

# Honey bees can perform accurately directed waggle dances based solely on information from a homeward trip

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**Abstract** Honey bees were displaced several 100 m from their hive to an unfamiliar site and provisioned with honey. After feeding, almost two-thirds of the bees flew home to their hive within a 50 min observation time. About half of these returning, bees signalled the direction of the release site in waggle dances thus demonstrating that the dance can be guided entirely by information gathered on a single homeward trip. The likely reason for the bees' enthusiastic dancing on their initial return from this new site was the highly rewarding honeycomb that they were given there. The attractive nature of the site is confirmed by many of these bees revisiting the site and continuing to forage there.

**Keywords** Honey bee homing · Displaced bee navigation · Path integration · Waggle dance · Bee training

## Introduction

Foraging honey bees indicate the direction and distance of a food site from the hive by performing a waggle dance which encodes these parameters of the trip (von Frisch 1965/1967). An early study by Otto (1959) in which bees were displaced while feeding to a release site that lay in a different direction from the hive showed that bees can be guided by information gathered on both their outward and inward trips. But it is generally supposed that information from the outward trip contributes more (Lindauer 1948; von Frisch 1965/1967; Srinivasan et al. 1996; De Marco

and Menzel 2005). Here I show that information from a single homeward trip can suffice to provide precise directional information for the dance.

The technique used is to monitor at the hive what happens when honey bees have returned after being displaced to an unfamiliar release site from their hive. It is well known that honey bees carried to sites at different distances from their hive (Romanes 1885; Uchida and Kuwabara 1951; Becker 1958; Southwick and Buchmann 1995) will fly home. From displacements of a 100 m, homing can be rapid and reliable (Romanes 1885), but from distances of several kilometres fewer bees arrive, and it may take them several hours to reach the hive, suggesting that they did not home directly (Pahl et al. 2011). As honey bees normally start performing waggle dances after making several complete foraging trips to and from a food site (Lindauer 1948; von Frisch 1965/1967), it might be supposed that dances do not occur after such displacements. The new part of the procedure is to feed bees highly rewarding honeycomb at the release site. Bees then seem eager to dance and indicate the location of the site to potential foragers on reaching the hive and to revisit to the site themselves.

## Materials and methods

### Experimental area and general procedure

Hives were moved to the experimental area near the village of Marloffstein (49°36'51.76''N; 11°03'49.79''E) relatively late in the summer to minimise the likelihood that bees had foraged in and become familiar with the area of the release site before they were displaced there in tests. Colonies of *Apis mellifera carnica*, that were housed in a four frame observation hive with sufficient stored honey were taken

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from an apiary at the Landesanstalt für Bienenzucht, Burgberg, Erlangen, to the outskirts of Marloffstein 5 km away. In 1999, the first year of the reported study, the move was in mid July and in 2004 it was at the end of August. Before the experiments began, the bees were allowed ample time (2 days minimum) to explore their new surroundings.

In late summer and autumn, the open Bavarian countryside offers little forage to honey bees. It is almost devoid of nectar-bearing flowers and the long spells of fine weather make it an ideal time to attract bees to artificial feeders. At the time of the move in 1999, the surrounding meadows and fields were already harvested and ploughed, apart from a ca. 3000 square metre plot located 400 m NE of the observation hive where trefoil was in bloom. The transplanted colony found this (last) good source and visited it during the 2 days before that field was also cut and ploughed. One bee flying there performed as many as 205 dance circuits in one dance indicating that the dance threshold was very low, and that little natural forage was about. Once the tests had started the only dancing seen was by experimental bees after feeding at their release site. If there was additional (unnoticed) dancing, it could only have been to farm gardens lying more than 350 m north of the hive and well away from the area and directions of the release sites (Table 1).

To encourage unoccupied foragers in the hive to leave it and participate in an experiment, a trail of a few sucrose drops (15 % W/V) led from the hive to the landing ramp outside. About 20 bees were trapped on the ramp in a conical transparent plastic container (20 cm long with ends 8 and 15 cm in diameter). The wider open end of the container was closed with a perforated lid, the container placed in a black cloth sleeve and carried to one of the release sites listed in Table 1.

