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The flight paths of honeybees recruited by the waggle dance

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In the ‘dance language’ of honeybees^{1,2}, the dancer generates a specific, coded message that describes the direction and distance from the hive of a new food source, and this message is displaced in both space and time from the dancer’s discovery of that source. Karl von Frisch concluded that bees ‘recruited’ by this dance used the information encoded in it to guide them directly to the remote food source, and this Nobel Prize-winning discovery revealed the most sophisticated example of non-primate communication that we know of^{3,4}. In spite of some initial scepticism^{5–9}, almost all biologists are now convinced that von Frisch was correct^{3,4,10–14}, but what has hitherto been lacking is a quantitative description of how effectively recruits translate the code in the dance into flight to their destinations. Using harmonic radar^{15–17} to record the actual flight paths of recruited bees, we now provide that description.

There have been some important advances since von Frisch’s original experiments, and it has been believed for some time that the honeybee communication system does not instantly specify a food location to the recruits, without any hesitancy and with pinpoint accuracy¹⁸. In fact, detailed observations have shown that recruits may go through several iterations of dance session and resultant search flight before they eventually arrive at the indicated food source, and some never find the food at all^{3,19–21}. The current interpretation of the von Frisch hypothesis thus predicts that newly recruited bees should fly directly from the hive to the vicinity of a food source, and then proceed to search for its exact location using odour and other cues². This searching period would neatly account for the fact that the arrival of recruits at the source is often

very much later than would be expected for a direct flight between the hive and food source—the anomaly that caused the initial scepticism about the hypothesis.

We began our experiments by capturing recruited bees as they left our observation hive, attaching a harmonic transponder, and then releasing them. The hive was not equipped to make quantitative measurements of individual dance angles or frequencies, but we observed that, at any given time, the dances of bees that had been previously recorded at the feeder were almost all aligned about a common direction. At midday this direction was at about 90° to the vertical, and this confirmed our expectation that the bees were feeding exclusively at our artificial feeder that lay 200 m directly east of the hive, and that it was to this food source that the waggle dances referred. Neither the feed nor the feeder station itself carried any artificial scents at any time.

Most recruited bees released from the hive almost immediately undertook a straight flight of direction and length that brought them directly into the vicinity of the feeder, as shown by the 19 flight paths from the hive in the upper part of Fig. 1. Figure 2a demonstrates that the mean direction of these flights lay impressively close to the hive-to-feeder direction for the first 200 m or so but, in spite of this, only two of the recruits actually found and alighted on the feeder. This was not a surprising result, given that similar low rates of success in finding unscented feeders have been found in conventional studies of recruit flight²². At the end of their straight outward flights, some recruits promptly initiated fairly direct return flights to the hive, but more usually they engaged in what appeared to be local searching manoeuvres for several minutes. It was noticeable that searching bees occasionally passed within just a few metres of the feeder without finding it, and in a few cases, searches lasted as long as 20 min, taking recruits as far as 200 m from the feeder location. These bees often returned to the point at which they had begun their searching behaviour before flying back to the hive, but fairly direct homeward flights from other points were also seen.

In a parallel experiment, recruited bees captured leaving the hive were taken to three release points 200–250 m away, and then

