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The automatic pilot of honeybees

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Using scanning harmonic radar, we make visible for the first time the complete trajectories of 'goal-vector' flights in honeybees. We demonstrate that bees captured at an established feeding station, and released elsewhere, nevertheless embark on the previously learned vector flight that would have taken them directly home from the station, had they not been artificially displaced. Almost all of the bees maintained accurate compensation for lateral wind drift, and many completed the full length of the vector flight before starting to search for their hive. Our results showed that bees tend to disregard landscape cues during these vector flights, at least initially, and rely on the 'optic flow' of the ground beneath them, and their sun compass, to judge both direction and distance.

Keywords: honeybee; vector flight; navigation; harmonic radar; wind compensation

1. INTRODUCTION

Central-place insect foragers are faced with the perennial problem of returning safely to their nests after long and circuitous excursions into what is often unfamiliar territory. Honeybees (*Apis mellifera*) in particular are renowned for their homing feats and although these have been intensively studied (Von Frisch 1967; Lindauer 1976), a lack of knowledge of the bees' actual flight trajectories has left significant uncertainties about their navigational methods (Menzel *et al.* 1996; Collett & Collett 2000). Desert ants of the genus *Cataglyphis* are known to use a method of *vector navigation* in which they integrate their translational movements during foraging, and continuously compute the vector that would take them directly back home to their nests (Wehner & Srinivasan 1981). Throughout this process, and while following their direct return paths home, they gauge their direction of travel from the azimuth of the sun and from the pattern of polarization in skylight (Wehner 1976). It was originally thought that, in the case of ants, distance was estimated from the self-induced optic flow (ground image movement) over the ventral retina (Ronacher & Wehner 1995), but more recent work has shown that the their odometer is based mainly on mechanically sensed information (Ronacher *et al.* 2000). The same dead-reckoning or path integration mechanism is believed to explain the ability of honeybees to return directly to their hives from distant foraging sites (Collett 1996; Collett & Collett 2000; Dyer *et al.* 2002), but unlike the case with pedestrian ants, it has not previously been possible to confirm this by direct observation of the bees' return paths. The mechanism must in any case be more complicated for a flying animal, because it has no mechanical contact with the ground from which to gauge distance travelled and it must also be able to correct for wind drift. We have therefore used the harmonic radar technique (Riley *et al.* 1996; Riley & Smith 2002) to determine the nature of bees' homeward flights. We also made provision to estimate accurately the wind-field in which the bees were flying so that we could investigate their ability to compensate for cross winds.

2. MATERIAL AND METHODS

The bee flight observations were made over a large area of mown pastureland, *ca.* 1 km × 1.5 km, close to the village of Klein Lüben, which is *ca.* 150 km northwest of Berlin. This area was selected because the terrain was unusually flat and free from obstacles that would have obscured the radar's field of view. We introduced artificial landscape features in the form of two groups of brightly coloured, triangular pyramid 'tents', which were 3.2 m tall (figure 1). There were very few natural sources of pollen and nectar present during our study period (late July–early August 1999).

We began our study by establishing in our experimental bees (European species *A. mellifera carnica*) a 'vector memory' of the hive position relative to a sugar solution feeder positioned 200 m to the east of their hive. The feeder contained 0.2–1 M sucrose solution, and training the bees to a distance of 200 m was accomplished over 2 days. Once foraging flights between hive and feeder were well established, we captured bees after they had ingested sugar solution and quickly transported them individually in a closed box to one of eight release points, distributed around the hive and *ca.* 250 m from it. The bees were then fitted with a radar transponder and released, and their flight paths were recorded by harmonic radar.

