

Guidance by odors in honeybee navigation

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Abstract Animal navigation is guided by multiple sensory cues. Here, we ask whether and how olfactory stimuli emanating from places other than the trained feeding site redirect the flight paths of honeybees. The flight trajectories of individual bees were registered using harmonic radar tracking. Sensory cues (compass direction, distance, visual cues en route and close to the feeding site) associated with the trained flight route dominated wayfinding, but a learned odorant carried by air flow induced excursions into the wind. These redirections were largely restricted to rather small deviations from the trained route ($<60^\circ$, <200 m) and occurred only if the animal did not receive the trained odorant stimulus at the trained feeding site. Under certain conditions, larger excursions were observed. These findings are discussed in the context of odor guidance of honeybees over longer distances (>300 m from the hive).

Keywords Navigation · Odor cuing · Search strategies · Harmonic radar tracking · *Apis mellifera*

Introduction

Animals use multiple sources of information for navigation, which are organized hierarchically according to the sensory cues and cognitive processes involved (Wiener et al. 2011). At any moment animals integrate internal information from acquired (or innate) routines and external stimuli, leading to confirmation or deviating from the expected sensory conditions. The guiding role of odor cues

is particularly interesting, since these cues might allow localizing a goal on the basis of rather simple response categories (Jacobs 2012). It is thus essential for any navigation study to elucidate the potential guiding function of odor cues. The role of odorants in honeybees navigating over several hundred meters is a controversial issue. von Frisch (1923, 1942; review: von Frisch 1967) was criticized for using odorants at the feeding site and at the test locations in his studies on dance communication (Wenner et al. 1969; Johnson and Wenner 1970; Wells and Wenner 1973; but see Lindauer 1971 and von Frisch 1974a, b). It was argued that odor guidance rather than vector information conveyed by waggle dances was transferred from the dancing bee to the follower bee, allowing the recruited bee to preferentially select the test locations which had been set up in the field. Meanwhile, conclusive evidence exists to rule out odor guidance as the only factor in the performance of recruits and to reaffirm the informational value of the waggle dances (Gould 1974; Riley et al. 2005). Yet, recent works have shown that odorants may guide recruits because they are learned during dance communication (Farina et al. 2005, 2006; Diaz et al. 2007) and are used when searching for the dance-communicated location (Grüter et al. 2008; see also Grüter and Farina 2009; Brockmann and Sen 2009; Reynolds et al. 2009). The relative weight of these two components, the vector information provided by waggle dances and the olfactory information from food sources, remains to be determined in a large-field navigation context.

We address this issue in the context of foraging flights. To fully control learning of odorants in the context of large-field navigation, we chose to train bees to an odor-marked feeding site. Under these conditions, localizing the source of the odorant is well defined within the navigational system of each test bee which had been trained to fly

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along a route between the hive and the feeder. Under these conditions, bees have learned a flight vector and may relate the source of the odorant to its visually guided navigation system as it is also known to be the case in a walking insect, the desert ant *Cataglyphis* (Wolf and Wehner 2000; Buehlmann et al. 2012). The most informative experiments by von Frisch (1967) (p. 160 ff), the fan-shaped experiments examining direction coding in the waggle dance, used multiple scent plates arranged at the same distance from the feeding site for the dancing bees (250–280 m) and at angular deviations from the direct route to the feeder of $\pm 15^\circ$, $\pm 30^\circ$, $\pm 45^\circ$ and $\pm 60^\circ$. Our experimental design was modeled accordingly, with wind direction and speed being measured continuously. We record the flights of bees using harmonic radar tracking (Riley et al. 1997; Menzel et al. 2005, 2011) to test over which distances bees might be attracted by multiple sources of odorants deviating from the location where the odor was learned. Although down-wind trails of odorants appear to redirect the flight paths of trained bees in test situations, this redirection is limited to a rather narrow angular range.