Bees at the release site were free to feed *ad lib.* from honeycomb in a tray and afterwards to fly off. To induce bees to start feeding, the closed container was first placed vertically with its narrow closed end pointing upwards. The sleeve was removed at the top end so that all the bees inside were attracted by the sunlight to the top of the container. Honeycomb and tray were then moved under the opened lower end. As soon as the top end was darkened and the bottom end uncovered, bees moved to the comb. The container could then be removed without disturbing the feeding bees, which were marked with numbered discs or dabs of paint while they imbibed the honey.

The bees' departures from the food and arrivals at the hive (and vice versa) were recorded by observers stationed at both locations. The bees on their first departures from the release site, circled above the feeder and the area, some for half a minute, presumably learning the landscape around the feeder (Opfinger 1931; Lehrer 1993). The site was made conspicuous by a variety of objects. An anis seed

**Table 1** Overview of seven release experiments

Date locations Marloffstein (ERLANGEN vertical comb)	Release site		Number of dancing bees on first visit to hive	Number of dancing bees returned to food	Number of not dancing bees returned to food	Video-record (yes no)	Observer at site/hive	
	Compass direction (°)	Distance (m)						Time
30 July 99	287	560	15:45	23/19	7	3	2	No +/-
30 July 99	93	365	17:25	16/8	5	3	1	No +/-
17 Sept. 99 vertical test	273	300	15:05	12/10	6	5	1	No +/-
27 Aug. 04	287	560	16:05	37/35	9	7	3	Yes +/-
02 Sept. 04	93	365	13:20	28/19	9	8	4	No +/-
09 Sept. 04	187	300	13:42	Approx. 20/?	2	Observations	Interrupted	Yes --/+
09 Sept. 04	93	365	16:12	24/?	3	Observations	Interrupted	Yes --/+

scent plate was put next to the tray of honeycomb, white sheets were distributed on the ground and a large yellow umbrella-like object (1 m wide and 1.5 m high) placed nearby. Additionally, there was an observer seated in front of a table.

Bees were first recorded revisiting the feeder 15 min after their release, having already unloaded honey at the hive. Their erratic searching distinguished them from other individuals which had failed to find the hive and came back to the feeder still heavily laden with honey. Revisiting bees were aided in their search for the feeder by Nasonov's pheromone released by the bees that had not yet managed to reach the hive. To reduce the chances that bees from another hive might find the feeder, the honey was always removed after 50 min and the recording ended.

The moving of whole colonies at close range combined with feeding is a standard beekeeping method (Sklenar 1954), but it is also possible to train bees to a new foraging location in one step by temporarily bringing the whole hive to this site.

### Recording and analysing dances

Dances were made easy to observe and interpret by putting the hive on its side and giving bees on the dance area of the horizontal comb an unobstructed view of the sky. The waggle dances were then oriented by celestial cues rather than by gravity. Because the dances were then directed towards the foraging source that the bees were advertising (Lindauer in von Frisch 1965/1967; Edrich 1975, 1977; Tanner and Visscher 2010), they were easy for an observer to decode and record.

In 1999, the bees' behaviour at the release site and their dancing at the hive were observed by eye and whether or not the dances were direction to the release site was recorded on audiotape. Dance direction was estimated to a precision of about  $\pm 20^\circ$  using a  $360^\circ$  protractor that was centred over the dancing bee (von Helversen and Edrich 1974). The category 'directed to the release site' includes dances in which the direction of the waggle phase was within about  $\pm 20^\circ$  of the bearing from hive to feeder.

All the bees seen dancing had been marked before release and all except one dancing bee signalled the direction to the release site. The dances on the bees' first returns appeared unusual and in 2004 all dances were video-taped with a camera pointing downwards at the horizontal dance area. The camera was set to view most of the dance floor. Consequently, although the direction and divergence angles could be measured with an accuracy of about  $3^\circ$ , the resolution was often insufficient to pick out individual waggles in the straight segments. For this and other reasons explained below only a few dances could be used for decoding the distances that the bees signalled.

The long waggle dances of eight videotaped bees were analysed as representative examples of dancing seen on the bees' first returns from the release site and on subsequent returns after revisiting the site. More than eight dances were observed, but did not meet the criterion of more than 15 straight waggle segments. Some were incomplete. Some were masked by other bees. In other cases, the dancing bee moved out of the view of the camera or danced fewer than ten circuits because it was attacked by guard bees. Short dances were not analysed because they were mostly irregular with unequal ratios of clockwise and counter-clockwise segments and had frequent interruptions.