Bees fitted with transponders could be tracked while in flight within a 190° arc of radius 900 m, centred on the radar. Their positions were shown once every 3 seconds on the screen of a desktop Personal Computer and their coordinates recorded (Riley & Smith 2002). Wind speed and direction were monitored at 10 second intervals at a height of 2.7 m by anemometers and wind vanes placed at the corners of a 500 m × 600 m

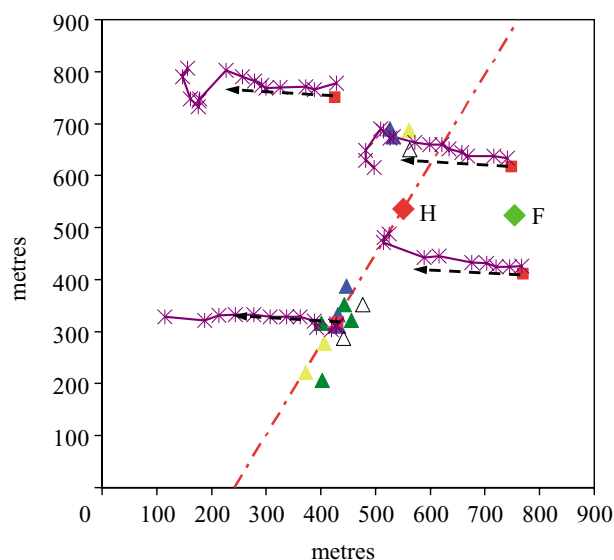*Author for correspondence (joe@radarent.freeserve.co.uk).

Figure 1. Four examples of vector flights by bees accustomed to flying between their hive (H) and an artificial feeder (F). The bees were captured at F after feeding, and then released at four different points (indicated by red squares) around the hive; their subsequent flights were recorded by the radar. Each radar position fix is marked by an asterisk, and the dashed line ending in an arrowhead extending from each release point represents the feeder-to-hive vector. The red broken line shows the delineation between the areas of pasture with grass of slightly different heights, and it can be seen that this is crossed by the feeder-to-hive vector from the release point to the north of F. Seven out of 10 bees flying from this point turned along the delineation when they encountered it 120 m into their westward flights. The positions of artificial landmarks are indicated by appropriately coloured triangles.

rectangle centred on the hive. Data from the four anemometers were averaged over the period of each vector flight, and then used to evaluate the coefficients in

$$V_{n_{xy}} = a_1 + a_2 x + a_3 y + a_4 y,$$

where $V_{n_{xy}}$ is the northerly component of wind speed at coordinates x,y, anywhere within the rectangle. An equivalent expression was used to derive the easterly component. These equations allowed us to calculate the mean wind vector at a height of 2.7 m at the mid-point of any vector flight within the rectangle.

To estimate the wind at other altitudes, we set up a mast near to the centre of the rectangle, holding anemometers at heights of 0.65, 1.3, 2.7 and 8.2 m, and a wind vane at 2.7 m. A second-order polynomial fit of the mast mean speed data to log height allowed us to estimate mean wind speed as a function of height at the mast position, for the duration of each vector flight. Since the area was very flat, we assumed that this function could be used to scale the 2.7 m mean wind vector, calculated for the vector flight midpoint, to the bee's height of flight. This height was estimated on the assumption that height = $v/3.5$, where v was the bee's mean ground speed over the vector flight, in m s^{-1}, and 3.5 rad s^{-1} its preferred optical flow rate (Riley *et al.* 1999; Riley & Osborne 2001). To find a bee's mean airspeed and heading during a vector flight, we calculated the mean wind vector at the midpoint of its track and at the estimated height of flight (Riley *et al.* 1999) and subtracted this from the insect's ground speed vector, as determined from the radar measurements.
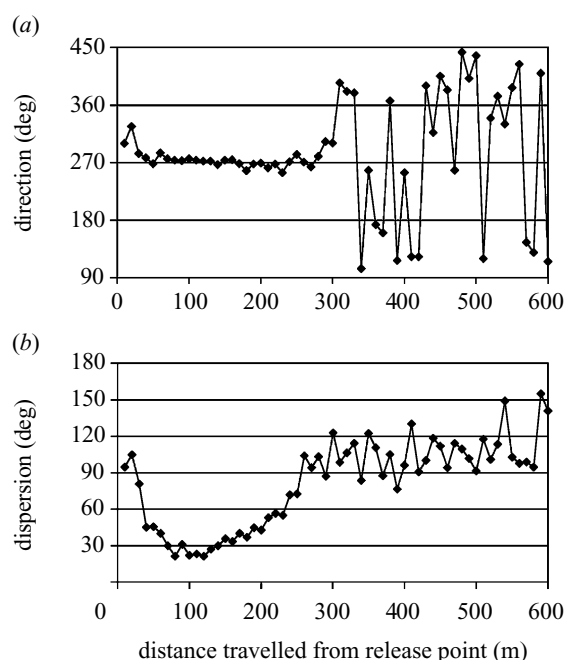
Figure 2. Accumulated data on vector flights ($n = 90$) of bees captured at the feeder and released at different points around the hive in July–August 1999. (*a*) The mean displacement direction. (*b*) The spread of directions (the angular dispersion of the flight paths, calculated using the 'doubling the angles' method described in Mardia (1972)). Both figure parts are plotted as a function of distance along the flight trajectory. The direction of the hive from the feeder was 273°.

