

Variability in the encoding of spatial information by dancing bees

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SUMMARY

A honeybee's waggle dance is an intriguing example of multisensory convergence, central processing and symbolic information transfer. It conveys to bees and human observers the position of a relatively small area at the endpoint of an average vector in a two-dimensional system of coordinates. This vector is often computed from a collection of waggle phases from the same or different dancers. The question remains, however, of how informative a small sample of waggle phases can be to the bees, and how the spatial information encoded in the dance is actually mapped to the followers' searches in the field. Certainly, it is the variability of a dancer's performance that initially defines the level of uncertainty that followers must cope with if they were to successfully decode information in the dance. Understanding how a dancer's behaviour is mapped to that of its followers initially relies on the analysis of both the accuracy and precision with which the dancer encodes spatial information in the dance. Here we describe within-individual variations in the encoding of the distance to and direction of a goal. We show that variations in the number of a dancer's wagging movements, a measure that correlates well with the distance to the goal, do not depend upon the dancer's travelled distance, meaning that there is a constant variance of wagging movements around the mean. We also show that the duration of the waggle phases and the angular dispersion and divergence of successive waggle phases co-vary with a dancer's orientation in space. Finally, using data from dances recorded through high-speed video techniques, we present the first analysis of the accuracy and precision with which an increasing number of waggle phases conveys spatial information to a human observer.

Key words: *Apis mellifera*, communication, spatial information, waggle dance, variability.

INTRODUCTION

Karl von Frisch (von Frisch, 1946) discovered that a highly stereotyped, still variable motion pattern that honeybees perform on the comb surface conveys to bees and human observers the circular coordinates of relatively well-defined locations. The term 'waggle dance' denotes a form of this pattern, which conveys information about targets located fairly far from the hive (von Frisch, 1967). Compelling evidence indicates that the waggle dance is at the core of a series of communication systems enabling a honeybee colony to coordinate the activity of its members during foraging and nest-site selection (e.g. Lindauer, 1961; Seeley, 1995; Dyer, 2002; Sherman and Visscher, 2002). This is possible because those colony members that keep close contact with a dancing bee, usually called dance followers, appear to detect a variety of signals emitted by the dancer, and process them in such a way that their ensuing behaviours may greatly depend upon the content of these signals (von Frisch, 1967). In the waggle dance, a returned, successful forager moves forward on the comb surface while wagging its body from side to side at about fifteen times per second. This straight portion of the dance is called a 'waggle phase'. Typically without interruption, it then moves on along a rather semicircular trajectory, and returns to a position close to the starting point of the recent waggle phase; this portion is called a 'return phase', and tends to be alternatively performed clockwise and counter-clockwise along the dance. Once at this position, the dancing bee repeats the forward, wagging portion of the dance. The number of waggle phases can

vary significantly across dances, thereby revealing regulatory responses and amplification phenomena on the signal production side of the communication process (e.g. Seeley, 1986; De Marco et al., 2005).

Intriguingly, a dancer's motion pattern is strongly linked to its recent navigation experience. Flying honeybees use the sun as a reference to maintain a course, and the average orientation of a dancer's successive waggle phases relative to the direction of gravity approximates the angle between the direction toward the goal and the sun (von Frisch, 1967). Honeybees also gauge the distance they travel toward their various goals [most likely by integrating self-induced optic flow during flight, i.e. the net amount of image motion over the retina accumulated during movement (e.g. Esch and Burns, 1996; Srinivasan et al., 1996)], and the average duration of a dancer's successive waggle phases correlates well with the amount of visual flow experienced on the way to the goal (Srinivasan et al., 2000; Tautz et al., 2004; De Marco and Menzel, 2005), and, consequently, also with the travelled distance (von Frisch and Jander, 1957). These two correlations convey to a human observer the position of a relatively well-defined area surrounding the endpoint of an average vector in a two-dimensional system of coordinates. The waggle dance is thus an intriguing example of multisensory convergence, central processing, motor coordination, and symbolic information transfer.

Six decades after von Frisch's original discovery (von Frisch, 1946), however, the process of decoding information in the dance

still remains elusive [see Michelsen (Michelsen, 1999) for a comprehensive account of the current hypotheses]. One reason is probably to be found in the striking variability of the multiple dance signals. The body contacts between dancers and followers most likely convey meaningful stimulation to potential recruits (e.g. von Frisch, 1967; Bozic and Valentincic, 1991; Rohrseitz and Tautz, 1999), and the same can be said about chemical cues, both environmental (von Frisch, 1967) and semiochemicals (Thom et al., 2007), coupled to a dancer's wagging movements. Three dimensional fields of particle oscillations produced by the dancers' vibrating wings (Michelsen et al., 1987; Kirchner and Towne, 1994; Michelsen, 2003) and substrate-borne vibrations caused by their wagging movements (Tautz, 1996) also appear to be a source of meaningful stimulation. However, the question of how a dancer's behaviour is mapped to that of its followers remains open, most probably as a result of the use of sub-optimal methods to trace the behaviour of dancers and followers, both inside and outside the hive. Furthermore, the study of a dancer's manoeuvres and a follower's response to the dance have long been addressed either independently (e.g. Towne and Gould, 1988; Riley et al., 2005) or without pondering the relative influence of simultaneous, guiding cues (e.g. von Frisch and Lindauer, 1961), e.g. olfactory cues that followers use to pinpoint their targets. [An exception here is the work by Esch (Esch, 2001) and colleagues, which simultaneously addressed the encoding of distance information in the dance and the distribution of field searches by recruits.] In addition, the influence of a follower's experience on the process of decoding information in the dance remains obscure. Currently, unemployed foragers appear to follow no more than a few waggle phases before resuming their flights to natural goals, and they do so by following those seemingly indicating familiar sites (Biesmeijer and Seeley, 2005). Such a small number of dancing events provides spatial information only roughly to a human observer (De Marco and Menzel, 2008), thereby posing the question of how informative (Haldane and Spurway, 1954) such a 'sample' can be to the followers. This is probably the reason why a distinction between experienced and novice foragers would prove fruitful for a deeper understanding of the dance communication system.

Dance studies typically focus on an average vector whose endpoint roughly corresponds to the location of a goal, and such a vector is often computed from a variable – and usually small – collection of waggle phases, from the same or different individuals. With only a few exceptions (e.g. Haldane and Spurway, 1954; Esch, 1978; Weidenmüller and Seeley, 1999; Beekman et al., 2005; Tanner and Visscher, 2006), variations in a dancer's manoeuvres are rarely discussed in the context of information transfer, even when it is unclear whether and to what extent followers average information from multiple waggle phases. Certainly, it is the variability of a dancer's motion display that initially defines the boundaries of the stimulation that followers must cope with if they are to successfully decode information in the dance. Such variability also defines the level of uncertainty that a human observer must cope with while dealing with samples of limited size. Hence, a first and utterly important step in the elucidation of how a dancer's behaviour is eventually mapped to that of its followers relies on the analysis of the accuracy and precision with which foragers map the position of a goal. Since the waggle phase is the main source of spatial information for both bees and human observers (von Frisch and Jander, 1957; von Frisch, 1967; Michelsen, 1999) our study is based upon thousands of waggle phases from hundreds of dances recorded through high-speed video techniques, and presents an analysis of the accuracy and precision with which an increasing number of waggle

phases conveys to a human observer the direction of and distance towards a desirable goal.

