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Honey bee dance communication: waggle run direction coded in antennal contacts?

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Abstract The behaviour of 38 honeybee dance followers and the patterns of antennal contact between followers and dancer were monitored during ten waggle runs for a feeding site 1200 m from the hive. The analysis was restricted to waggle runs with a maximum of 5 followers, allowing the followers to choose between different positions around the dancer. At the beginning of the waggle run, followers are rather evenly spaced around the dancer. During the waggle run, the followers tend to accumulate at the rear end of the dancer. At the end of the waggle run, all followers are found in a $\pm 60°$ arc behind the dancer. The body orientation angles of the followers depend on their position relative to the dancer. The follower bees have intense antennal contact with the dancer. At least one temporal parameter of the contact pattern may inform the followers about their position relative to the dancer, may guide the dance followers to the rear end of the dancer and may allow them to extract information about the location of the food source advertised by the dance. The role of antennal contact for dance communication appears to have been underestimated in previous studies.

Keywords Waggle dance · Dance language · *Apis mellifera* · Tactile communication · Information transfer

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Introduction

Honeybees can recruit nest mates to new feeding places (von Frisch 1965). Important for recruitment is the waggle dance, which is performed by the successful forager on the comb inside the hive (von Frisch 1923; Esch and Bastian 1970). The waggle dance can be regarded as a repetition of stereotype movements consisting of a waggle "run" and a return run. During the waggle run, the dancer swings her body from side to side in a pendulum-like manner, 13–15 times per second, and she produces dance sounds by vibrating her wings dorsoventrally (Esch 1961; Wenner 1962). The bee moves her body continuously forward, but her legs do not move at all or perform only a few slow-motion strides (Tautz et al. 1996). In the return run, the dancer circles back to start a new sequence.

Some parameters of the waggle run are correlated with the location of the advertised feeding site. The angle between the sun's azimuth and the direction to food in the field equals the angle between gravity and waggle run, which is called waggle run angle. The distance to the food source is indicated in the duration of the waggle run: The longer the duration of the waggle run, the further away is the feeding site (von Frisch 1965).

Dance followers mostly accompany the dancing bee. The interaction between dancers and dance followers can be broken up into the following successive steps: First, bees motivated to follow a dancer detect, localise and approach the dancer (Tautz and Rohrseitz 1998). Second, they accompany her, often for many circuits (Esch and Bastian 1970; Mautz 1971) and thus become dance followers. Third, after following a number of dances (Esch and Bastian 1970; Mautz 1971), they often fly out and find the indicated food source.

Since the discovery of the dance language by von Frisch, a major problem has been understanding how the information, visible to us in daylight, but invisible to the bees in the darkness of the hive, is transmitted to the follower bees, and how the follower bees perceive it.

Von Frisch (1965) proposed two communication channels: (1) tactile contact between the dance followers and the dancer, and (2) vibrations generated by the dancing bee and transmitted through the comb. Michelsen et al. (1986) checked the vibration hypothesis, but they did not find any dance-correlated 250-Hz vibrations perpendicular to the surface of the comb. Tautz (1996) suspected that waggle dancers do produce vibrations, but parallel to the surface of the comb. Rohrseitz (1998) showed that these vibrations can be sensed by the followers, but only under certain circumstances. Tautz et al. (unpublished observations) provide further insight into that topic.

Michelsen et al. (1987) dealt with another promising route of information transfer between dancer and dance follower bee: a complicated pattern of air flows around a dancing honeybee, that originates from the wing vibrations (producing the dance sounds) and from the wagging movements. More details are given by Storm (1998).

The main goal of this study is to describe the antennal contacts between followers and the dancer and to answer the question of whether antennal contact patterns enable the followers, at least from a theoretical point of view, to determine the direction of the indicated food source. In order to find the feeding site, a follower must know the waggle run angle. The simplest way is to stand directly behind the dancer and having the body aligned parallel with the dancer's body. In this case the follower's position relative to gravity equals the waggle run angle. Bees can perceive their orientation relative to gravity (Markl 1966; Sandeman et al. 1997). However, the waggle run angle can also be calculated for other follower positions according to Fig. 1. A follower must know her orientation relative to the waggle run direction. Assuming that a follower only has discovered the dancer, however, without knowing the dancer's waggle run direction, she must find out where she stands relative to the dancer (position angle, Fig. 2) and how she is oriented at that particular position (body orientation angle, Fig. 2). Thus, in order to answer the question of whether antennal contact patterns help in aligning with the dancer or contain the needed information for calculating the direction of the waggle run, we must check the relationship between the position of followers relative to the dancer and the antennal contact pattern.