3. RESULTS

The person releasing the bees noted that most flew initially in small circles or landed briefly, but irrespective of the position of the release point relative to the hive, their subsequent radar-tracked flight paths were always to the west. Figure 1 shows four examples where bees were released at different points, but maintained straight flights to the west for *ca.* 200 m, before beginning searching flights. These straight flights were almost exactly along the feeder-to-hive direction for their entire lengths, even when bees were released near to prominent artificial landmarks that were not present along the real feeder-to-hive path. The striking degree to which our experimental bees maintained their vector flights is illustrated in figure 2*a*, which shows that the mean direction of displacement of all the bees remained very close to the feeder-to-hive direction for at least 270 m. Although individual bees initially flew off in widely different directions, the differences between them fell rapidly in the first 70 m of flight (figure 2*b*). During the vector phase, the bees' mean ground speed (5.3 m s^{-1} ± 0.68 (s.d.), $n = 90$) was significantly higher than in their subsequent hive-seeking flight (3.85 m s^{-1} ± 0.27).

In both studies, bees showed no signs of drifting off the vector flight directions in cross-winds, and to test the accuracy of their compensation for lateral wind drift we plotted the components of the wind, and of the bees' air speeds, perpendicular to the hive–feeder axis (figure 3). The slope of the regression line (−0.97) and high correlation coefficient (0.83) demonstrates that, in the range of wind speeds (up to 5 m s^{-1}) and directions experienced
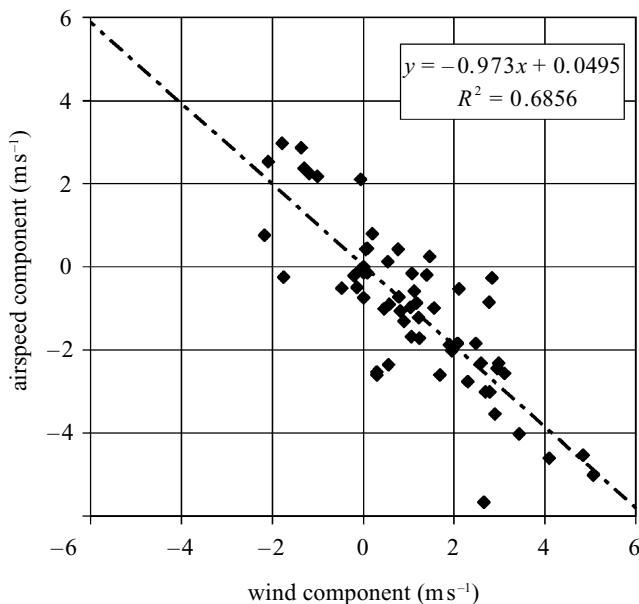
Figure 3. Accumulated data on wind compensation. The component of the wind (at the estimated flight height of each bee), at right angles to the homeward vector, is plotted against the same component of the bees' air speed. Northward components of the vectors are counted positive. A slope of -1 would indicate perfect compensation for cross winds.

during our field study, the bees were able to reduce lateral wind drift to negligible levels.