During slow-motion playback of video tapes waggle segments and the crescent segments were traced onto transparencies fixed to the screen of the video monitor (Edrich 1975). The directions of waggle segments relative to north were measured with a protractor to an accuracy of  $3^\circ$  and the means of the directions of each of the eight dances computed using circular statistics (Batchelet 1981). The straight segment of each circuit of the dance is usually directed alternately left and right of the mean direction (von Frisch 1965/1967), and the mean divergence angle between alternate segments was calculated (Table 2).

For the few dances for which it was possible, the number of waggles during individual waggle segments was counted during slowed down replay of the video to provide a measure of the distance indicated by the dance (e.g. Esch and Burns 1996; De Marco and Menzel 2005). On the bees' first returns individual waggle segments were absent in 12 % of the 223 segments analysed and these segments were excluded from analysis. Ideally, the number of waggles per circuit on dances after bees had revisited the site can provide a distance calibration for the number of waggles in dances after the bees' first returns from the site. The average number of waggles per complete figure of eight circuit on dances after revisiting the site at 560 m from the hive were for two bees 11.4 (SD  $\pm 2.4$ ) and 14.5 ( $\pm 2.2$ ) waggles/circuit. The values for two bees revisiting the site at 300 m from the hive were 2.8 ( $\pm 1.4$ ) and 2.0 ( $\pm 0.8$ ) waggles/circuit. This large non-linearity for the two distances makes the values from the dances recorded after the bees' first return hard to evaluate. There are first return data for only one bee leaving the 560 m site [3.1 ( $\pm 3.7$ ) waggles/circuit] and for two bees leaving the 300 m site [2.8 ( $\pm 1.4$ ) and 2.0 ( $\pm 0.8$ ) waggles/circuit]. Clearly, more data are required before any conclusions can be drawn.

### Results

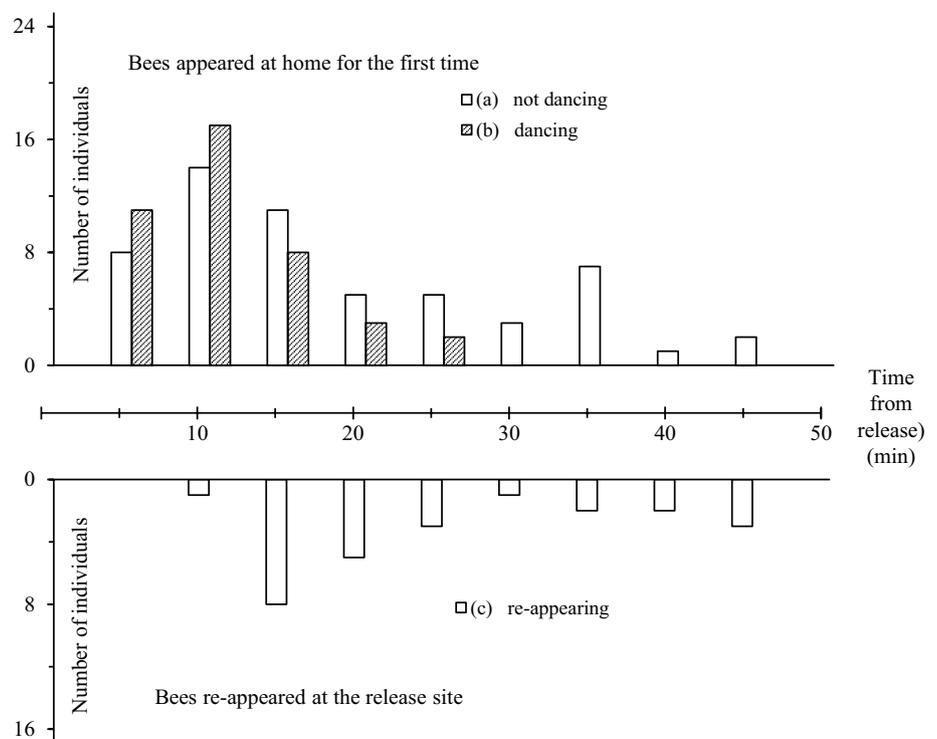
Of 160 honey bees released from 5 different directions with respect to their hive, 97 homed within the 50 min observation period of the experiments. The average homing time