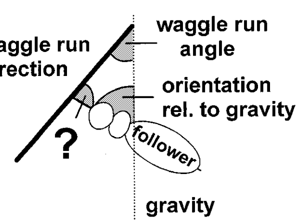


Fig. 1 Angles for measuring the waggle run angle of a dancer by a follower bee. The waggle run angle is the angle between gravity and the direction of the waggle run. In order to read the waggle run angle, a dance follower must know her own orientation relative to gravity and her orientation relative to the waggle run direction, indicated by "?"

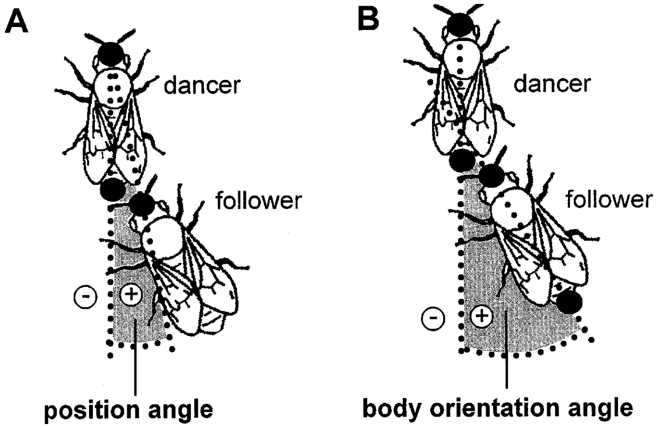


Fig. 2A,B Measures taken to quantify the position of a follower relative to a dancer. At each middle position of the pendulum-like waggle movements of the dancer the coordinates of the followers were monitored at the sites marked by the *filled circles* and both angles were calculated

Materials and methods

Video recordings

High-speed video recordings (NAC HSV 400; 200 frames s^{-1}) were made in a colony of *Apis mellifera carnica* Pollm., living in a two-frame observation hive at the bee station of the University of Wuerzburg in July 1995. Marked foragers were trained to visit artificial feeders with 2 mol l^{-1} sucrose solution, 1200 m from the hive. To check the possible influence of the stroboscopic light necessary for the high-speed video recordings, we also performed video recordings under infrared light (λ = 875 nm, 40 Hz frames s^{-1}).

Analysis

A computer-based video analysis system (Unimark 3.6) was used for digitising and analysing the recordings. Aided by this software, we monitored the Cartesian coordinates of several body parts of the dancers and the followers.

We define a follower as a bee close to the dancer (maximally one bee length away) and "interested in the dance", i.e. facing the dancer for at least one whole waggle run. We restricted our analysis to waggle runs with maximally five followers (median of the numbers of followers was 3.5, which is a typical number: Tautz and Rohrseitz 1998), so that the followers had been able to choose between different positions relative to the dancer. A second condition was that the number of the followers had to be constant for the whole waggle run. The analysis was performed on ten waggle runs of seven different dancers.

The positions of the follower bees were taken at the middle position of the dancer's pendulum-like movements during the waggle run (precision ca. ±1°), starting with the first waggle and ending with the last waggle of the waggle run.

We have measured the following angles (Fig. 2). *Position angle*, the angle between the long axis of the dancer and the connection between the head of the dancer and the head of the follower. A positive position angle means that the follower is standing on the right side of the dancer. *Body orientation angle*, the angle between the long axis of the follower's thorax and the long axis of the dancer. We did not choose the long axis of the follower, since a follower often bends her abdomen against the thorax during the waggle run (Spaethe et al. 1997). The angles were taken for dances performed on combs with open and empty cells.