MATERIALS AND METHODS

We performed two experimental series. In both series, we used a colony of *Apis mellifera carnica* L. bees placed indoors in a two-frame observation hive. The entrance to the hive and the dance floor faced north and west, respectively. The first series focused on within-individual variations in the encoding of distance information. Marked bees were trained to forage on outdoor feeders – one feeder per experimental session – placed at 137, 248 or 360 m from the hive, and aligned along two different flight directions: 82°SW and 3°NW. The waggle dances of newly recruited bees foraging on these feeders were filmed at 25, 125 and 250 frames per second under red illumination. The feeders offered unscented 1.8 mol l⁻¹ sucrose solution. Each recording session involved only one of the two flight directions. We first allowed ten marked bees to forage on the outdoor feeder. Ten newly recruited bees were then marked with numbered tags. Next, any unmarked bee, as well as any other bee whose behaviour had previously been recorded, was caged and released at the end of the day. Our experimental subjects were thus marked and filmed on the same day, and lacked foraging experience with our particular feeder prior to the video recordings. Such recordings began 15 min after the marked bees were first presented with sucrose solution. For each of the three different distances, each recording session lasted approximately 60 min. Each marked bee performed a maximum of 8–15 foraging trips per session, depending on the flight distance. We measured the duration of the waggle phases for each distance, and the number and duration of the dancers' wagging movements, or lateral displacements of the body, from one side to the other, occurring during the waggle phase. Data were analysed by means of linear regressions, one-way ANOVAs, *t*-test for independent samples, Kruskal–Wallis tests, Tukey comparisons, Dunn multiple comparison tests, Kolmogorov–Smirnov goodness-of-fit test and Runs test (Zar, 1984; Sokal and Rohlf, 1969).

The second experimental series focused on the variability in the encoding of both distance and direction information. Bees foraged on an outdoor feeder placed at 215 m from the hive along a single flight direction: 82°SW. The feeder offered unscented 1.46 mol l⁻¹ sucrose solution. This sucrose concentration, slightly lower than that of the first series, was chosen to attenuate recruitment and to carry out our recordings more efficiently. The bees were individually marked and their dances filmed at 87 frames per second under red illumination. We used 87 frames per second because it provided us with a favourable temporal resolution for our subsequent analyses, and also with optimal values for the rate of information transfer from the camera to the computer in which the digital videos were stored. The time of day of each video recording was also noted. Owing to an apparent lack of differences between the dances of trained and newly recruited bees, we recorded dances from both groups of bees, provided that all of them had already been individually marked; this helped us to enhance our rate of data collection. In addition, several bees were repeatedly recorded. Next, we analysed the digital videos frame by frame by means of specially designed software, allowing precise measurements of a dancer's movements and body orientation in space. In order to quantify the direction of each waggle phase, we measured the angle formed by the direction of gravity and a line connecting the centre of the dancer's head, the junction between its thorax and abdomen, and the tip of the wagging abdomen when it was in the middle of its trajectory from one side to the other. We recorded this angle twice for each waggle phase, within its first and third portion, as calculated

from the total number of wagging movements involved in such a phase. Next, the mean from these two measurements was computed as the waggle-phase orientation relative to gravity. In doing our measurements, we recorded 38 waggle phases (out of 1452) with no apparent wagging movements of the dancer's body; in all these cases, the waggle-phase orientation was calculated based on a dancer's straight and forward motion occurring between consecutive return phases. Bees tend to regularly alternate between left and right turns when dancing, and the waggle phases made after one type of turn (either to the left or to the right) tend to have a different direction than the waggle phases made after the other one, particularly when the duration of the waggle phase is short. Hence, we separately analysed the waggle phases made after either left or right turns, and calculated the mean angle of left and right waggle phases. The mean angle of the entire dance was computed as the average between left and right mean angles. In all cases, means were computed only when the dance consisted of at least four left and four right waggle phases. For each side, either left or right, the angular dispersion was defined as the average magnitude of the differences between the angles of the single waggle phases and the mean from all the waggle phases of the respective side. The angular divergence, in addition, was defined as the difference between the angles of alternation (i.e. left vs right) in consecutive waggle phases. We also calculated the 'Missweisung' (von Frisch and Lindauer, 1961), or misdirection of the dance, as the difference between the direction encoded in the dance and the actual direction toward the goal. In addition, we counted the number of wagging movements occurring during the waggle phase, as well as any interruption in a dancer's manoeuvres occurring during the dance. For each side, either left or right, the dispersion of the number of wagging movements was defined as the average magnitude of the differences between the number of wagging movements of the single waggle phases and the mean from all the waggle phases of the respective side. In evaluating the encoding of distance information, we excluded the 38 dancing events (see above) lacking a dancer's characteristic wagging movements. Overall, 1452 waggle phases were recorded throughout 145 dances performed by 29 individuals. All angles are indicated clockwise with respect to either north or upward vertical, and their means were calculated using rectangular coordinates (Batschelet, 1981). To confirm some of the results of the first series, we repeated the analysis of the relationship between the flown distance and the duration of the waggle phase with a new group of bees. The slope of the ensuing linear regression gave 0.038 wagging movements per meter of travelled distance, thus matching our previous results (see below). With this new calibration curve, we computed the locations encoded in the single waggle phases of all dances for 215 m. Next, we estimated the level of uncertainty associated with the mean direction and the mean number of wagging movements as a function of the number of observed waggle phases. To this end, for each chosen number of observed waggle phases, we randomly resampled 50 000 times all waggle phases from dances with at least four left and four right waggle phases, and calculated the proportion of those resamples for which the means fell within each of a series of intervals around the overall mean.