Methods

The experiments were conducted during the summer of 2012 in a grass field close to Klein Lüben (Brandenburg, Germany). The pasture was rather homogenous in character with discernible landmarks only on the ground (patches with varying grass lengths, clover flowers). A line of bushes formed the southern border of the field behind the harmonic radar device (Fig. 1). Two water channels ran in an NNE direction roughly perpendicular to the bushes. A natural

food supply was provided by blooming clover in the SW at distances >900 m and in the S at distances >1.5 km, as judged by radar tracking of foraging bees in a parallel experiment and by occasional inspections of food recruitment dances. There was no natural food supply in the regions from NW to SE, i.e., the area covered by our test bees. The hive consisted of two combs with an extended space of 4 cm to the front glass window, allowing the transponder-carrying bees to walk freely inside the hive and to be observed through the window. Bees (approximately 2,500 in number) could build wax cells only on one side of a wooden board. Also, the hive exit was enlarged allowing bees to enter and leave the hive without damaging their vertically mounted radar transponders. A group of 10–20 bees were trained from the hive to a feeder 300 m southeast of the hive. The bees were marked with colored number tags and equipped with the radar transponder at the feeding site. The feeding site consisted of a small (40×50 cm) white table with a sucrose-containing jar and the source of the odorant (see below). During radar tracking, only the bees with transponders traveled between the hive and the test stations, and all trained bees without transponders were caged. The tracked bees were not individually identified during tracking, and had already traveled between the hive and the feeder several times. Usually, no more than three transponder-carrying bees were in the air at one time. If more than one transponder-carrying bee was in the air it was always possible to distinguish between the tracks of different bees. Notice that the tracks of single bees could not be assigned to a particular bee; therefore the same bee may have been tested under varying conditions of the experiment (see below). A total of 49 tracks were recorded, 40 were complete and were therefore used for analysis.

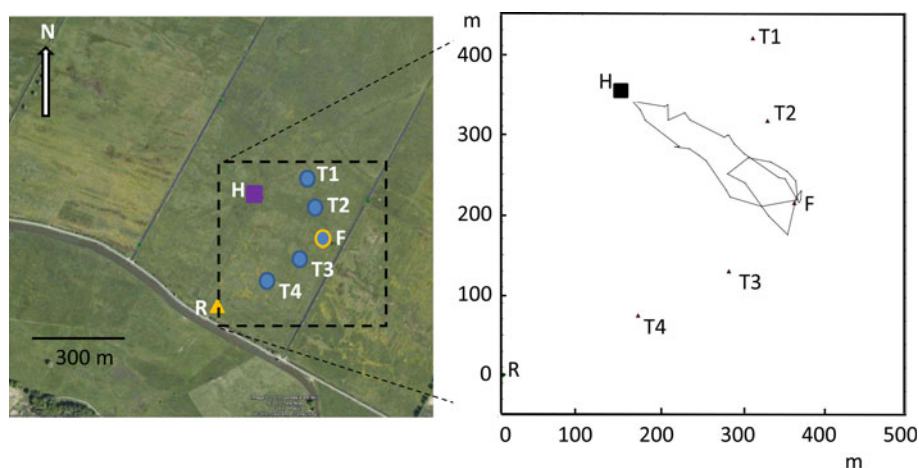


Fig. 1 Layout of the experiment. The position of the hive (*H*), radar (*R*), feeder (*F*) and the four test stations (*T1–T4*) are arranged such that the complete flights of the test bees could be recorded. The right graph shows the part of the test area which is displayed in the figures of the “Results” together with one flight track of a bee tested under

conditions in which the sucrose solution was removed from the feeder, but otherwise the feeder location was visible by the small white table, and the odor marks were provided both at the feeder location and at the test stations. Scale: m as measured from the radar station