For every video frame, that is every 5 ms, we checked whether the antennae of the followers were in contact with the dancer or not.

Statistics

For Fig. 3 a goodness of fit test was performed (Kolmogorov-Smirnov goodness of fit for continuous data; Zar 1996). $P < 0.05$ was considered to indicate significant differences. For Figs. 7A, 7C and 7D correlation coefficients were calculated separately for positive and negative position angles.

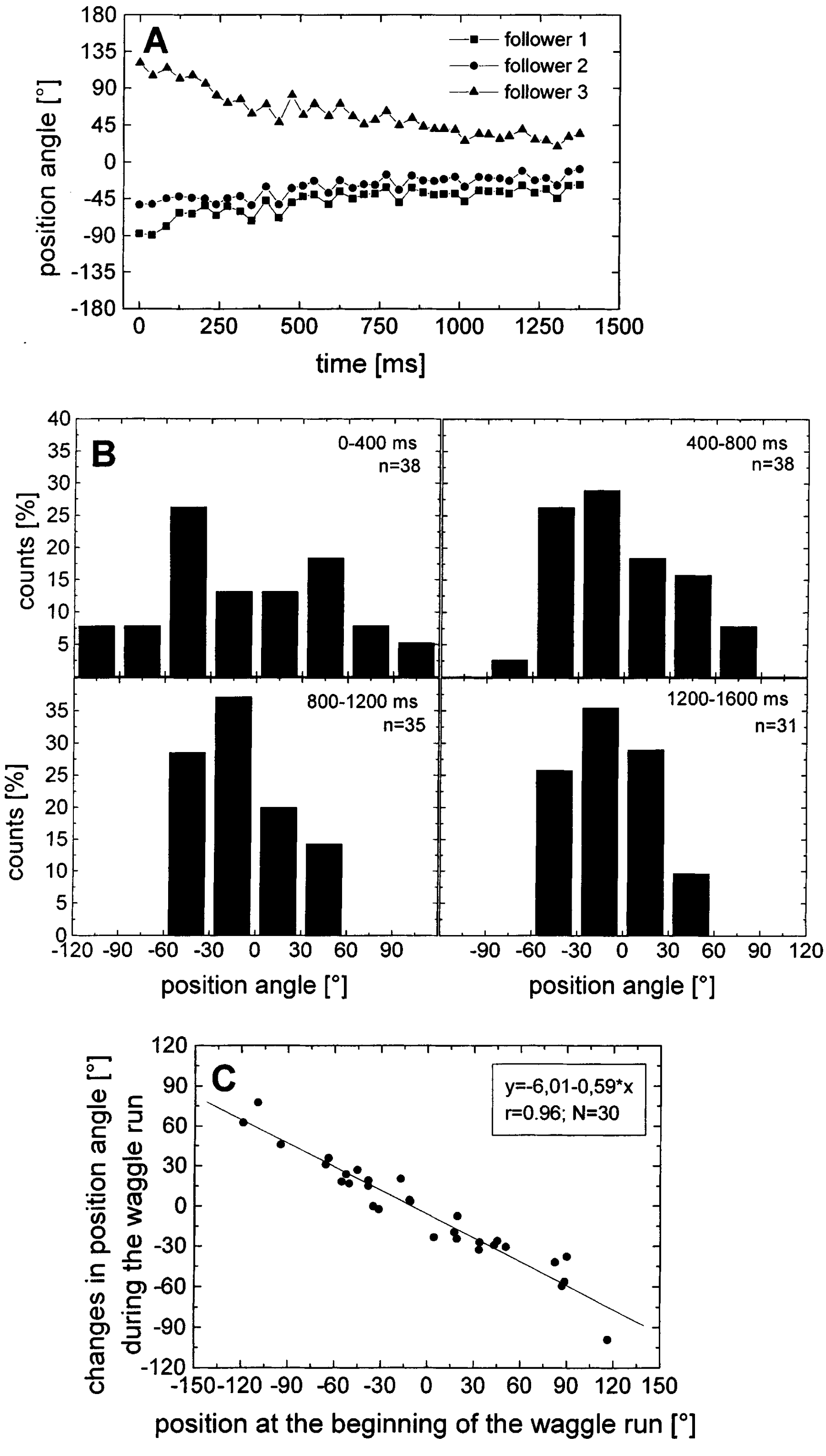


Fig. 3A–C The position angles (see Fig. 2) of followers of waggle dances performed on a vertical comb with open and empty cells and indicating food sources 1200 m distant from the hive. The position angle was always determined in the middle position of the dancer's pendulum-like waggle movements (Fig. 2), beginning with the first waggle movement and ending with the last waggle. **A** The changes in the position angle of three followers during a waggle run. **B** Histograms showing the position angles of 38 followers during ten waggle runs of different dancers. Each waggle run was divided in 400-ms intervals, and the mean position angle was calculated. **C** The changes in position angles are correlated to the follower's position angle at the beginning of the waggle run

Results

Position of the followers relative to the dancer

In Fig. 3A, the *position angles* (see Fig. 2) of three followers during a waggle run are shown. In the beginning of the waggle run, the followers were dispersed around the dancer and two of them were even standing around her head (indicated by the large position angles), but the longer the waggle run lasted, the smaller the position angles became. This means that the followers accumulated around the dancer's abdomen.

We repeated this analysis for another nine waggle runs, divided each of them into 400-ms intervals, calculated the mean angle for every follower ($n = 38$) in every interval, and plotted histograms for every interval (Fig. 3B). Again, the followers were scattered around the dancer at the beginning of the waggle run, but were increasingly found in a lateral-posterior position to the dancer as the waggle run came to an end. For all intervals, the distributions differ significantly from a uniform distribution (Kolmogorov-Smirnov goodness of fit; range from −180° to 180°). The first and the last distribution are also significantly different from each other (Kolmogorov-Smirnov goodness of fit). The more anterior to the dancer the followers started watching the waggle run, the more their positions changed during the waggle run (Fig. 3C).