RESULTS

Within-individual variations in the encoding of distance information

For each of the three different distances of the first series, we quantified the duration of the single waggle phases and the number and duration of the single wagging movements of a dancer's body. For each of the two different flight directions, we then analysed the

relationship between the duration of the waggle phase and the distance to the feeder (henceforth, flown distance). In doing this, we used dances that had been filmed at 25 frames s^{-1} . As expected for both directions (von Frisch, 1967), the waggle-phase duration increased linearly with the flown distance (82°SW: $r^2=0.78$, $P<0.0001$; 3°NW: $r^2=0.80$, $P<0.0001$; linear regression). Neither the slopes ($F_{(1,56)}=2.72$, $P=0.11$; linear regression) nor the elevations ($F_{(1,57)}=0.03$, $P=0.86$; linear regression) of the two regression lines were statistically different, and the pooled slope gave 1.61 ms of waggle-phase duration per meter of travelled distance; this result matches published data obtained in our particular outdoor landscape (De Marco and Menzel, 2005). Next, we repeated the analysis with dances recorded at 125 frames s^{-1} , and found no statistical differences in either the slopes ($F_{(1,56)}=0.01$, $P=0.91$; ANCOVA) or in the intercepts ($F_{(1,57)}=0.60$, $P=0.44$; ANCOVA) of the regression lines obtained with either 25 or 125 frames s^{-1} . Owing to a greater sample size, we focused on the former video-recordings (25 frames s^{-1}) in order to analyze the frequency distribution of the within-individual variations associated with the encoding of distance information. To compare information from different bees and distances, the data from each waggle phase was incorporated into a frequency distribution using the difference between the duration of that waggle phase and the mean duration from all the waggle phases of a dancer, and dividing this difference by the individual mean. Each of these values is referred to as the 'divergence' between the distance information encoded in a single waggle phase and that from all of a dancer's waggle phases. Fig. 1A–C shows the relationship between the flown distance and the frequency distribution of these divergences (as percentages). The distributions of the different distances were not normal (137 m: $P=0.043$; 248 m: $P=0.011$; 360 m: $P=0.004$; K–S goodness-of-fit test), although those corresponding to 248 and 360 m did not deviate from a Gaussian model (248 m: $R^2=0.97$, $P=0.064$; 360 m: $R^2=0.91$, $P=0.568$; runs test). Skewness and Kurtosis were 1.0 and -0.2 , 1.7 and 1.5, and 2.0 and 3.2 for 137, 248 and 360 m, respectively. The percentage of waggle phases (from different dances and individuals) for which the duration differed less than 10% with respect to that of the mean was 14.4% (Fig. 1A), 20.5% (Fig. 1B) and 25.4% (Fig. 1C) for 137, 248 and 360 m, respectively. Thus, the scatter of the distribution decreases as the flown distance increases (Fig. 1A–C).

How does the precision of the distance indication change with increasing waggle phase duration? In order to answer this question, we first quantified the number and duration of the dancers' wagging movements (WMs) by using our high-speed video recordings (125 and 250 frames s^{-1}), and then used these measurements to recalculate the distributions of the divergences described above according to the number of WMs of the single waggle phases (Fig. 1D–F). Each wagging movement was computed as an excursion of the tip of a dancer's abdomen, from one side to the other. We recorded 10.1 (± 0.7), 12.8 (± 0.7) and 19.7 (± 1.0) WMs (mean values \pm s.e.m.) for 137, 248 and 360 m, respectively. The mean duration (\pm s.e.m.) of the single WMs, in ms, was 69.3 (± 1.4), 68.1 (± 1.1) and 67.9 (± 2.0) for 137, 248 and 360 m, respectively, and did not vary with the flown distance ($F_{(2,30)}=0.22$, $P=0.8$; one-way ANOVA). Next, we used the ratio between the mean duration of the waggle phase and that of the WMs to re-examine the observed within-individual variations in the encoding of distance. Both the mean duration of the waggle phase and that of the WMs are depicted in Fig. 1D–F, whereas the distance between the grey dashed lines signalling '0' and either '+100' or '-100' in each of the three plots corresponds to the mean duration of the waggle phase, and the distance between the grey dashed line signalling '0' and each of the dark-grey dashed