Tracking bees by harmonic radar was described in Riley et al. (1996, 2005) and Menzel et al. (2011). We used a system with a sending unit consisting of a 9.4 GHz radar transceiver (Raytheon Marine GmbH, Kiel, NSC 2525/7 XU) combined with a parabolic antenna providing approximately 44 dB. The transponder fixed to the thorax of the bee consisted of a dipole antenna with a Low Barrier Schottky Diode HSCH-5340 of centered inductivity. The second harmonic component of the signal (18.8 GHz) was the target for the radar. The receiving unit consisted of an 18.8 GHz parabolic antenna, with a low-noise pre-amplifier directly coupled to a mixer (18.8 GHz oscillator) and a downstream amplifier with a 90 MHz filter. A 60 MHz signal was used for signal recognition. The transponder weighed 10.5 mg and was 12 mm in length. We used a silver or gold wire with a diameter of 0.3 mm and a loop inductance of 1.3 nH. The range of the harmonic radar was 1 km radius, and the spatial resolution was better than 5 m radius. The height of the tracked bee could not be determined, but since we collected complete tracks and determined reliable radar signals between 0.7 and 6 m (measured at a distance of 900 m) we estimate that the bees flew within this height range.

The feeder and the four test stations were equipped with an odor source consisting of a plastic tube (diameter 3 cm) filled with filter paper and arranged horizontally such that the wind could blow through the tube. The filter paper was impregnated with 2 μ l undiluted geraniol at 9 am and at 2 pm. The sources of odorants were tested subjectively and no obvious loss of smell was detected at the end of the morning or afternoon session. We also inspected whether differences in flight trajectories may be related to the time of testing and did not find dependence. The time of testing is given for the flight trajectories in the respective figure legends. The four test stations consisted of wooden boards (10 \times 10 cm) fixed to a 1 m high stick and had a different visual appearance than the feeding station. The idea was to reduce the visual attraction of the test stations and to imitate as closely as possible the conditions in von Frisch's fan-shaped experiments where the dance-recruited bees searched for a source of the odorant whose visual appearance they did not know. The four test stations were located at the same distance from the hive as the feeder (300 m) and arranged at angles of $\pm 30^\circ$ and $\pm 60^\circ$ from the line between the hive and the feeder (Fig. 1). Again, this arrangement closely resembles the conditions in many of von Frisch's fan-shaped experiments. Due to the ownership of the grassland in the north of the test area, the distance to test stations T1 and T2 were shorter than to T3 and T4.

Wind speed was measured with a weather station within the test area 1.90 m above ground, and an average was calculated for the period of the particular test flight.

Circular data were analyzed according to Batschelet (1981) using Oriana, Version 1.06, Kovach Computing Services.