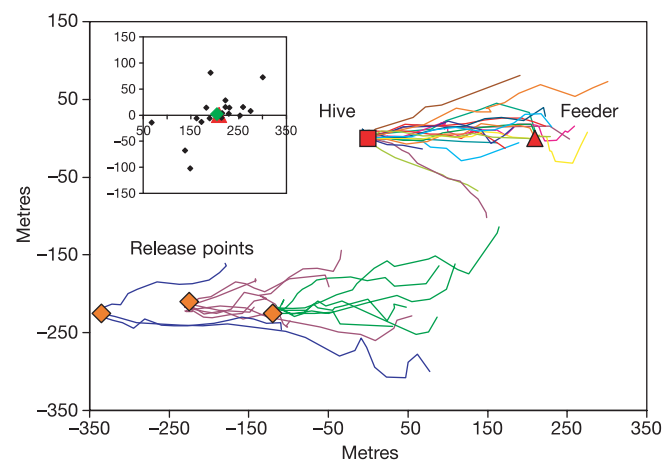


Figure 1 Flight paths of bees leaving the hive or other release points, after they had followed a waggle dance. Initial flight paths of 19 recruits leaving the hive (individual tracks in different colours) and of 17 recruits taken to locations southwest of the hive (different colour for each release point) before being released. The majority flew very close to the hive-to-feeder direction (90°), irrespective of where they were released. The tracks were truncated where they deviated by more than 90° from the hive-to-feeder direction over a track distance of more than 8 m, and this gave a mean length of 206 ± 53 m (s.d.) for hive-released bees, and 188 ± 94 m for the displaced bees. The corresponding straightness ratios (start–end point separation/track length) were 0.89 ± 0.07 and 0.82 ± 0.08. The end-point scatter of the hive-released recruits (inset) illustrates the imprecision of the dance communication/flight navigation system, but the close proximity of the mean end point (green diamond) to the feeder (red triangle) shows that, on average, the system is remarkably accurate.

released. These bees did not fly towards the actual position of the feeder, but instead made straight flights on the vector that would have taken them to the feeder had they not been displaced (lower tracks in Fig. 1, and mean direction in Fig. 2b). Their flights were thus exactly like those of recruits released at the hive, and similarly often extended to searching behaviour at the expected feeder position. Unable to locate the feeder, the bees then returned to their release site. The processes by which they eventually returned to their hive are described elsewhere²³.

The wind fields in which the bees were flying were almost always uniform, with no evidence of large-scale mixing eddies or back flow (see the example in Fig. 3a). The flow was predominantly from the west or southwest during our experiments (Fig. 3b), typically at 2–4 m s⁻¹, and this guaranteed that no odours from the feeder could possibly have been available to guide the recruits leaving the hive. As one would expect in these circumstances, the flight paths showed no evidence of the casting or upwind zigzagging that is known to characterize odour-following flight in other insects^{24–26}. These two facts, and the flight path data shown in Figs 1 and 2a, together carry the very convincing inference that recruits leave the hive with prior knowledge of the direction and distance of a food source that they have never previously visited. By themselves, these observations thus provide extremely strong, direct support for von Frisch's hypothesis that recruited bees 'read' the waggle dance, but the most compelling evidence comes from the flights of displaced recruits. These bees made direct flights to where the feeder should have been (Figs 1 and 2b), and did so without the aid of

any landscape or odour cues that might have existed on the true hive-to-feeder route. There was also, of course, no possibility that they were following either regular foragers directly, or ephemeral odour trails left in the hive-to-feeder flight corridor by regular forager traffic.

It is important to note that, although the feeder was in the overall downwind direction from the hive, the recruits were not simply flying downwind. For example, Fig. 3a shows how a feeder-bound recruit adopted a heading of 28° to the south of its track direction so as to compensate for the northerly drift that would otherwise have been produced by the southwesterly wind. This ability to compensate for lateral wind drift appears to be common to both bumble bees²⁷ and honeybees²⁸ and it was clearly demonstrated in most of the recruits that we observed (see examples in Fig. 3b). In spite of wind compensation, the translation by individual recruits of information encoded in the waggle dance into flight to the intended destination was rarely perfect (see scatter diagram inset, Fig. 1). While the diagram shows that the mean of the outward vector flights was impressively close to the target (within 6 m), most ended tens of metres from the feeder. Thus some form of terminal guidance would normally be essential for successful homing on the target and, in the case of natural food sources, this would usually be available in the form of visual and odour cues, and sometimes from experienced foragers manoeuvring over the source²².