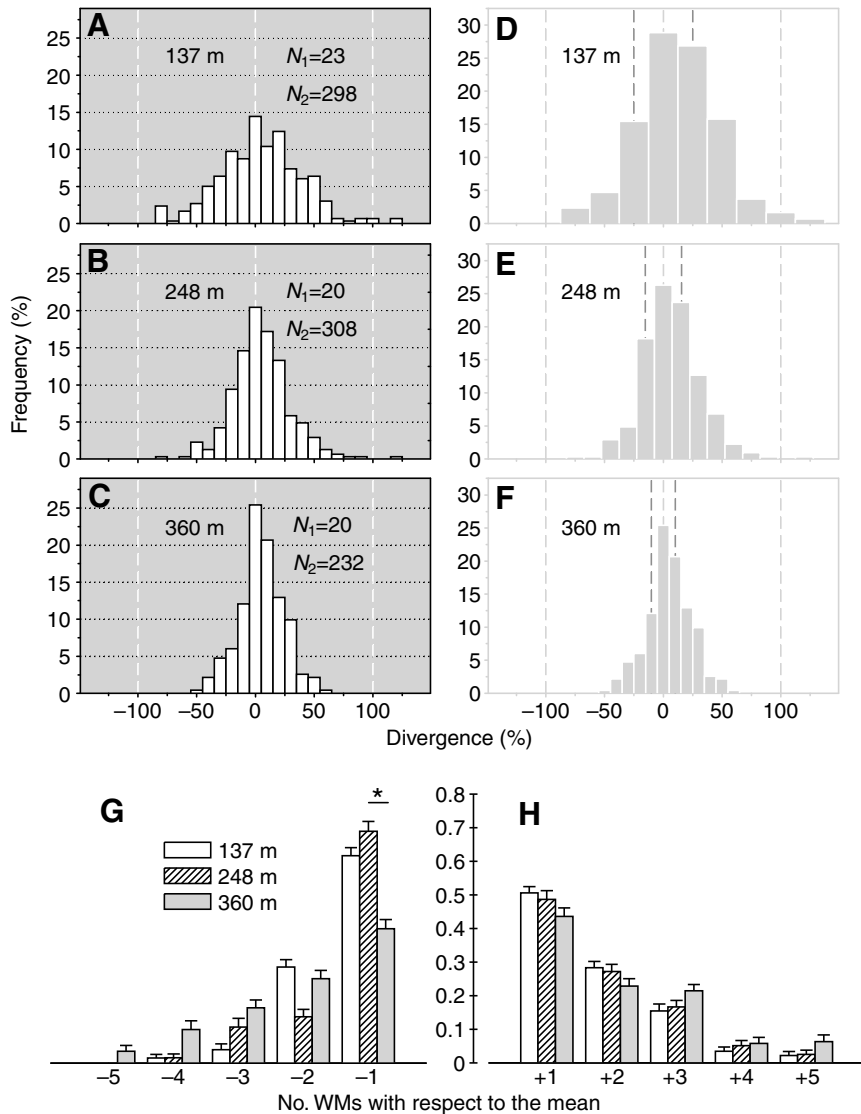


Fig. 1. An analysis of within-individual variations in the encoding of distance information in the dance. To compare information from different bees and distances, the data from each waggle phase was incorporated into a frequency distribution using the difference between the duration of that waggle phase and the mean duration from all the waggle phases of the dancer, and dividing this difference by the mean. Each of these values is referred to as the 'divergence' between the distance information encoded in a single waggle phase and that from all of a dancer's waggle phases. The relationship between the flown distance and the frequency distribution of such divergences, in percentages, is shown in (A–C); the variance of the distributions decreases as the flown distance increases. (D–F) To answer how the precision of the distance indication changes with increasing waggle-phase duration, we used the number and duration of the dancers' wagging movements (WMs) to re-calculate the distributions of the divergences according to the number of WMs of the single waggle phases. Within-individual variations in the encoding of distance thus appeared to be invariant to the actual flown distance. (G,H) To confirm this, we analyzed the relationship between the flown distance and the frequency distribution of 'actual' divergences, i.e. those involving at least one WM of a dancer's body, either below (G) or above (H) the mean. The values obtained for each category were divided by the total number of individual measurements. Data from different bees were then averaged, and the resulting frequency distributions were separately analyzed according to the flown distance. N_1 , number of dancers; N_2 , number of waggle phases. The asterisk in G denotes statistical differences between the corresponding bars (see Results for statistics and details.)

lines corresponds to the mean duration of the WMs. The distribution of the divergences for 137 m then appeared to be normal ($P>0.10$; K-S goodness-of-fit test), and Skewness and Kurtosis gave 1.0 and -0.7 m, 1.6 and 1.1, and 2.1 and 3.7, for 137, 248 and 360 m, respectively. Furthermore, the percentage of waggle phases whose number of WMs was similar to that of the mean did not differ across distances: 28.9% (Fig. 1D), 26.3% (Fig. 1E) and 25.4% (Fig. 1F) for 137, 248 and 360 m, respectively. Thus, within-individual variations in the encoding of distance appeared to be invariant to the actual distance towards the goal. To confirm this result, we then analyzed the relationship between the flown distance and the frequency distribution of the divergences involving 'at least one WM' of a dancer's body, either below (Fig. 1G) or above (Fig. 1H) the mean. We thus focused on those waggle phases with numbers of WMs that actually diverged from the mean number of WMs. Each divergence was calculated as the number of WMs of a single waggle phase minus the mean number of WMs from all the waggle phases. The values obtained for each bin category (e.g. +1 WM, +2 WMs, and so on) were divided by the total number of individual measurements. (Hence, for any given distance shown in Fig. 1G, for example, a relative frequency of 1.0 for the type of event '–1' would have meant that all the waggle phases whose numbers of

WMs were below the mean eventually diverged from the mean by only one WM.) Data from different bees were then averaged, and the resulting frequency distributions were separately analyzed according to the flown distance. Overall, the frequency distribution of the waggle phases whose number of WMs was lower than that of the mean did not change with the flown distance (Fig. 1G, '–2': $H_3=4.8$, $P=0.09$; '–3': $H_3=5.6$, $P=0.06$; '–4': $H_3=1.6$, $P=0.46$; '–5': $H_3=4.4$; $P=0.11$, Kruskal–Wallis test), with the exception of those with only one WM below the mean (Fig. 1G, open, hatched and grey bars: $H_3=8.9$; $P=0.012$, Kruskal–Wallis test): their frequency decreased as the flown distance increased from 248 to 360 m (Fig. 1G, hatched vs grey bars, $P<0.05$; Dunn's multiple comparison tests). We found similar results for the waggle phases with a higher number of WMs than that of the mean (Fig. 1H, '+1': $H_3=2.1$, $P=0.34$; '+2': $H_3=1.1$, $P=0.58$; '+3': $H_3=3.5$, $P=0.17$; '+4': $H_3=0.4$, $P=0.81$; '+5': $H_3=1.1$, $P=0.57$; Kruskal–Wallis test).

The number of wagging movements does not vary between right and left waggle phases, but changes with the overall dance orientation

Bees tend to regularly alternate between left and right turns when dancing, and the waggle phases made after one type of turn (either

to the left or to the right) tend to have a different direction than the waggle phases made after the other one. Hence, we asked if the duration of the waggle phase changes depending on whether it follows a right or left turn. Moreover, it has long been reported that the misdirection associated with the encoding of the direction of a goal varies together with a dancer's orientation in space (von Frisch and Lindauer, 1961; Lindauer, 1963). As described by von Frisch (von Frisch, 1967): "One sees that the 'direction' indications are quite precise when the dances are directed upward or downward or approximately horizontally to left or right." It has remained unknown, however, whether the distance indication also varies together with the overall dance orientation. We asked, therefore, whether the encoding of distance information also varies together with a dancer's orientation in space. In the second experimental series, the scatter of WMs around the mean was asymmetrical in the waggle phases following right turns ($P < 0.001$), and symmetrical in those following left turns ($P = 0.091$). We found similar scatters when the data from both sides were compared, with variances of 6.75 and 6.34 WMs for waggle phases following left or right turns, respectively (Pearson's $\chi^2 = 9.68$, $P = 0.64$); 90% of the divergences fell within 4.5 WMs around the mean (Fig. 2A), thereby matching the results of the first series (Fig. 1B). Furthermore, the mean number of WMs changed together with the overall dance orientation: it was smaller in horizontal ($\sim 60\text{--}90^\circ$) than in downward dances (Fig. 2B,C).

Within-individual variations in the encoding of direction information

The scatter of the directions of the single waggle phases around the mean was asymmetrical ($P < 0.01$) and similar for waggle phases following left and right turns (Pearson's $\chi^2 = 22.68$, $P = 0.091$; Fig. 3A). The variance from waggle phases following left and right turns was 126° and 133° , respectively. Overall, 90% of the single directions were within 17° around the mean. The scatter also changed with the overall dance orientation, meaning that the angular dispersion was greater in horizontal ($\sim 90^\circ$) than in downward dances (Fig. 3B,E,F), irrespective of whether the waggle phases followed right or left turns. The misdirection gave an average of 3° , with higher and more variable values in the early afternoon (14:00–16:00 h; Fig. 3C), when the direction toward the sun was perpendicular to that of the dancers' flights. The latter result is in agreement with previous reports (von Frisch, 1967).

The angular divergence co-varies with the overall dance orientation

The mean angular divergence gave maximum and minimum values in horizontal ($\sim 90^\circ$) and downward ($\sim 180^\circ$) dances, respectively (Fig. 3D, white circles), but the distributions of these divergences were independent of the overall dance orientation (Fig. 3D). The mean and distribution of divergences were intermediate in upward ($\sim 0^\circ$) dances. These variations could only be partially explained on the basis of simultaneous variations in the scatter of the single waggle phases (Fig. 3B), because there was a notable increase in the mean angular divergence in horizontal dances (Fig. 3D, white circles), and a simultaneous, much smaller increase in the corresponding scatter of the waggle phases following either left or right turns (Fig. 3E,F, respectively).