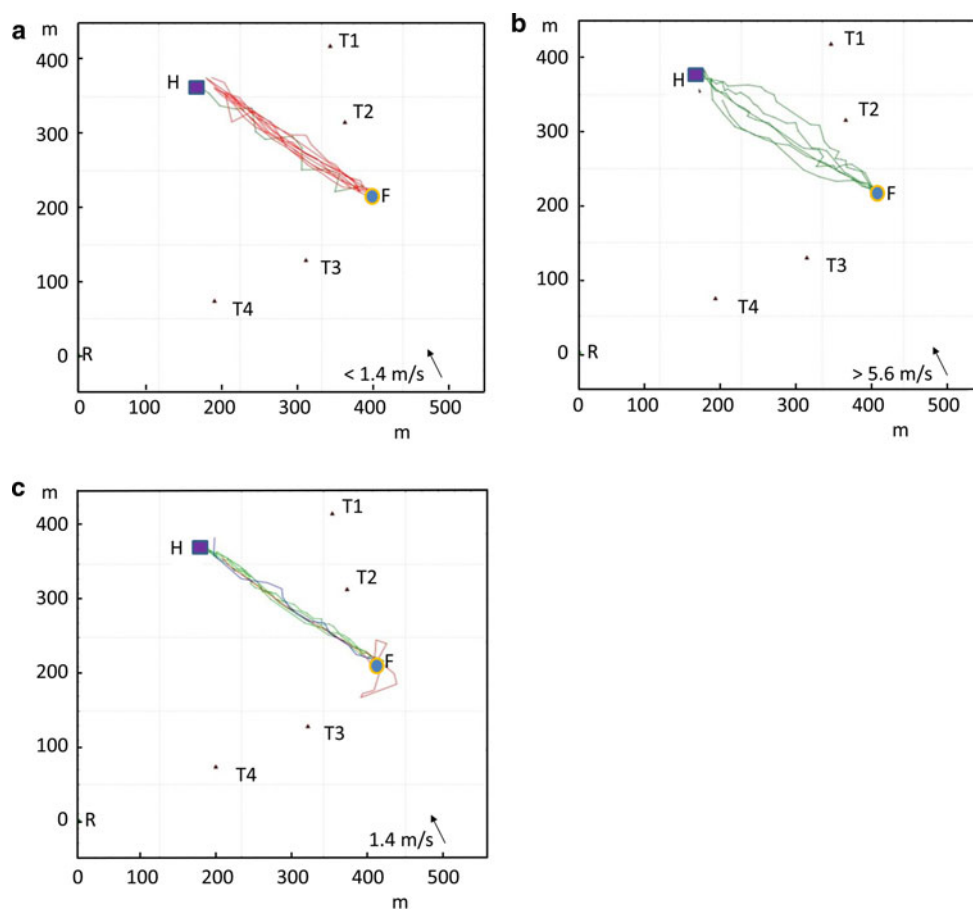
Results

First, we tested whether bees equipped with a transponder can be radar tracked during training. This requires that the transponder fixed to the number tag on the thorax does not get lost when the bee returns to the colony. Another requirement is that the transponder does not lose its function due to mechanical stress (e.g., bending and distortion) and social contacts inside the hive. About half of the transponders remained functional for more than 3 days, and about 10 % of the transponder-carrying bees were radar tracked, some for more than 10 days. Figure 2a–c shows training flights under three different conditions (Fig. 2a feeder open, no wind, Fig. 2b feeder open, rather strong wind from SSE, Fig. 2c feeder empty, wind, < 1.4 m/s). In all three cases, the test stations T1–T4 were not equipped with an odorant in an attempt to test whether the test stations or the surrounding area are attractive for other reasons. Very narrow flight routes were observed during still wind conditions, whereas the outbound flights were shifted to the north and the inbound flights to the south when the wind blew from SSE. When the feeder was empty, the animals landed, searched for food in very narrow loops around the feeder and then returned to the hive without exploring the area. Both outbound and inbound flights followed a very narrow corridor, and no excursions to a test station were performed.

Since the animals searched only within the close vicinity of the feeder when it was empty possibly guided by the visual and olfactory signals of the feeder, we removed the feeder and all equipment around it during test conditions. Thus, no visual or olfactory signals were provided at the feeder location during tests, and only the four test stations were equipped with the odorant which the animals had learned at the feeder, but without any reward. Figure 3a–c shows the results for different wind conditions. Three flights were recorded without wind (< 1.4 m/s). The straight outbound flight was followed by rather narrow search loops close to the former feeder location. Then the animals returned to the hive along the trained route. The first sharp turn occurred close to the virtual feeder location and was directed to SSW in one animal, to NNE in the second and to S in the third, indicating that there was no preferred direction for excursions. Flights in Fig. 3b were performed under wind directions from SSE and wind speed varying from 5.6–7.0 m/s. The outbound flight paths were already skewed to the south (average angle of the outbound flight path as measured 100 m away from the hive: $218^\circ \pm 18^\circ$

Fig. 2 Training flights and test flights with the empty feeder.