In summary, we have provided the first quantitative and direct description of the degree to which recruits translate information encoded in the waggle dance into flight to the vicinity of the designated destination. Our results have shown that although this

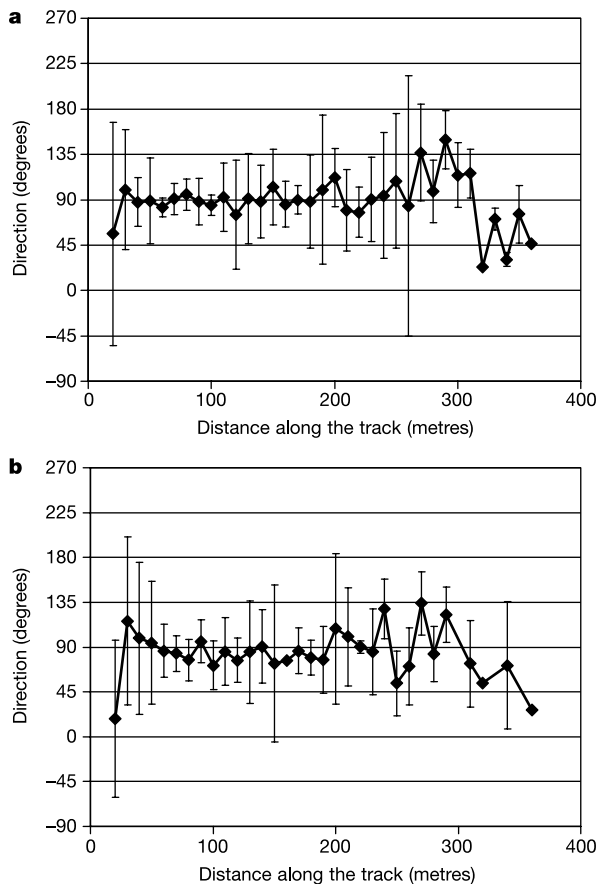


Figure 2 Circular mean of direction of travel as a function of distance along flight path. **a**, The 19 hive-departing recruits (see Fig. 1). The mean remains very close to the hive-to-feeder direction (90°) to beyond 200 m. **b**, The 17 recruits displaced to the south-west before release. The mean is again very close to 90°: the expected direction to the feeder, had the recruits read the dance. Vertical bars indicate the angular dispersion (spread of directions among individuals).

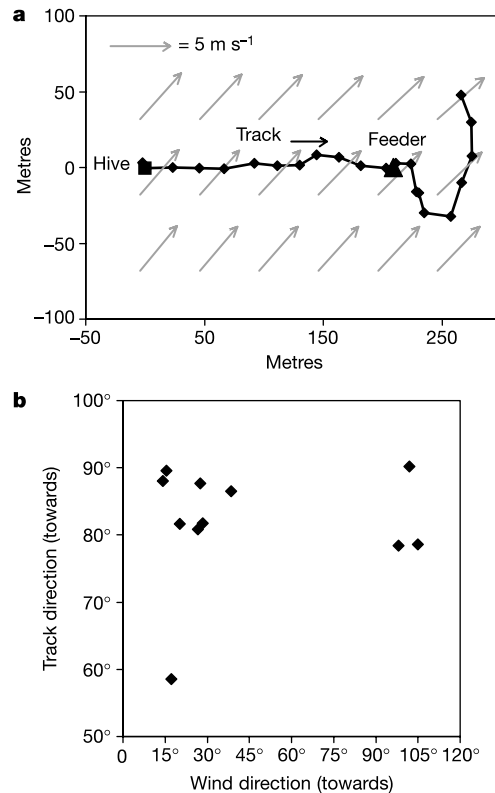


Figure 3 Wind compensation. **a**, Flight path of a recruit leaving the hive in a cross-wind (grey arrows). Over the straight part of the track (towards 87°), its ground speed was 6.8 m s⁻¹, implying a flight height of 1.9 m (refs 16, 27). The mean wind at this height was 3.3 m s⁻¹ towards 38°, showing that the bee's air speed was 5.2 m s⁻¹ and that it had adopted a heading of 115° to avoid drifting northwards. **b**, Comparison of wind and track directions for 11 recruits leaving the hive, when the wind field was particularly uniform. All compensated for lateral wind drift. Note also that the hive was never downwind of the feeder.

process is highly effective, most recruits would not reach the intended food sources without the use of odour and visual cues in the final stages of their flight. We hope that together with earlier studies, particularly those of Gould¹⁰, Srinivasan *et al.*¹³ and Esch *et al.*¹⁴, our results will also be accepted as a vindication of the von Frisch hypothesis. □