Accuracy and precision in the encoding of spatial information

We examined the accuracy and precision of the encoding of spatial information in the dance, as related to the field locations indicated by the single waggle phases of all dances from our second series (Fig. 4). Of the endpoints of the vectors indicated by the single

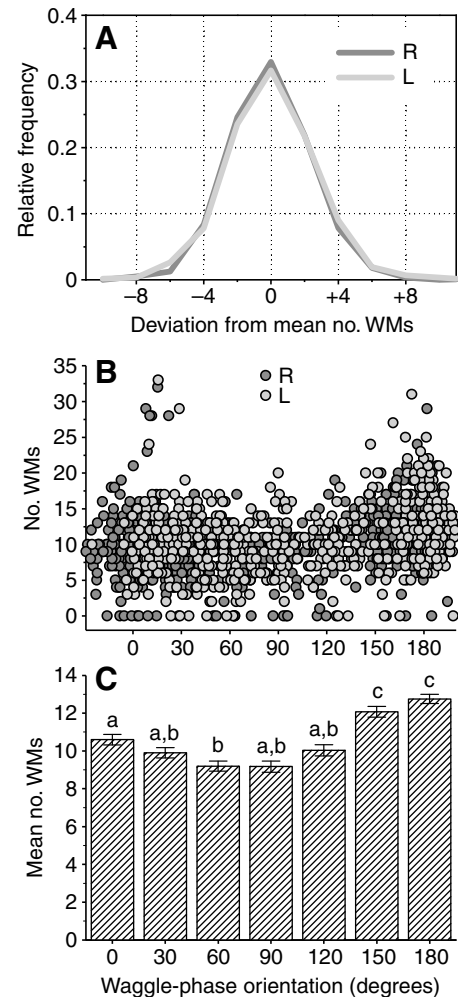


Fig. 2. (A) An analysis of the scatter of a dancer's number of wagging movements (WMs) around the mean. Data from waggle phases following either left (light grey) or right (dark grey) turns are shown separately. (B) The number of WMs occurring during the waggle phase as a function of the dancer's mean orientation with respect to vertical; left and right waggle phases (see Materials and methods) are shown separately. (C) Mean number of WMs as a function of the dancer's mean orientation with respect to vertical. Data from left and right waggle phases were pooled separately; vertical lines indicate 95% C.I.; different letters denote significant differences between groups ($P < 0.05$).

waggle phases, 15% corresponded to field locations that fell well within an area centred at the feeder of a radius of 50 m, and 90% fell within an area of a radius of 180 m. The totality of the indicated locations fell within a circular surface of 101.800 m^2 (Fig. 4). The mode of the signalled locations was slightly closer to the hive, and 3°S from the actual position of the feeder (Fig. 4). This agreed with both the asymmetry found in the scatter of the dancers' wagging movements (Fig. 2A) and the average misdirection (Fig. 3C).

The relationship between the accuracy and precision of the dance and the number of waggle phases

We conducted a random resampling analysis based on an increasing number of waggle phases to examine the relationship between a given number of waggle phases and the precision of its corresponding mean angle and duration, thereby gauging the level of uncertainty associated with the encoding of both direction and

distance information (Fig. 5). We used data from dances with at least four waggle phases per side (i.e. following either left or right turns), and calculated the precision of the mean from each resample as the average of the modules of the differences between either the angle or duration (i.e. number of WMs) of the single waggle phases and the mean angle or duration from all resamples with the same number of waggle phases. For each given number of waggle phases, we used 50 000 random resamples and computed the proportion of those resamples yielding a certain level of precision. This gave us an estimate of the level of uncertainty arising from a variable collection of waggle phases.

Fig. 5 shows the results of this analysis. Depicted is the level of uncertainty, as related to both direction (A,C) and distance (B,D), derived from dances for a goal placed 215 m from the hive, as a function of the number of observed waggle phases. One sees the proportions of resamples with mean values falling within each of the several categories, in turn defined on the basis of their respective deviation from the mean direction and distance. Thus, the cumulative frequencies denote the probability of achieving a certain level of precision based on an increasing number of waggle phases. For the sake of comparison, the results shown in Fig. 5A and B are also depicted in C and D, where the precision in the encoding of distance is shown in meters. For example, a deviation of 5° with respect to

the mean direction encoded in the dance is more likely to be achieved by extracting directional information from 40 waggle phases, a sample size yielding a cumulative frequency of 1, than from only two waggle phases, a sample size that yields a cumulative frequency of 0.6 (Fig. 5A,C). Similarly, an average deviation of ≤ 20 m with respect to the mean distance encoded in the dance can simply not be ‘read’ out of a dancer’s wagging movements, irrespective of the number of observed dancing events (Fig. 5B,D).

DISCUSSION

There are several dance components ascribed to convey spatial information (e.g. von Frisch, 1967; Seeley et al., 2000; Michelsen, 2003). For a human observer, the spatial information is encoded in the direction relative to gravity and the number of wagging movements of the waggle phase (von Frisch, 1967). If these two measures correlate well with a follower’s estimate of the direction of and distance towards the goal, our results then reflect the amount of variability that a follower must cope with while decoding information in the dance.

Is there a built-in ‘noise’ in the encoding of distance?

We measured the overall duration and the number of wagging movements of waggle phases for different distances, thereby