**Table 2** Single Bees' dance directions and dance speeds from video-taped release experiments

Date	Direction and distance of release site from hive	Bee identification	Mean of dance angles for CCW and CW turns	Dance divergence (see Fig. 2)	Mean dance direction	Vector length (dance scatter)	Cycle number in calculations/total cycles
Dancing after first return							
27.08.04	287°560 m	#41	ccw 274.1 cw 303.9	29.8	285.0	0.89	54/60 plus
09.09.04	93°365 m	TQ	ccw 57.1 cw 109.2	52.1	80.2	0.82	55/63
09.09.04	187°300 m	GR	ccw 167.1 cw 217.1	50.0	190.9	0.85	88/89
09.09.04	187°300 m	WL	ccw 180.4 cw 213.7	33.3	189.6	0.80	26/27
Dancing after subsequent trip to release site							
27.08.04	287°560 m	#31	ccw 263.5 cw 274.0	10.5	265.7	0.95	60/124 plus
27.08.04	287°560 m	#14	ccw 265.9 cw 281.0	15.1	275.6	0.96	43/45
09.09.04	187°300 m	GL	ccw 202.2 cw 217.6	15.4	207.3	0.91	42/43
09.09.04	187°300 m	WR	ccw 186.5 cw 204.5	18.0	202.1	0.91	15/17

CW clockwise, CCW counter-clockwise

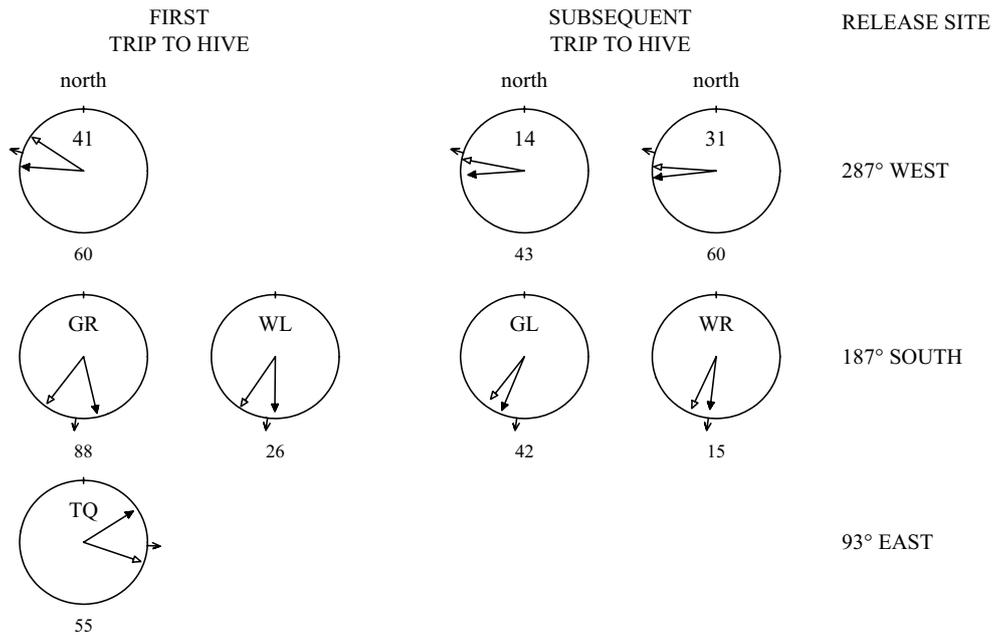
**Fig. 1** Distribution of times bees take to reach the hive on their first return home and then to arrive back at the feeding site. The *top histogram* shows the arrival times of bees that reached the hive and danced (*hatched columns*) and of bees that reached the hive but did not dance (*open columns*). The *bottom histogram* with data plotted downwards gives the arrival times at the feeder of those bees that revisited. *Abscissa* time taken to reach goal. Bin width is 5 minutes. *Ordinate* number of bees in each bin. Data were collected from 91 marked bees reaching the hive within 50 min after release. 41 of these individuals danced upon their first arrival at the hive



was 15.2 min (SD 9.6, range 4–48,  $N = 97$ ). The distribution was skewed with a peak at about 10 min (Fig. 1). 41 out of 91 bees observed in the hive danced, with those reaching the hive early in the 50 min more likely to dance than those that took longer to fly home (Fig. 1; Table 1).