a Five outbound and inbound training flights under wind speed <1.4 m/s, wind direction: SSE. Test times: 12:30; 15:27; 10:15; 9:45; 11:44. **b** Three outbound and inbound flights under wind speed >5.6 m/s, direction: SSE. Test times: 12:00; 11:56; 11:01. **c** Four outbound and inbound flights under wind speed 1.4 m/s, direction SSE. Test times: 12:00; 10:45; 15:27; 15:40. The flight direction of all flights shown in **a–c** as measured 100 m away from the hive: $129.7^\circ \pm .6$ standard error. Scale: m as measured from the radar station. The arrow indicates wind direction; wind speed is given in m/s

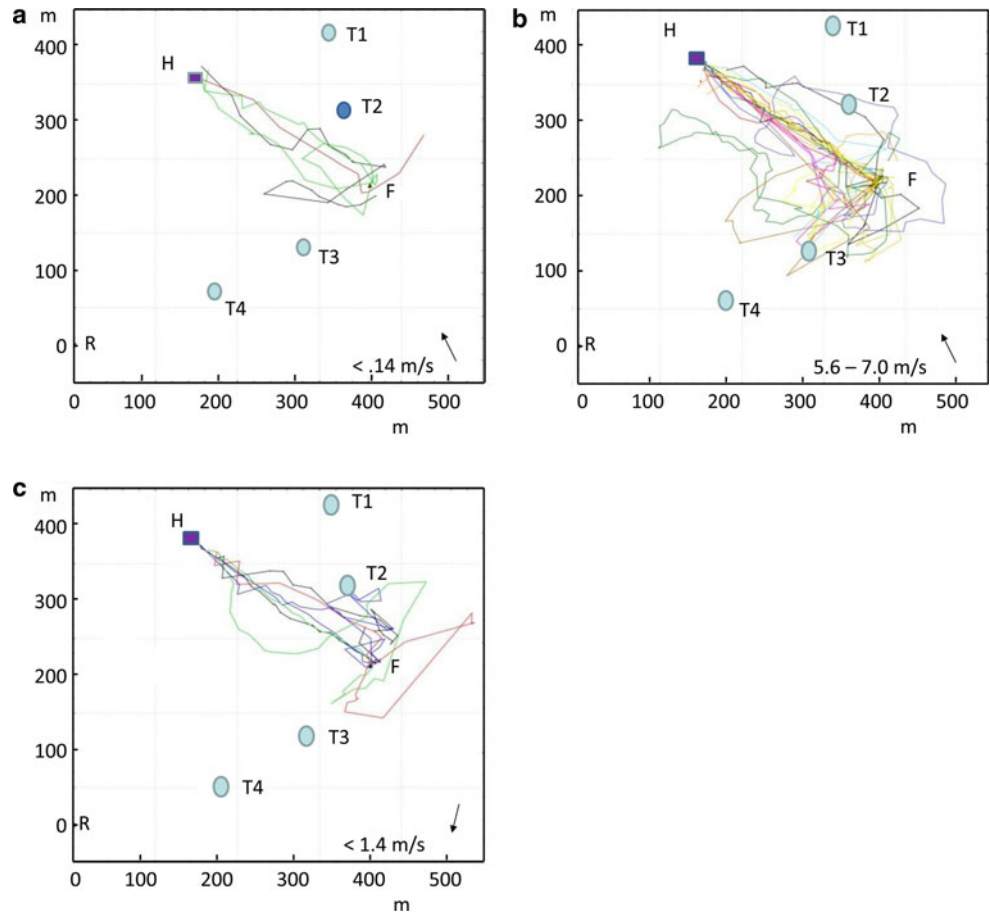


standard error, statistically significantly different from the flights during training as shown in Fig. 2, $p < .001$, $F = 42.7$). Four out of ten animals reached T3, the closest test station to the south, on their outbound flight. Two animals came as close as 50 m to T3 on their outbound flights. Two animals flew back to the hive crossing over T2, the next test station to the north. Also in these animals, the first sharp turn appeared very close to the feeder location and was directed to the S in four animals, to the SSW in five animals and to the NNE in one animal. None of the animals came close to T4, the farthest test station in the S. Wind speeds (<1.4 m/s) from varying directions were recorded during test flights shown in Fig. 3c, but wind drift from the north dominated. The outbound flights were skewed to the north (average angle of the outbound flight path as measured 100 m away from the hive: $42^\circ \pm 75^\circ$, significantly different from the flights during training (Fig. 2, $p < .001$, $F = 11.8$) and significantly different from the flights shown in Fig. 3b, $p = .02$, $F = 7.79$). One out of four animals reached T2 and the others came close to T2 (within 50 m). The first sharp turns close to the feeder location were to NNE, NNW, SW (for a short distance and then NNE) and N.

Figure 4a–c gives three examples of individual flights with interesting properties. The only animal (out of 40) that