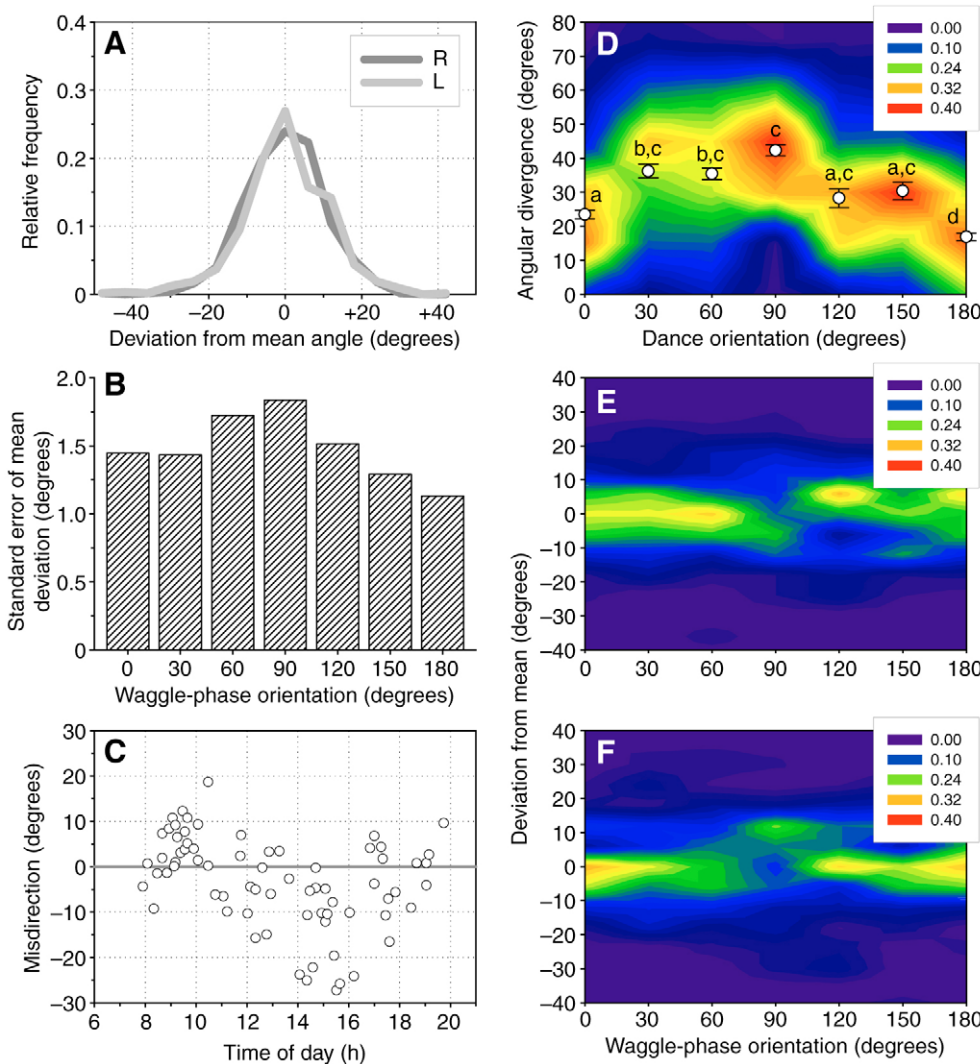


Fig. 3. (A) An analysis of the scatter of directions of single waggle phases around the mean. Data from waggle phases following either left (light grey) or right (dark grey) turns are shown separately. (B) Average standard error (s.e.), in degrees, of the mean direction of a dancer’s waggle phases as a function of the average dance orientation; for each orientation, we averaged standard errors from 10 different random resamplings in order to balance the sample size across categories. (C) The ‘residual misdirection’ of the dance as a function of the time of day. (D) The angular divergence of the dance as a function of the average dance orientation; white circles denote the mean angular divergence (\pm s.e.m.), whereas colours depict the frequency distribution of the divergences as a function of the average dance orientation. Different letters denote significant differences ($P < 0.05$) across groups. (E,F) Frequency distribution of the scatter of directions of left (E) and right (F) waggle phases around the mean as a function of the average dance orientation.

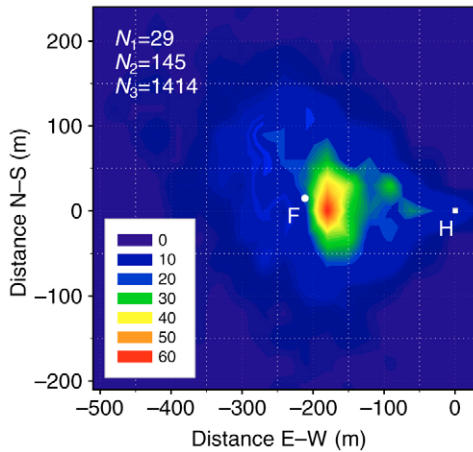


Fig. 4. The accuracy and precision of the encoding of spatial information in the dance, as related to the field locations indicated by the endpoints of the vectors encoded in 1414 waggle phases (N_3) from 145 dances (N_2) by 29 dancers (N_1). Data are from the second experimental series. The colour scale refers to the absolute number of observations within categories (bin size=10) in a two-dimension system of coordinates. The square denotes the position of the hive (H), and the circle that of the feeder (F).

quantifying within-individual variations in the encoding of distance information. We recorded dances from the early morning until the evening for all the three different distances, meaning that the different orientations of the dancers' bodies with respect to the direction of gravity were equally represented in the different groups. We also measured the duration of each of the pendulum-like wagging movements of the waggle phases, and found that this measure did not change either across distances (see Results) or throughout each of the single waggle phases (data not shown). We show that the precision of the distance indication increases with the flown distance (Fig. 1A–F), a result that is in close agreement with published data (Esch, 1978; Beekman et al., 2005). This happens

because the scatter of a dancer's wagging movements around the mean from its various waggle phases remains constant across distances (Fig. 1G,H), which means, in turn, that the number of wagging movements above and below the mean can be relatively large in dances for close (<300 m) goals. Such variations account for more than 25% of the mean number of wagging movements in waggle phases for goals located well within the foraging range of a colony. The former result indicates that within-individual variations in the encoding of distance information are scale-invariant, and do not depend upon a stored estimate used by a dancer as a reference to set an average waggle phase duration. We also found a regular dispersion of wagging movements around the mean (Fig. 2A). This finding is in agreement with previous reports (Beekman et al., 2005), and fits predictions from the tuned-error hypothesis (Haldane and Spurway, 1954; Towne and Gould, 1988). According to that hypothesis, the scatter of signalled locations roughly corresponds to a circular distribution. We found such a distribution, although twice the magnitude of that reported by Towne and Gould (Towne and Gould, 1988) for a similar distance. Comparisons are not straightforward, however, because we measured the scatter of the signalled locations, instead of that of the followers' searches.

The duration and direction of a waggle phase co-vary with the overall dance orientation

The number of wagging movements (Fig. 2B,C), the directional scatter of the single waggle phases (Fig. 3B,E,F) and the angular divergence between successive waggle phases (Fig. 3D) co-vary with the overall dance orientation. In contrast to horizontal ($\sim 90^\circ$) dances, downward ($\sim 180^\circ$) dances had more wagging movements (Fig. 2C) and showed smaller directional scatter (Fig. 3B) and angular divergence (Fig. 3D), whereas upward ($\sim 0^\circ$) dances gave intermediate values for these measures. The distribution of the angular divergences between successive waggle phases was independent of the overall dance orientation (Fig. 3D, colours), and the greater mean divergence found in horizontal dances (Fig. 3D, white circles) was accompanied by a simultaneous, much smaller increase in the scatter of the single waggle phases (Fig. 3B,E,F).