All 41 dances were directed at the feeding site within about  $\pm 25^\circ$  of the bearing from hive to feeder.

26 of the bees that had returned to the hive were seen afterwards to revisit the release site (Fig. 1). Of these 26 bees, 16 had danced before returning to the release site and



**Fig. 2** Examples of dance directions in vector form. The mean dance directions of individual bees on their first trip home and after their subsequent trip to the release site are indicated by two arrows in each circle. Filled arrow heads give directions of waggles segments that precede clockwise crescents, open arrow heads those that precede counter-clockwise crescents. Lengths of arrows show mean resultant waggles vectors as a proportion of the radius of the bounding circle. Each row gives the data from a different release site with a different direction from the hive as specified in column 3 and by arrows out-

side the circles. The circles are arranged in three rows according to three release sites with compass directions from the hive West 287°, South 187° and East 93° (arrows outside the circles). The number below each circle shows how many straight segments contributed to the mean. The angular difference between the two arrows gives the mean divergence angle of adjacent waggles segments for each dance, indicating a larger divergence angle in dances performed on a bee's first return to the hive than after a subsequent foraging trip

10 had not. Although more dancers than non-dancers revisited the release site, the numbers as a proportion of the total numbers of dancers or non-dancers are not significantly different. Thus, 16 out of 41 dancers and 10 out of 50 non-dancers revisited the feeder ( $P = 0.0623$ , Fisher's exact test, 2-tail).

Quantitative details of eight long waggles dances (Fig. 2; Table 2) show that the four dances performed after the bees' first return to the hive and the four dances performed after a repeated trip were equally well directed at the release site. But there are some clear differences between the first and subsequent dances. Most obviously, the divergence angle is much larger on the dances after first returns than it is after subsequent returns from the feeder—a finding that will be elaborated on in the "Discussion" on subsequent dances. Because of the large and unexpected reward, the first returns tend to be faster.

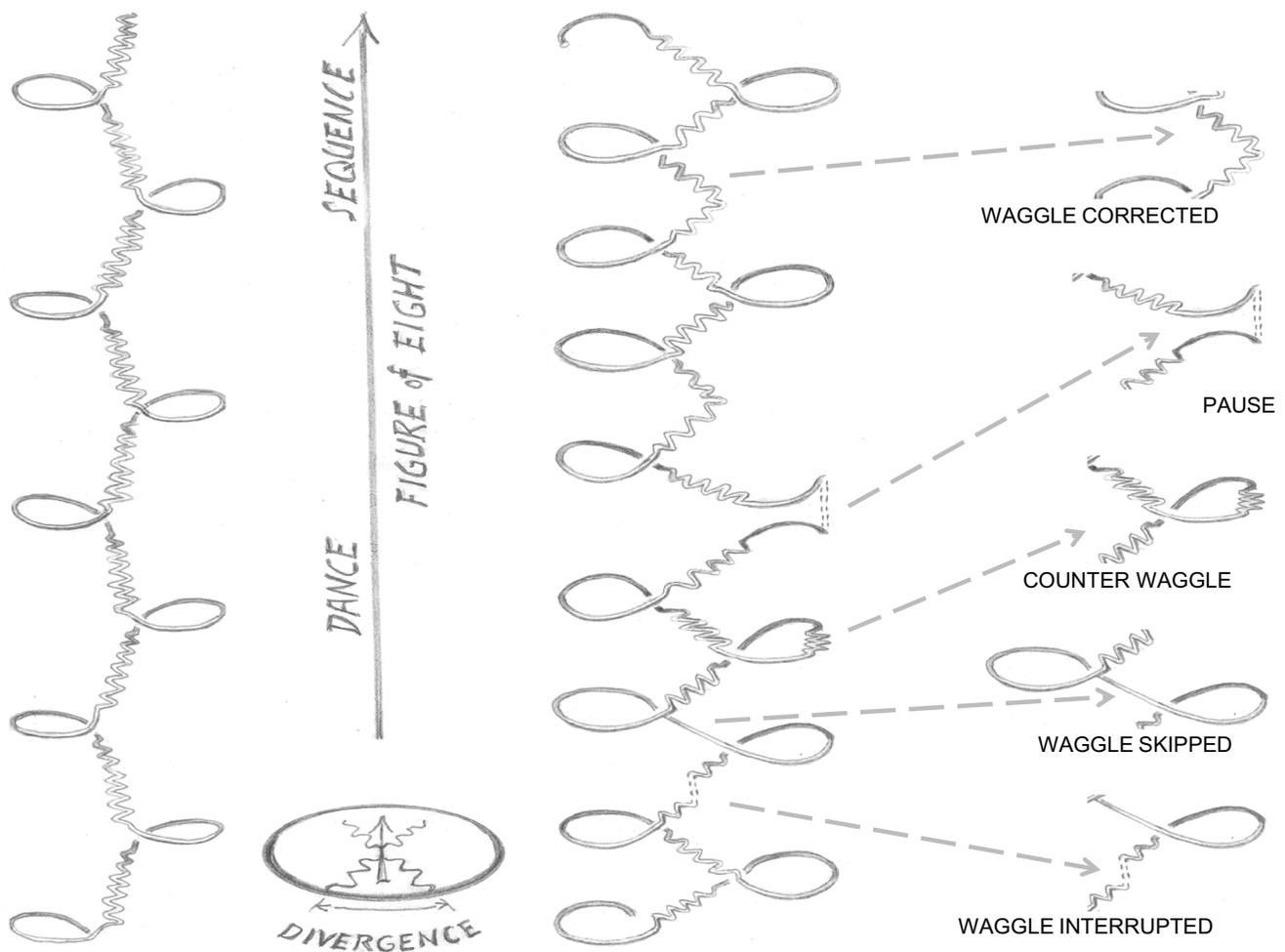
There are also marked qualitative differences between the first dances and those after revisiting the feeder (Fig. 3). Dances on the first trip home appear disordered in several ways: the strict alternation between clockwise and counter-clockwise crescents is sometimes disrupted; a waggles segment may be performed in the reverse direction, or waggles movements inserted into a crescent. Dances on the first