directly flew from the hive to one of the test stations (here T2) is shown in Fig. 4a. Wind conditions during this flight were: speed 1.4 m/s, direction from NE. The straight outbound and inbound flights are surprisingly straight and rapid. Since there were no natural nectar or pollen sources in the area of T2, and T2 was never rewarded, these straight flights and the lack of search flights close to T2 are indeed surprising. Figures 4b and c shows flights which reached farthest away from the feeder location of all flights recorded. The wind conditions during the flight as shown in Fig. 4b were: wind speed (<1.4 m/s), direction from SW. Thus the wind conditions were favorable for an odor-guided excursion to the SW. Interestingly, the animal did not approach T3, but extended its flight toward T4, which, however, it did not reach. At the most southern point the animal turned back toward the hive, first along a shortcut to the hive, but then flew back to the feeder location once it came to the route between hive and feeder. The flight shown in Fig. 4c is characterized by two loops, the first one around the feeder location including the test location T2 and the second one south of T3 including an excursion 150 m south of T4. The wind conditions were: wind speed (<1.4 m/s), from NE. The southern loop brought the animal back to T3, and from there it applied the correct vector component for an inbound flight from the feeder to the

Fig. 3 a–c Flight routes during test conditions. **a** Three flights under wind speed < 0.14 m/s. The inbound flight component of the animal depicted in *blue* was not recorded. Test times: 14:46; 15:54; 12:30. **b** Ten flights under wind 5.6–7.0 m/s, direction: SSE. **c** Four flights under wind speed < 1.4 m/s, wind direction: NNE. Test times: 12:30; 12:00; 13:43; 15:55; 15:45; 12:15; 12:25; 12:34; 12:56; 15:39. Scale: m as measured from the radar station. The arrow indicates wind direction; wind speed is given in m/s



hive. An interpretation of these three flights will be offered below.