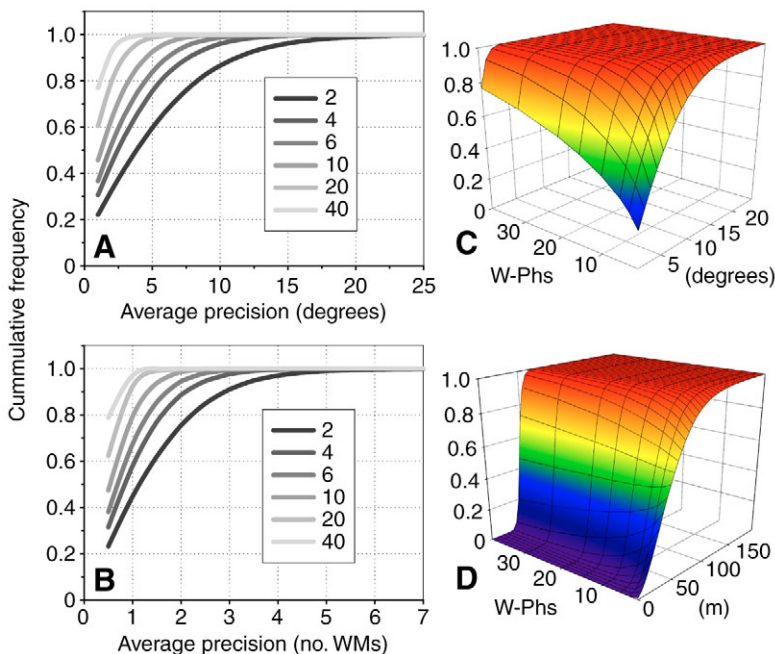


Fig. 5. An analysis of the level of uncertainty associated with the encoding of both direction (A,C) and distance (B,D) information as a function of the number of observed waggle phases. For each given number of waggle phases, we used 50 000 random resamples and computed the proportion of those resamples yielding a certain level of precision, defined on the basis of their respective deviations from the mean. Cumulative frequencies thus denote the probability of achieving a certain level of precision based on an increasing number of waggle phases. In A and B, each line corresponds to a different number (sample size) of observed waggle phases. For the sake of comparison, the same results are shown in C and D, where the precision in the encoding of distance is shown in meters; 'W-Phs' is the number of waggle phases; the average precision for direction and distance information is shown in degrees (C) and meters (D), respectively.

This means that variations in the directional scatter of the single waggle phases (Fig. 3B) can account only partially for the divergences found in horizontal and downward dances (Fig. 3D, white circles). The ‘residual misdirection’ of the dance also covaries with a dancer’s orientation relative to gravity, as well as with its previous flight direction relative to the azimuth of the sun (von Frisch and Lindauer, 1961; von Frisch, 1967). Since *Apis mellifera* dancers transfer visual information gathered during their foraging flights to a reference system defined by proprioceptive input, a process called ‘transposition’ (von Frisch, 1967), their residual misdirection was initially thought of as being reliant on a ‘built-in error’ in the transposition system (von Frisch, 1967). Evidence indicates, however, that its magnitude can systematically be changed by manipulating the strength and direction of the earth’s magnetic field (Lindauer and Martin, 1968), suggesting that it also depends upon the bees’ magnetoreception system (Kirschvink et al., 2001).

As the distance to a goal increases, the average angular divergence decreases and the duration of the waggle-phase increases (von Frisch, 1967). We found that horizontal dances have greater divergences and signal closer locations than downward dances. This suggests that a common pathway underlies the circuitry controlling these two tightly connected features of the dance. Little is known of the mechanisms controlling the direction and duration of the waggle phase, and our results help in describing features to be modelled while addressing the regulation of a dancer’s manoeuvres. However, the source of the dance variations described above still remains unknown. They may arise from (1) ‘built-in’ variations in the processing of proprioceptive input that depend upon a dancer’s orientation in space (von Frisch, 1967), (2) self-promoted variations in the strength and direction of the earth’s magnetic field, derived from a dancer’s own motion (Lindauer and Martin, 1968), and (3) variations in the processing of navigation information prior to the dance, depending on a dancer’s recent flight direction relative to the azimuth of the sun and the pattern of polarized skylight (Rossel and Wehner, 1982). Further experiments based upon manipulation of the orientation of the comb surface, the position of the goal, and the navigation information available to dancers are necessary to distinguish between these alternatives.

Gathering information from variable dances

The transfer of spatial information from dancers to followers seemingly depends upon input derived from the dancers’ wagging movements and wing vibrations. A dancer’s vibrating wings produce near field air flows (Michelsen et al., 1987; Michelsen, 1999) and narrow jet air flows (Michelsen, 2003) oscillating with the frequency of its wagging body. Moreover, a wagging dancer repeatedly deflects the followers’ antennae, either directly, by contact between its body and the follower’s antennae (Rohrseitz and Tautz, 1999), or indirectly, *via* the air flows produced by its vibrating wings. It has recently been shown that air-born antennal deflections, as those caused by the 250–300 Hz dance sounds, can elicit signals conveyed by the Johnston’s organ (Tsujiuchi et al., 2007). In addition, the number of a dancer’s wagging movements is mapped to the number of a follower’s antennal deflections (R.J.DeM., unpublished observations). These observations suggest that followers rely on mechanosensory input to compute estimates of the direction and duration of the waggle phase, and it would be interesting to examine how the variability described above is actually mapped to that of a follower’s mechanosensory input during the waggle phase, especially when dancers and followers have different orientations relative to gravity.

It is not yet clear whether and how followers average stimulation from multiple waggle phases. Several studies reported that bees tend to follow just a few dancing events before resuming their flights to a goal (von Frisch and Jander, 1957; Esch and Bastian, 1970; Mautz, 1971; Bozic and Valentincic, 1991; Judd, 1995; Biesmeijer and Seeley, 2005), although bees can also follow tens of waggle phases during dances for artificial sources of sugar solution (R.J.DeM., unpublished observations). Gathering information from only a few dancing events can lead a human observer to experience a relatively large discrepancy between the virtual and the actual position of a goal (Fig. 5), and it seems reasonable to ask whether followers may also experience such a discrepancy. Moreover, if followers average information from several waggle phases, including left and right waggle phases, variations in the average angular divergence of the dance might have minor effects on the scatter of recruits. However, it remains to be determined whether followers tend to follow mainly right or left waggle phases during dances with considerable angular divergences; if this were the case, the angular divergence might have a significant, measurable effect on the scatter of recruits. It also remains unknown whether and to what degree the number of waggle phases followed by potential recruits depends upon their foraging experience within the area of the goal.