returns also tend to be faster than after subsequent re-returns, corroborating observations that dances are particularly fast and vigorous after a first encounter with an unexpectedly rich food source (c.f. Edrich et al. 1995; Seeley et al. 2000).

### Discussion

This study adds a significant new finding to the vast body of knowledge concerning the honey bee dance and navigation. It is that bees can perform waggles dances in the hive after their first return from an unknown release site to which they were carried from the hive. The dances were consistently directed towards the release site. Because the bees were unfamiliar with the release site and so probably took a circuitous route (see below), this finding suggests that the direction of the release site from the hive was obtained through some kind of path integration performed on the way home and that the directional signal derived from path integration was inverted to guide the dance.

Before discussing these results further, it is worth rehearsing the evidence that the release site itself was unfamiliar, even though bees probably performed orientation flights (Opfinger 1931; Capaldi et al. 2000) around the hive



**Fig. 3** 3-D-presentation of two waggles, one on a first return to the hive and the other after revisiting the food site. The spirals with waggles ordered in time are to be read upwards from the bottom of the figure (see lettering on a separate axis). The free hand drawings are based on video clips of two dances, depicting 26 s of their dance. The number of waggles depicted is not accurate. *Left column* dance performed by bee #31 after a subsequent trip to the feeder. *Right column* dance of bee #41 performed immediately after its first

trip home. The direction of the release site is indicated by the arrow in the ellipse at the bottom of the vertical axis, here pointing away from the observer through the plane of the drawing. Several oddities of a first-trip dance (*right column*), as mentioned in the results, are illustrated in *insets* on the far right. Other characteristics of lively dances are expressed in greater speed of dancing, large divergence angles, and larger area covered by the dance

to survey the new landscape immediately after the hive was transferred into the experimental area before the experiments started. First, the author saw no bees around the experimental sites and no more than a few unvisited flowers in the surrounding grass fields. Second, on visits to the hive between experiments the author noticed occasional dances, but these pointed at village gardens to the north, a direction that was not used for releases. Third, the bees took much longer to fly to their hive than the 30–50 s, it took the bees to fly home once they were experienced with the location of the release sites and flew directly home; although, without monitoring the bee's homeward path, it remains possible that bees landed and rested *en route*. Fourth, the bees' dances differed in several respects from normal ones and

those seen on their returns after revisiting the feeding site (Fig. 3). Fifth, some bees which homed successfully did not reappear again at the release site, despite performing dances and leaving the hive.