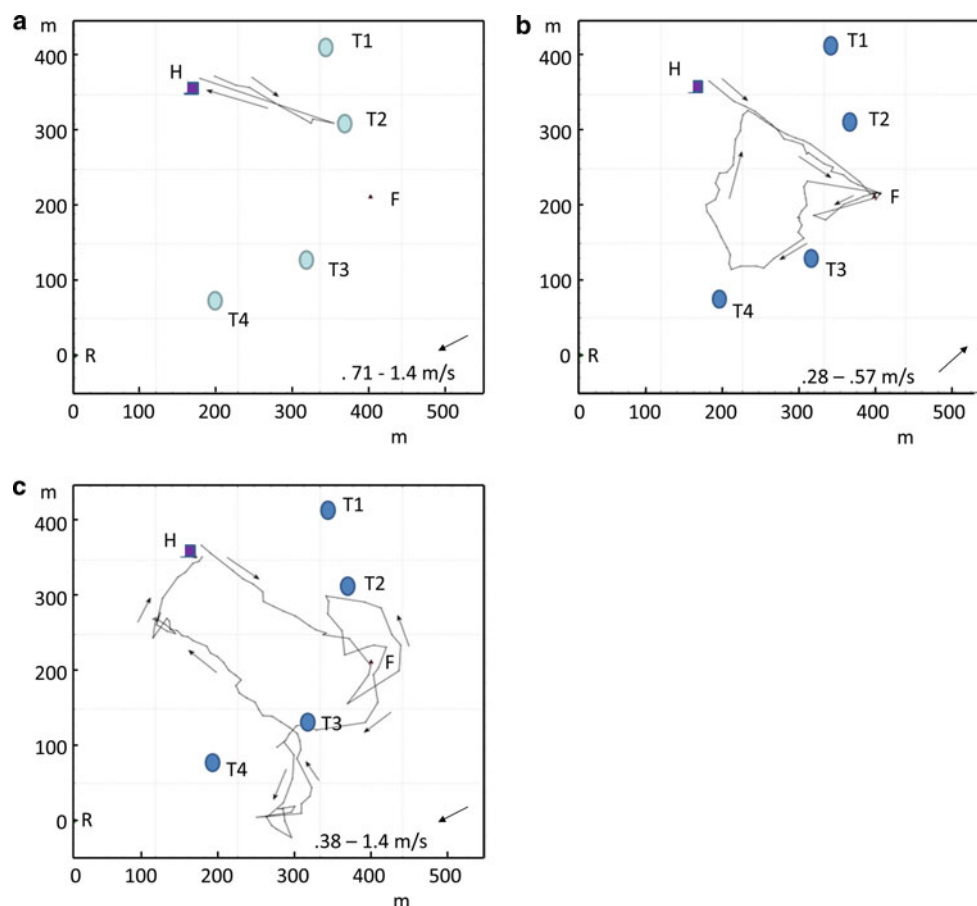
The most distant test stations, T1 and T4, were not visited under any of the test conditions indicating that sources of the odorants appearing under angular deviation of $> 30^\circ$ and > 100 m distance from the learned feeder location failed to redirect outbound flight routes or search flights under our test conditions.

Discussion

A commonly applied paradigm in navigation studies is to introduce competition between the actual and the expected external cues by constraining specific sensory functions, dislocating the animal, or eliminating or introducing a particular sensory stimulus. The latter procedure was applied here. Honeybees had learned a flight route to a feeder that offered besides its visual features (location relative to the hive, surrounding landmarks, appearance of the feeder) an olfactory stimulus. This stimulus was offered at four locations T1–T4 (Fig. 1) with a different visual appearance than encountered during training. This situation allow us to ask whether and under which conditions the

animals deviate from their flights toward the expected feeder and search for the origins of the salient odor stimulus. Our experimental design is particularly relevant to honeybee navigation because it has frequently been argued that honeybee navigation, in general, and guidance by social communication by the waggle dance, in particular, relies predominantly (Grüter and Farina 2009) or exclusively (Wenner et al. 1969) on the spatial distribution of sources of odorants. The layout of our experiment mirrors that of von Frisch (1967, p. 160 ff) in which he tested whether recruits of the waggle dance applied the directional information embedded in the dance performance. He needed to set up scent plates to count the recruits flying past or landing on the plates. Like von Frisch, we offered multiple (4) scent plates and tested the bees over a similar range of distances and angular distributions of the test stations. Like in von Frisch's experiments, the outbound bees that aimed to fly along a vector either learned from a dancing bee or learned during former flights. In our case, the distance of the training site from the hive was 300 m, and the distances of the test stations from the training site were ± 150 and ± 350 m. Redirection by odors was found to be limited to the nearby test stations corroborating von Frisch's conclusion that even under his test conditions