Methods

Harmonic radar

Most of our knowledge of insect flight behaviour at high altitudes has been derived from the use of radar modified for entomological observations²⁹. More recently, it has become possible to apply this technique to low-flying insects by tagging them with tiny harmonic transponders, weighing only a few milligrams (6–20 mg, depending on the degree of mechanical robustness required). The transponders return signals to the radar at twice the original transmitted frequency, and because these signals can be distinguished from returns from ground features and other unwanted targets, the position of tagged insects can be determined while they are in flight^{15–17}. In our experiments we caught bees as they exited their hive, attached transponders, and released them from the hive (or from remote release points), and recorded their subsequent flight trajectories. Nineteen of the 23 recruits (83%) released from the hive flew off satisfactorily, and produced good radar tracks, all to the east. Of the remaining four, three also went east, but were not detected by the radar enough times to produce a satisfactory track, probably because they were flying very low. Only one failed to leave the vicinity of the hive. Similar results were achieved for the remote releases, except during a period when the tubes in which the recruits were being transported became accidentally contaminated with sucrose solution, with the result that these bees did not fly away from the release point.

Experimental arena

The flight observations were made over a carefully selected³⁰, large area of mown pastureland, approximately 1 × 1.5 km, where the terrain was unusually flat and free from obstacles that would have obscured the radar’s field of view²⁸. The radar was positioned on the southern edge of the arena, so that it overlooked an observation hive and a feeding station 200 m to the east of the hive. Three release points were set 200–250 m in the sector to the southwest of the hive. There were very few natural sources of pollen and nectar present during our study period (late July/early August 2000).

Description of the wind field

Wind speed and direction were recorded at 10-s intervals at a height of 2.7 m by anemometers and wind vanes placed at the corners of a 500 m × 600 m rectangle centred on the hive. We also 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. The clocks of the recording data loggers were synchronized each morning with a master clock at the radar to ensure that wind data were recoverable for the duration of each individual recorded flight. Using interpolation methods described elsewhere^{16,27} the data collected by these instruments were then combined to describe the mean wind field within which each of the flights recorded by the radar took place.

The observation hive

We used a two-frame colony, equipped with a transparent side panel that faced directly into a small, low tent attached to the hive. From within this darkened enclosure we could observe the dance behaviour of the bees, and their entry into and exit from the hive. Most of the bees in the small colony were marked with numbered tags. The entrance to the hive was in the form of clear plastic tube, so that observers stationed outside the tent could also observe entry and exit, and capture selected bees for tagging with transponders.

The flight experiments

We began our study by establishing in our experimental bees (European species *Apis mellifera carnica*) a route memory of the position of a feeding station relative to the hive. The feeder was placed directly to the east of the hive, and supplied with 0.2–1 M sucrose solution, and training to a distance of 200 m was accomplished over two days. No artificial odour cues were used in the procedure. From the start, observers at the feeder recorded the identification number of every marked bee that arrived there, and the hive was never opened unless an observer was at the feeder. Once foraging flights between hive and feeder were well established, observers in the tent watched the waggle dances. Whenever a numbered bee was seen to follow a dance and then move directly towards the exit, an observer outside the tent was alerted to catch the bee as it attempted to leave. If its identification number indicated that it had never previously visited the feeder, the bee was confirmed as a recruit, and a transponder attached. The bee was then either released directly from the hive exit, or taken in an opaque tube to one of three release points 200–250 m from the hive, and allowed to fly from there. Bees fitted with transponders could be detected while in flight within a 190° arc of radius 900 m, centred on the radar; their positions were shown once every 3 s on the screen of a desktop personal computer, and their coordinates recorded¹⁷.

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The origin of bursts and heavy tails in human dynamics

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The dynamics of many social, technological and economic phenomena are driven by individual human actions, turning the quantitative understanding of human behaviour into a central question of modern science. Current models of human dynamics, used from risk assessment to communications, assume that human actions are randomly distributed in time and thus