Body orientation angle of the followers

We also determined the body orientation angle of the followers during waggle runs. The *body orientation angle* was defined as the angle between the long axis of the follower's thorax and the long axis of the dancer (Fig. 2). There was a strong correlation between the body orientation angle of the followers and their position relative to the dancer (Fig. 4).

For follower positions between ±60° (the middle part of the data in Fig. 4), the body orientation angle of the followers was proportional to their position angle, with the thorax orientation angle being larger than the position angle (see Fig. 2). This means, that the followers were not arranged radially around the head of the dancer. In the semicircle around the head and prothorax of the dancer (position angles between 60° and 150° to each side), however, the followers kept their body orientation angle constant and independent of the position angle.

Combining these findings, the following conclusions can be drawn: bees that began to follow a dancer from a position near her head did not turn their body before reaching the thorax of the dancer. They then started to turn their body continuously, while approaching the rear end of the dancer. From the video recordings we could see that the followers exhibited the stereotyped body orientation immediately after the start of the waggle run.

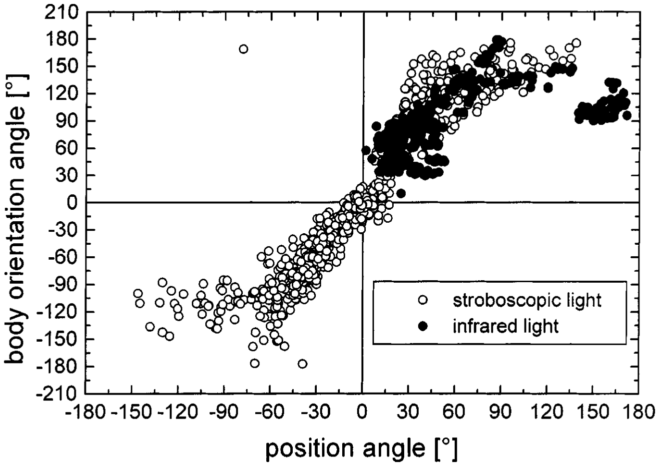


Fig. 4 Pooled data of body orientation angles (see Fig. 2) of follower bees (23 followers of six waggle runs, $n = 791$; $r = 0.93$) under stroboscopic flashlight illumination visible to bees (○) and under infrared illumination (●; $\lambda = 875$ nm; 11 followers of five waggle runs; $n = 381$; $r = 0.59$) invisible to bees

As shown in Fig. 4, the followers achieved the same body orientation angles under IR light. We therefore conclude that the arrangement of the followers was independent of light and not an artefact of the stroboscopic illumination necessary for the high-speed video recordings.