That bees can use the direction of their homeward trip to direct dances to a feeder is not unexpected. The work of Otto (1959) and of De Marco and Menzel (2005) showing that bees combine directional information from food-ward and homeward trips already tells us that information from the return flight can be transformed, so that it can contribute to dance performance. In desert ants too, the intimate connection between the two directions is apparent: recalibration of the home-vector induces similar re-calibration of the food-ward vector (Collett et al. 1999).

Dances on a bee's first return (after a normal outward flight) are very rare. Lindauer (1948) observed them in a colony with almost no honey reserves in their hive. Dances immediately after displacement from the hive to a release site have to my knowledge been reported only once in an unpublished PhD thesis (Brines 1978). Brines using the same training method as here (which he learnt from the author) displaced bees 200 m from the hive along a flight corridor that was familiar to them. He also recorded dances directed to the release site, but did not analyse second return dances nor estimate the distances that the dances signalled. Interestingly, in Brines' study the bee dances were more similar to those of well-established foragers, and probably had normal divergence angles. The large divergence angles seen in my experiments are likely to be a consequence of the unfamiliarity of the release site. When the site is familiar, the homeward route can be direct, but when the site is unknown the route is likely to be circuitous. This difference provides further support for a model of path integration that I developed earlier (Edrich 1975).

Through path integration a bee flying between a feeding site and its hive continuously monitors a sometimes circuitous path and converts it into a straight line vector representing the direction and distance it has travelled. So, once arrived at the hive, the bee has a record of the vector between the feeding site and hive (e.g. Mittelstaedt 1983; Collett and Collett 2000; Tautz et al. 2004). To generate an outward trip to a known feeding site, the bees fly the remembered vector in the food-ward direction.

Dances of honey bees based only on the outward trip could use the path integration state attained when a bee has reached the feeder. Dances based solely on the homeward trip, as in the present study could be guided by inverting the path integration vector at the hive. By definition path integration converts a circuitous path into a straight line vector and this is seen in the small scatter of the directions of the dances that the bees performed on their first return. But do the dances exhibit any sign that this first homeward trip was probably circuitous? There is an evidence that the divergence angle between alternate segments gives some indication.

As with so much about the bee dance, the first discovery that dance divergence varies with details of the flight came from von Frisch (von Frisch 1965, pp. 63, 148, 185; von Frisch 1967, pp. 62, 147, 181; Edrich 1975). An intriguing pattern of results has emerged. First, the angle of divergence is large when bees forage between 80 and 200 m and is usually smaller as foraging distance increases and the precision of directional information presumably becomes greater. Second, divergence varies when the input from the light compass is more erratic than usual. Third, divergence is large when a bee must circumvent an obstacle or, as in the present experiments, when bees unfamiliar with their surroundings take circuitous paths (as predicted in Edrich

1975). Lastly, dance divergence increases when the gravitational input that bees use to orient their dance on vertical comb in a darkened hive is reduced by tilting the hive (Edrich 1975).

While it is commonly assumed that the divergence angle indicates the imprecision of a bee's directional information (Tanner and Visscher 2010), I suggested that the divergence reflects more a dynamic process related to the changes in direction that a bee experiences during its flight path (Edrich 1975). A flavour of the idea is given by considering a bee flying in sunlight. It records the route as superimposed 'after images of the sun's position in a retinotopic neural array. The more circuitous the route, the larger is the area of the array covered by after-images. Suppose that when dancing one edge of the array occupied by the sun's after-image triggers a straight waggle run on a clockwise circuit and the other edge the successive one on a counter-clockwise circuit. Then the bigger the area covered by the sun the larger will be the divergence angle under the prevailing stimulus distribution, although the mean of the adjacent straight waggle runs will correctly indicate the bee's intended direction. A good review of this concept (Edrich 1975) is given by Tanner and Visscher (2010). The model is expanded and supported by training experiments on wood ants in which the scatter of compass directions was related to different experimentally imposed light distributions (Scharstein 1975).

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#### Compliance with ethical standards

Guidelines for the care and use of animals were followed.

