landmark in the immediate

path integration system, provided that bees had not reached this point by following a straight path from the hive.

There are several reasons for supposing that bees did not fly directly to the site of the new feeder. First, we found that the majority of foragers did not take a direct route from the hive to the feeder even during training. Instead, they first steered towards the landmark, and then turned towards the feeder (Fig. 1). This landmark piloting behavior was not observed in bees returning homewards from the feeder. Thus, even from the point at which the landmark is detectable on the way towards the feeder in Exp. 1, bees would not

reach the feeder by a direct route. Second, it was recently shown that bees will ignore local landmarks indicating the position of the feeder when the landmarks are displaced by 30° or more from their familiar compass bearing, provided that a feeder is set up at the trained compass bearing [5]. Consequently, we assume that if in our experiments bees arrived at the feeder displaced 30° from its training direction, these bees must have first visited their training feeder site. They then "discovered" that the feeder was not in its place, and reached the novel feeder only after a search that originated at the site of the training feeder. Third, because of the

surrounding of the feeder (Exp. 1, Fig. 2b), as they do during training, path integration is not used. It is likely that bees first flew towards the training site and, near the end of the trained flight vector, searched for familiar landmarks for the precise localization of the target [7]. When these landmarks are not encountered at the expected site, it makes little sense for the bee to rely on path integration for its further course, since the bees' own distance and direction estimations have apparently failed. This may be due to passive displacement by wind, or errors inherent to the path-integration system [1, 2]. In such a situation, the only possibility for bees to redirect their course is to locate a familiar landmark, reset their path-integration system, and use the appropriate flight-vector instruction that normally follows the encounter of that landmark [9]. This is exactly what the bees appear to be doing in Exp. 1 (Fig. 2b), using a simple compass-based direction estimation and steering a course parallel to the correct flight path from the training site to the hive. Further experiments are necessary to determine whether this behavior is caused by the absence of the landmark at the trained site, its presence at the novel site, or both.

In contrast, those bees that reached the novel site in Exp. 2 (Fig. 2c) used path integration to fly into the correct hive direction. We presume that these bees had also flown towards the training site first, and found that the arrangement of blue cardboard and landmark was in place; only the feeder was absent. This is equivalent to a natural situation when a floral patch is no longer profitable. Being motivated to feed, they then started a search for a *novel* food source. Some of these bees eventually arrived at the new site, which, in contrast to the training site, was not marked by a landmark. They correctly assessed their arrival at a previously unknown food source, and thus strongly weighted the home direction as estimated by path integration. Under these conditions, path integration is essential for homing, particularly in an environment devoid of landmarks. In conclusion, we therefore propose that path integration is mainly used when bees explore novel routes, whereas when moving on familiar territory, a sequence memory for flight-vector instructions and landmark memory retrievals is used.

1. Jander, R.: Z. vergl. Physiol. *40*, 162 (1957); Müller, M., Wehner, R.: J. Comp. Physiol. A *175*, 525 (1994)
2. Müller, M., Wehner, R.: Proc. Nat. Acad. Sci. USA *85*, 5287 (1988); Schmidt, I., Collett, T. S., Dillier, F.-X., Wehner, R.: J. Comp. Physiol. A *171*, 285 (1992); Wehner, R., Srinivasan, M. V.: ibid. *142*, 315 (1981)
3. Frisch, K. v.: The Dance Language and Orientation of Bees. Cambridge: Belknap 1967
4. Giurfa, M., Vorobyev, M., Kevan, P., Hempel, N., Menzel, R., in: Goettingen Neurobiology Report, p. 422. Stuttgart-New York: Thieme (1995); Lehrer, M., Bischof, S.: Naturwissenschaften *82*, 145 (1995)
5. Chittka, L., Geiger, K.: Ethology *99*, 117 (1995)
6. Batschelet, E.: Circular Statistics in Biology. London: Acadamic Press 1981
7. Chittka, L., Kunze, J., Geiger, K.: Anim. Behav. *50*, 23 (1995)
8. Fisher, N. I.: Statistical Analysis of Circular Data. Cambridge Univ. Press 1993
9. Collett, T. S., Fry, S. N., Wehner, R.: J. Comp. Physiol. A *172*, 693 (1993)