Tactile behaviour of the followers

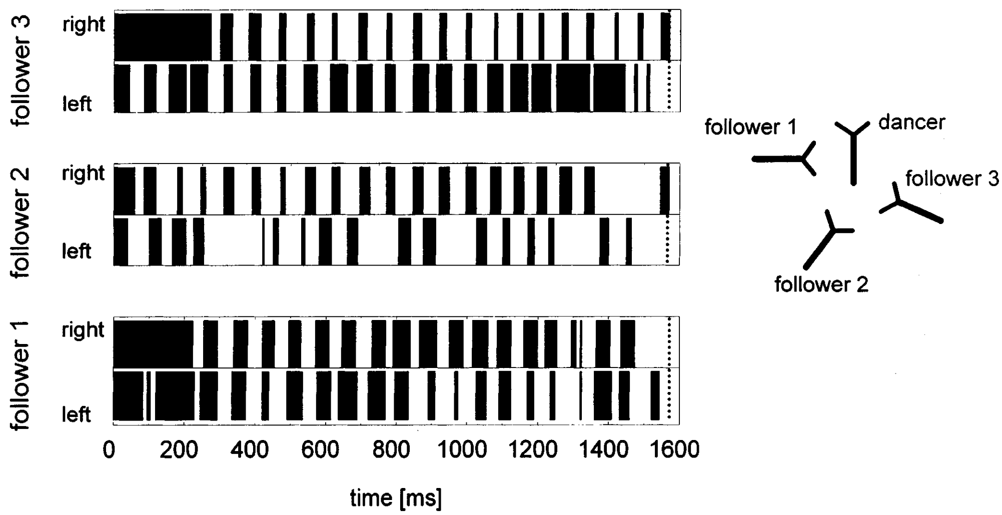
From the video recordings we observed that the followers had intense antennal contact with the dancer during the whole waggle run. Most of the contact was quite intense due to the wagging movements of the dancer and the small distance between dancer and followers. During periods of contact, the antennae of the followers were bent outwards by the dancer. The points of contact on the dancer were mostly at her body, sometimes at her wings. While wagging, the dancer occasionally struck even the heads of the followers. No avoidance behaviour of the followers was observed in these cases. Bees approaching the dancer from the head, showed an intense antennal waving and they often later followed the dancer.

We monitored the antennal contact between dance followers and dancers. Examples of individual contact patterns of 3 followers of one waggle run are given in Fig. 5. The antennal contact patterns of 38 followers in ten waggle runs were analysed in detail. For 62% (SD = ±12%) of the duration of the waggle run, a follower had tactile contact with the dancer, at least with one antenna (Fig. 6). A single contact with one antenna lasted for 34 ms on average (SD = ±11 ms).

Correlation between the temporal properties of the contact pattern and the position of the followers

Are temporal properties of the contact patterns correlated with the mean position angle of a particular

Fig. 5 Representative examples of the contact patterns between the antennae of dance followers and dancers in one waggle run with three followers. *Black* indicates contact with the antenna, *white* marks periods with no contact. The drawing shows the mean position angles of the three followers relative to the dancer



follower and thus enable the follower to read the waggle run angle? In Fig. 7, the analysed temporal patterns and their relationship with the position angle of the followers are shown. The total contact time with one antenna during the waggle run showed no correlation with the position of the follower (Fig. 7A), neither did the time difference between consecutive contacts with the two antennae (Fig. 7B). However, the mean duration of a single contact with one antenna (Fig. 7C) was weakly dependent on the angular position of the follower. This relation was not unambiguous, because both bees behind the dancer and around the thorax had longer contact times than the others. The strongest relationship was found for a feature that we called coincidence (Fig. 7D). This is the duration of simultaneous contact with both antennae. The slopes of the U-shaped curve were strongest for follower positions between 60° and 30° to each side, the range all followers pass through (Fig. 3).