Encoding and decoding spatial information in the dance

Our findings raise the question of how a dancer’s behaviour is ultimately mapped to that of its followers. By using harmonic radar techniques, Riley et al. (Riley et al., 2005) traced the flight paths of displaced bees seemingly recruited through dances for a feeder placed 200 m from the hive. Based on the direction of and distance to a virtual goal, the displaced bees exhibited well-directed flights of an average – and not so variable – distance of 188 m, only 12 m less than the initial hive-to-feeder distance (Riley et al., 2005). Their post-displacement flights in the absence of additional guiding cues were thus remarkably accurate and precise. Yet, our resampling analysis shows that such levels of accuracy and precision can simply not be ‘read’ out of the number of a dancer’s wagging movements (Fig. 5B,D). Two different views might help to explain these contradictory results. On the one hand, the accuracy of the followers’ traced flights (Riley et al., 2005) could be accounted for by two separate, but still complementary concepts. The first one is based upon the idea that the dance conveys highly accurate, still unknown signals allowing followers to gather accurate and precise distance information, whereas the second relies on multiple ‘built-in’ compensatory mechanisms embedded in a follower’s response to the dance. That is, prior to its flight, a follower may correct deviations arising from waggle phases with systematically variable angles and durations. Thus, a follower may be able to counterbalance (1) the residual misdirection of the dance (Fig. 3C), as long as it is the subject of the same source of variation that influences a dancer’s performance; (2) the differences across the angles of left and right waggle phases, if it can reliably distinguish between both types of waggle phases, and then compensate for their variable (Fig. 3B) deviations from the mean direction of the dance; (3) variations in the angular divergence of the dance (Fig. 3D), if it is able to average the angles of left and right waggle phases, and resolve the angular divergence that correlates well with the overall dance orientation; and (4) variations in the number of wagging movements that depend upon a dancer’s orientation relative to gravity (Fig. 2B,C), if a form of template allows it to correct its estimate of the duration of a waggle phase based on proprioceptive input. These concepts are plausible, and constitute a reasonable basis for future research,

especially if one were to study the neural basis of dance communication.

On the other hand, an interaction may exist between two sources of spatial information that a follower might access simultaneously, namely, the dance signals and its own navigational memories (Menzel et al., 2005; Menzel et al., 2006; De Marco and Menzel, 2008). Such an interaction is a fundamental feature of any communication process. Communication depends upon reproducing a symbolic entity selected and transmitted by a sender, but the entity that a receiver finally reproduces depends upon stored variants of it, which the receiver computes together with the transmitted signals. One needs to ask whether a follower also recollects stored information while decoding information in the dance. Biesmeijer and Seeley (Biesmeijer and Seeley, 2005) reported that no more than a quarter of the lifetime field excursions of a bee are preceded by dance following, and that bees tend to follow dances seemingly indicating familiar goals. These findings match previous results by von Frisch (von Frisch, 1968), who reported that dances for familiar goals lead to more effective recruitment. Biesmeijer and Seeley (Biesmeijer and Seeley, 2005) also found that experienced bees follow only a few waggle phases before resuming their foraging flights, a 'sample' that provides spatial information only roughly to a human observer (Fig. 5).

A possible interaction between dance information and a follower's spatial memory may seem inappropriate at first glance to account for the discrepancy between the accuracy and precision of the followers' post-displacement flights described above (Riley et al., 2005) and that of a dancer's performance, as revealed by our data, simply because the bees whose flights were traced by harmonic radar had never foraged on the advertised goal. Flying honeybees, however, mark and pinpoint the position of desirable sources of food and water by releasing volatiles produced by their Nasonov glands (e.g. von Frisch, 1967; Pflumm, 1969; Núñez, 1971; Free and Williams, 1972; Free, 1987). They also use the flights of conspecifics as a source of visual cues to pinpoint their targets (Tautz and Sandeman, 2002), a phenomenon also found in stingless bees (Nieh, 2004). Moreover, stingless bees visually track the piloting flights of experienced conspecifics, and these movements can guide them for at least part of the distance to a food source (Esch et al., 1965; Esch, 1967; Kerr, 1969). Stingless bees do not exhibit waggle dances, however, meaning that recruits would more strongly rely on signals and cues that are different from those used by honeybees. Nevertheless, several species of highly social insects exhibit local enhancement and orient toward the visual presence of foraging conspecifics (Slaa et al., 2003), which suggests, in turn, that outdoor interactions with conspecifics may constitute a robust strategy in the context of collective foraging. Furthermore, dance followers fly out and return to the dance floor several times before reaching their goals, and the duration of these interruptions increases together with the number of followed waggle phases (R.J.DeM., unpublished observations). Consequently, it is reasonable to ask to what degree a follower experiences a given hive-to-goal trajectory before finding its foraging target. It might do this in between its dance following performance, by using semiochemicals and visual cues derived from the flights of conspecifics, and then use the spatial information gathered through dances as well as that derived from its recent, 'truncated' flight excursions in order to pinpoint the goal. The wonder might arise on the number and frequency of the pre-displacement excursions of the bees whose post-displacements flights were later traced by radar techniques (Riley et al., 2005). Unfortunately, neither their dance-following behaviour nor their pre-displacement excursions have been reported. Clearly, if one ignores

the possibility that bees are able to use this form of 'outdoor' information from conspecifics in conjunction with information gathered through dances, then the hypothesis described above does not apply to the experiments reported by Riley (Riley et al., 2005) and colleagues. However, direct evidence stresses the synchronicity of the flights of bees foraging on the same goal, as well as the role of semiochemicals and visual cues in the context of recruitment (Tautz and Sandeman, 2002).

Open questions

Studying the variability of the waggle dance may prove fruitful for improving our understanding of the honeybee dance communication system. We suggest that such a system has at least two functional levels that are hierarchically organized. Thus, an active follower may first fly towards a recently experienced goal, especially if goal-related cues are coupled to current dances for the same or a different goal. This primary level would thus rely on the interplay between a follower's past experience and the presence of 'arousing' cues associated with such dances, which eventually trigger the recollection of specific route memories allowing the follower to resume its flights to previously visited locations. Semiochemicals emitted by dancing bees (Thom et al., 2007) and olfactory cues associated with the nectar brought into the colony (von Frisch, 1967; Ribbands, 1954) are examples of such arousing cues; the role of 'taste' still remains elusive in this context. Next, depending on both the availability of resources at these past locations and the strength and duration of the current dances for a different goal, a follower might also gather further stimulation from these dances, and focus its subsequent searches within the area of a currently advertised goal. This second level would involve gathering repetitive stimulation from waggle phases, as well as several flight excursions and returns to the dance floor before reaching the goal. On the basis of these two levels, the efficiency of the honeybee dance communication system would largely depend upon the spatial knowledge shared by dancers and followers. Future work should examine to what extent the dance system depends upon a follower's ability to acquire, store and recall navigational memories; it would be interesting, for example, to manipulate a follower's experience with single or multiple goals, and to evaluate its subsequent responses to dances for a different one. Combining high-speed video recordings and harmonic radar techniques in such a context would prove useful not only to distinguish dance variability from actual noise, but also to reveal the functional structure of the honeybee dance communication system.

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