Fig. 4 Three examples of individual flights with characteristic features. **a** This animal flew directly from the hive toward $T2$, and also returned to the hive directly without search flights. Wind conditions: speed .71–1.4 m/s, direction: NE. Test time: 13:50. **b** This animal flew a large loop to the south without targeting $T3$ or $T4$ closely. Wind conditions: speed .28–.57 m/s, direction: SW. Test time: 13:24. **c** This animal performed two large loops, the first between the feeder location and $T2$ and the second between $T3$ and a southern location (but not $T4$). Wind conditions: speed .38–1.4 m/s, direction: NE. Test time: 13:02. Scale: m as measured from the radar station. The arrow indicates wind direction; wind speed is given in m/s



recruited bees were guided predominantly or exclusively by the directional information of the waggle dance. It thus appears that redirection by odor is bound to a narrow range as defined by the visually guided navigation strategy confirming conditions as found in a visually guided walking insect, the desert ant *Cataglyphis*. Both the home entrance (Buehlmann et al. 2012) and a food source (Wolf and Wehner 2000; Wolf et al. 2012) are located by *Cataglyphis* by upwind streams of odorants, but only within the vicinity of the source of the odorant. Thus as in honeybees vicinity is defined by visually guided navigation, although the long distance navigation strategies applied in walking *Cataglyphis* and flying honeybee may be quite different. The design of our experiment, however, does not allow drawing direct conclusions to the experiments in which the role of odor guidance was explored in dance communication, since bees may attend to odors differently in foraging flights and in dance-communicated flights.

It has been proposed that bees may apply a kind of random walk search strategy when confronted with a conflict between visual and olfactory guidance (Reynolds et al. 2009), a proposal that is not supported by our data. Our experimental design differed from that of Reynolds et al. (2009) who trained and tested over shorter distances

(100 m) and used only one scented plate (25–75 m away from the trained site). An additional difference to the Reynolds et al. (2009) experiments relates to the visual appearance of the test stations. They set up two test stations (one scented, one unscented) with similar visual appearance to the feeding station. We purposely varied the visual appearance of the feeding and test stations to reduce or even eliminate the visual attractiveness of the test stations, and in an attempt to closely match the conditions faced by dance-recruited animals who do not receive information about the visual appearance of the goal. We consider the different scales and the mismatch between the visual appearance of the learned and the test stations important because the search strategies and the distribution of the scent plumes originating from the test stations may be qualitatively different from the conditions tested by Reynolds et al. (2009). Indeed, Reynolds et al. (2009) describe narrow search loops in the region of the feeding site. Such narrow search flights were seen in our experiments only when the empty feeding site provided the same visual and olfactory stimuli as during training. Reynolds et al. (2009) show that the search strategy applied during these narrow loops were found to be best described by a Levy flight strategy, indicating that distributions of angular deviations

and flight stretches appear not to follow any systematic heading of the flight trajectories.

The three single flight paths shown in Fig. 4 document flight paths toward a test station in head wind direction under wind conditions with unique characteristics: the first one is the only direct flight from the hive to an odor-marked test station (T2); the second describes a far-ranging excursion toward the furthest test station in the south (but not reaching it); and the third flight shows an excursion with a return flight component which resembles the inbound vector to the hive at a southern region. Since we do not know how many test flights an animal might have already performed, it might well be that these three trajectories come from animals whose trained flight route was partially extinguished during several unrewarded test flights. It is conceivable that under such conditions, the relative impact of odor guidance may increase but even then deviation from the visually guided vector flight is limited. The flight pattern shown in Fig. 4c lends itself to the following interpretation. When the animal returned to T3 and became exposed to the odorant while in a motivational state for homing, it may have recruited the home vector which it had associated with the feeder odor, applied this memory and ended up about 100 m south of the hive. There it corrected its flight and headed straight NNE toward the hive. We cannot exclude that the animal may have seen the hut with the hive from this southern position, but we know from earlier experiments that a beacon is not necessary to initiate a straight homing flight (Menzel et al. 2005).

Taken together, our results prove that bees are indeed attracted by the odor learned at the feeding site when this odor comes from other directions. However, the effect is rather small and only redirects the searching animal within a rather narrow angle that deviates from the straight flight route by less than $\pm 60^\circ$. Furthermore, the redirecting effect does not appear to be stronger under stronger wind conditions, but rather trails of odorants carried by light wind may be attractive over longer distances.

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