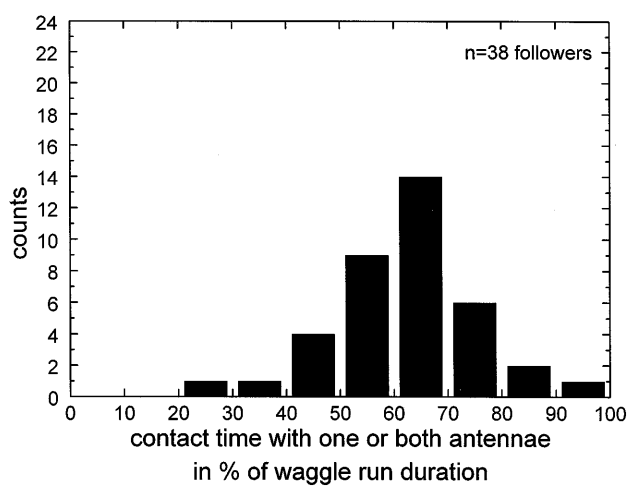


Fig. 6 Total contact time with one or two antennae for 38 followers of ten waggle runs performed by different dancers. The duration of contact is given relative to the whole duration of each waggle run

In Fig. 8 the changes in coincidence during a waggle run are shown for eight followers. When the followers approached the rear end of the dancer, the individual coincidence was decreasing.

Discussion

Followers have intense antennal contact with the dancer during the waggle run

A quantitative analysis of the antennal contact revealed that followers have, on average, antennal contact with the dancer for more than 60% of the duration of the waggle run. Such extended antennal contact should enable a flow of information from the dancer to the follower (see below).

Our results confirm findings by Mackenroth (1990) and Dreller (1993), who used an indirect estimation of this parameter. However, they are in contrast to Michelsen et al. (1987), who found a shorter total contact time. The reason for this difference could be a different definition of what a dance follower is. On a crowded dance floor, there are many bees that stand in the vicinity of the dancer without being interested in the dance.

Dreller (1993) also investigated the total contact time for *Apis dorsata* (16%) and *Apis florea* (25%). In contrast to *A. mellifera*, these tropical honeybees are open nesters and dance in daylight. Therefore, vision might reduce the importance of antennal contact in these species.

Cues and signals that could be transmitted between dancer and follower bees

Antennae are well equipped with different types of sense organs such as mechanoreceptors (e.g. Esslen and Kaissling 1976), chemoreceptors (Lacher and Schneider 1963; Vareschi 1971) and temperature receptors (Lacher