#### References

- Batchelet E (1981) Circular statistics in biology. Academic Press, London
- Becker L (1958) Untersuchungen über das Heimfindervermögen der Bienen. *Z vergl Physiol* 41:1–25

- Brines ML (1978) Skylight polarisation patterns as cues for honey bee orientation. Thesis, Rockefeller University, New York
- Capaldi EA, Smith AD, Osborne JL, Fahrbach SE, Farris SM, Reynolds DR, Edwards AS, Martin A, Robinson GE, Poppy GM, Riley JR (2000) Ontogeny of orientation flight in the honey bee revealed by harmonic radar. *Nature* 403:537–540
- Collett M, Collett TS (2000) How do insects use path integration for their navigation? *Biol Cybern* 83:245–259
- Collett M, Collett TS, Wehner R (1999) Calibration of vector navigation in desert ants. *Curr Biol* 9:1034
- De Marco R, Menzel R (2005) Encoding spatial information in the waggle dance. *J Exp Biol* 208:3885–3894
- Edrich W (1975) The waggle dance of the honeybee; a new formulation. *Fortschr Zool* 23:20–30 and 48–51
- Edrich W (1977) The interaction of light and gravity in the orientation of the waggle dance of honey bees. *Anim Behav* 25:342–363
- Edrich W, Farina W, Kramer E, Nunez JA (1995) Soliciting behaviour of Africanized honey bees studied in Salta, Argentina. In: Proceedings of the international conference on tropical bees & the environment, 1994. Mardan M, Sipat A, Yusoff, KM, Kiew HMSR, Abdullah MM (eds) Jutaprint, 2 Solok Sungei Pinang 3, 11600 Penang, Malaysia, pp 34–38. The author will send a reprint on request
- Esch H, Burns J (1996) Distance estimation by foraging honeybees. *J Exp Biol* 199:155–162
- Lehrer M (1993) Why do bees turn back and look? *J Comp Physiol A* 172:549–563
- Lindauer M (1948) Über die Einwirkung von Duft und Geschmacksstoffen sowie anderen Faktoren auf die Tänze der Bienen. *Z vergl Physiol* 31:48–412
- Mittelstaedt H (1983) The role of multimodal convergence in homing by path integration. *Fortschr Zool* 28:197–212
- Opfinger E (1931) Über die Orientierung der Bienen an der Futterstelle. *Z vergl Physiol* 15:431–487
- Otto F (1959) Die Bedeutung des Rückflugs für die Richtungs- und Entfernungsangabe der Bienen. *Z vergl Physiol* 42:303–333
- Pahl M, Zhu H, Tautz J, Zhang S (2011) Large scale homing in honeybees. *PLoS One* 65:e19669. doi:10.1371/journal.pone0019669
- Romanes GJ (1885) Homing faculty of Hymenoptera. *Nature* 32:630
- Scharstein H (1975) Der Mechanismus der Sollwertverstellung bei der Kursregelung der roten Waldameise. Doctoral thesis: Ludwig-Maximilian Universität München
- Seeley TD, Mikheyev AS, Pagano GJ (2000) Dancing bees tune both duration and rate of waggle- run production in relation to nectar-source profitability. *J Comp Physiol A* 186:813–819
- Sklenar G (1954) Imkerpraxis, 7th edn. Weber-Sklenar H Selbstverlag, Mistelbach Zaya, Niederösterreich
- Southwick EE, Buchmann SL (1995) Effects of horizon landmarks on homing success in honey bees. *Am Nat* 146:748–764
- Srinivasan MV, Zhang SW, Lehrer M, Collett TS (1996) Honeybee navigation en route to the goal: visual flight control and odometry. *J Exp Biol* 199:237–244
- Tanner DA, Visscher PK (2010) Adaptation or restraint? Reference dependent scatter in honey bee dances. *Behav Ecol Sociobiol* 64:1081–1086
- Tautz J, Zhang S, Spaethe J, Brockmann A, Aung S, Srinivasan MV (2004) Honeybee odometry: performance in varying natural terrain. *PLoS Biol* 2. doi:10.1371.Journal.pbio.20211
- Uchida T, Kuwabara M (1951) The homing instinct of the honeybee, *Apis mellifica*. *J Fac Sci Hokkaido Univ* 10:87–96
- von Frisch K (1965) Tanzsprache und Orientierung der Bienen. Springer, Berlin, Heidelberg
- von Frisch K (1967) Dance language and orientation of bees. Belknap Harvard University Press, London
- von Helversen O, Edrich W (1974) Der Polarisationsempfänger im Bienenauge: ein Ultraviolettzeptor. *Comp Physiol* 94:33–47