4. DISCUSSION

On the basis of his short-range visual observations of honeybees captured at an established feeding station and released elsewhere, Wolf suggested that displaced bees embark on the previously learned flight that would have taken them home from the station, had they not been artificially displaced (Wolf 1927; Ribbands 1964). Our results demonstrate that displaced bees do indeed make return 'vector' flights, and do not deviate towards the actual location of their goal, as suggested by Gould (1986). Our data also strikingly confirm Wolf's conjecture that many bees complete the full length of the homeward flight before starting to search for their hive. In a more recent study, we repeated the homing vector experiments, but we also captured trained bees as they left the hive, displaced them, and examined the degree to which their outward flights corresponded to the hive-to-feeder vector (J. R. Riley (and 12 others), unpublished data). We found that these bees, too, usually made vector flights, regardless of where they were released, but this time the flights were in the hive-to-feeder direction. In our studies, almost all of the bees maintained accurate compensation for lateral wind drift. It has been argued elsewhere (Collett *et al.* 1993; Riley *et al.* 1999; Riley & Osborne 2001) that drift compensation could be achieved if bees simply adjust their headings until the ground image movement over their retinas occurs at the angle relative to the sun's azimuth that corresponds to their intended tracks. This rather straightforward mechanism obviates the need for complicated correctional computations of air speed and heading of the type envisaged by Von Frisch (1967, p. 186). It also pre-

dicts that compensation can be maintained in the complete absence of landscape features normally associated with the desired track—a prediction now confirmed by our observations. Esch & Burns (1996) have shown that bees estimate the distance they have travelled by integrating the optic flow of ground image movement over their ventral retinas, a conclusion supported by more recent laboratory observations (Srinivasan *et al.* 2000). In our studies, where bees frequently adopted cross-track headings to compensate for side winds, the ground images would have moved obliquely over the ventral retina, so it seems that the optic flow integration mechanism is not restricted to image movements along the insects' longitudinal axes.

Our results demonstrate that bees tend to disregard landscape cues during vector flights, at least initially, and that flights were maintained even when this entailed flying in the vicinity of conspicuous visual features not present along the true hive-to-feeder path. This persistence suggested that the bees' response to unfamiliar landscape features was largely suppressed, and that in this sense, they were flying in an 'automatic pilot' mode. But there was one exception to this general rule. We had noticed in our 1999 experiments that after completion of their vector flights, if hive-seeking bees intercepted a line running approximately SSW–NNE across our flight arena, they often turned to fly along it. It subsequently became clear that this line corresponded to a previously unnoticed but perceptible edge between two areas of pasture mown at different times, and with grass of slightly different heights. The linear feature passed through the hive position, and it crossed the expected vector flight direction from one of our release points (figure 1), *ca.* 120 m to the west of it. Three out of 10 westward-bound bees released from this point over-flew the edge and completed their vector flights as normal, but when the other seven reached it they abandoned the homeward vector flight and turned to fly along the edge, most often in the hive direction. It thus appeared that in seven out of 10 cases, the 'automatic pilot mode' was over-ridden by a linear visual feature associated with the hive, with which the bees were familiar. This truncation of return vector journeys by a familiar linear feature is strikingly similar to that observed on a much smaller scale in early experiments with displaced foraging ants (Collett & Collett 2000), and suggests that airborne and pedestrian insect foragers may perhaps have similar elements in their hierarchy of homing strategies.

We note in conclusion that truncation of vector flights by some bees would not have been apparent without the ability of radar to reveal whole flight paths. This provides a cautionary illustration that establishing the relative importance of landscape-related and vector routes from traditional 'vanishing bearings' observations alone can be highly problematic (Collett & Collett 2000).

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