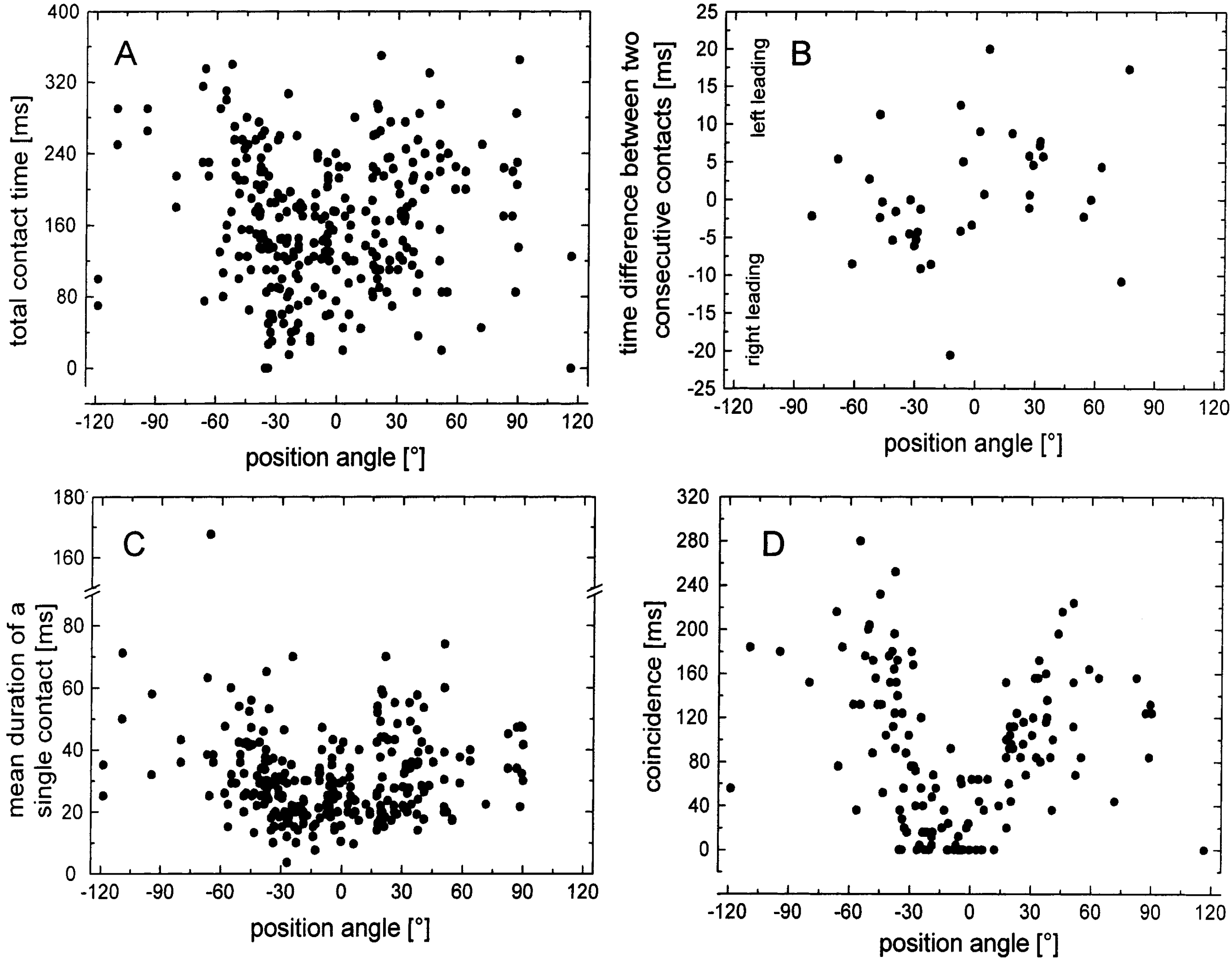


Fig. 7A–D Different temporal parameters of the contact pattern during the waggle run, and their relation to the mean position angle of the follower relative to the dancer. The analysis is based on ten waggle runs with a total of 38 followers. **A** The total contact time for one antenna each, per 400-ms intervals (for positive position angles $r = 0.35$; for negative position angles $r = -0.20$). **B** The time difference between two consecutive contacts with the two antennae ($r = 0.28$). **C** The mean duration of a single contact with one antenna, per 400-ms intervals (for positive position angles $r = 0.24$; for negative position angles $r = -0.46$). **D** Duration of coincidence, that is the period of simultaneous contact with both antennae, measured in 400-ms intervals (for positive position angles $r = 0.57$; for negative position angles $r = -0.69$)

1964). A dance follower can thus receive different cues and signals (a description of cues and signals in honey bee communication is given by Seeley 1998) emitted by a dancer: mechanical stimuli, the higher body temperature of the dancers (Stabentheiner et al. 1995) and pollen and scent from the flowers visited (von Frisch 1965).

Antennal contact patterns as a means of information transfer between dancer and followers

A dancer performs waggle movements that lead to complex contact patterns. It is most likely that these patterns are sensed by the mechanoreceptors. We suggest two possibilities of how followers might use these antennal contact patterns to find out the direction of the indicated food source. Firstly, a decreasing value of coincidence guides the follower to the rear end of the

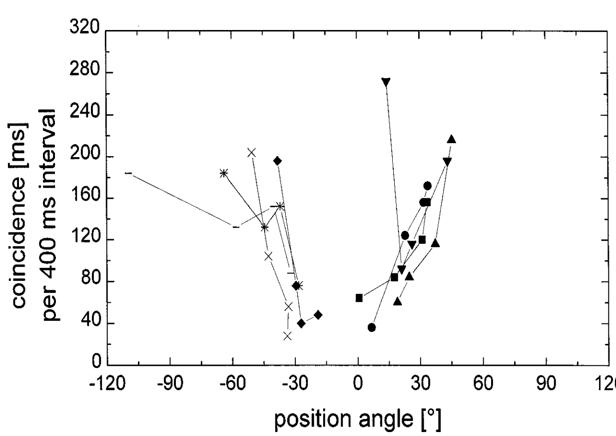


Fig. 8 Examples of individual changes of coincidence for eight followers during different waggle runs

dancer (Fig. 8), a favourable position for the determination of the waggle run angle (see below). Secondly, at least one temporal characteristic of the antennal contact patterns (Fig. 7D) is related to all positions of the follower relative to the dancer. A neural network analysis is under progress to address the question of how precisely the position can be determined by use of antennal contact patterns (Rohrseitz and Tautz 1998).

Compared to other tasks, that bees are able to perform by using their antennae (Martin and Lindauer 1966; Kevan and Lane 1985; Erber et al. 1998), it seems reasonable to assume that bees can measure these properties. For the determination of both parameters no detailed information about the stimulus (like amplitude or direction) is necessary. A simple measure of duration is needed.

However, the problem is not that simple, since the antennal contact patterns are not only influenced by the waggle movements of the dancer herself; they are also dependent both on the orientation of the followers relative to the dancer and on the nature of the active antennal movements. Two aspects of the follower behavior reduce the complexity of the situation: first, the followers have a stereotyped body orientation (Fig. 4). and second, we found that followers do not move their antennae actively while engaged in a waggle run; they keep them stretched.

How might this stereotyped body orientation pattern be achieved? Is it simply an arrangement by which the maximal number of followers can be spaced around the dancer? This assumption can be ruled out, because the maximal number of followers did not exceed five in the waggle runs under research. Around a dancing bee there is space for at least ten follower bees. This stereotyped body orientation might result from the straight approach of the potential follower bees towards the dancer from a distance (Tautz and Rohrseitz 1998). Potential dance followers are mostly attracted to a dancer from distances further than the reach of the antennae (Tautz and Rohrseitz 1998), and therefore antennal contacts are not necessary. Other modalities like air flows (Michelsen et al. 1987; Michelsen 1993; Storm 1998) and comb vibrations generated by the dancer (J. Tautz et al. unpublished observations) might guide the bees to the dancer. Further studies on the role of the different possible modalities (e.g. tactile contact, air flows, vibrations) and their interactions in the honey bee dance language are needed.

The importance of the followers' antennae for recruitment

The importance of the antennae for being recruited to a new feeding site has been demonstrated by Bayer (1975) and by Dreller (1993). Bees without antennae have difficulties in performing this task, perhaps due to difficulties in gaining the dance information (tactile signals as well as air flows) or to worsened navigational abilities of the handicapped bees.

The followers accumulate around the dancer's abdomen

According to our results, the position of followers relative to the dancer during the waggle run is only constant for bees behind the dancer. For all the others, the positions change during the waggle run: towards the end of each waggle run more followers are found around the dancer's abdomen.

Other authors also investigated the followers' position during waggle runs. Michelsen et al. (1987) pooled the position data for whole waggle runs, and found that the most common position is around the dancer's abdomen. Judd (1995) tried to correlate a follower's position with the success in finding a new feeding site. He reports that successfully recruited bees followed the waggle run from position angles between $\pm 30°$. This fits well with our findings that followers free to choose their dance position accumulate around the abdomen of the dancer.

Why do the followers show a preference for a position around the end of the dancer's abdomen? One possibility is that a dance follower is guided, for example by coincidence, to the end of the dancer's abdomen and therefore knows that she aligned parallel to the dancer (see Fig. 4). Once having reached this position, she only has to monitor the angle between her walking direction and gravity to find out the waggle run angle. From all other positions, the bee must calculate the waggle run direction from her position and her orientation relative to the dancer and relative to gravity.

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