

Floral scents affect the distribution of hive bees around dancers

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Abstract Floral scents are important information cues used to organize foraging-related tasks in honeybees. The waggle dance, apart from encoding spatial information about food sources, might facilitate the transfer of olfactory information by increasing the dissipation of volatiles brought back by successful foragers. By assuming that food scents are more intensive on specific body parts of returning foragers, i.e., the posterior legs of pollen foragers and mouthparts of nectar foragers, we quantified the interactions between hive mates and foragers during dances advertising different types of food sources. For natural sources, a higher proportion of hive mates contacted the hind legs of pollen dancers (where the pollen loads were located) with their heads compared to non-pollen dancers. On the other hand, the proportion of head-to-head contacts was higher for non-pollen foragers during the waggle runs. When the food scent was manipulated, dancers collecting scented sugar solution had a higher proportion of head-to-head contacts and a lower proportion around their hind legs compared to dancers collecting unscented solution. The presence of food odors did not affect in-hive behaviors of dancers, but it increased the number of trophallaxes in-between waggle runs (i.e., during circle phases). These

results suggest that the honeybee dance facilitates the olfactory information transfer between incoming foragers and hive mates, and we propose that excitatory displays in other social insect species serve the same purpose. While recent empirical and theoretical findings suggested that the colony level foraging benefits of the spatial information encoded in the waggle dance vary seasonally and with habitats, the role of the dance as a compound signal not only indicating the presence of a profitable resource but also amplifying the information transfer regarding floral odors may be important under any ecological circumstances.

Keywords *Apis mellifera* · Waggle dance · Floral scent · Information transfer · Trophallaxis

Introduction

Communication is indispensable for the survival of animal societies. Within the insect taxa, honeybee (*Apis mellifera*) colonies are good models to study communication because they have efficient channels for transferring information about food source characteristics. The different communication mechanisms allow bees to exploit selectively the most profitable food sources in an often unstable environment (von Frisch 1967; Seeley 1995). The most studied and conspicuous behavior that involves signal transmission in honeybees is the waggle dance (von Frisch 1967). When foragers find highly profitable food sources nearby, they perform round dances, while waggle dances are displayed when food sources are far from the hive (von Frisch 1967). The waggle dance has been shown to encode spatial information about food sources (von Frisch 1967; Gould 1974; Esch et al. 2001; Riley et al. 2005). The duration and the rate of waggle-run production are tuned to the resource

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profitability allowing for an adaptive distribution of recruits among the various food sources (von Frisch 1967; Seeley et al. 1991, 2000). However, the benefits to hive foraging efficiency of the spatial information encoded in the waggle dance seem to depend on the particular environmental circumstances, e.g., the spatial and temporal distribution of food sources (Sherman and Visscher 2002; Dornhaus and Chittka 2004).

It has often been suggested that the dance serves at least two other informational purposes. Firstly, it increases the attention and activity of bees in the vicinity thereby communicating the presence of an attractive food source (von Frisch 1923, 1967; Božič and Valentinčič 1991). If a forager is performing a waggle dance, the increased attention of unemployed foragers will facilitate their perception of the acoustic–vibratory signals emitted by the intensive movements of the wings that conforms the acoustic near field of the dancer (Michelsen et al. 1987; Michelsen 2003). However, the dance display not only attracts potential foragers but also food processor bees that initiate trophallactic interactions with the incoming foragers, whereby the latter would receive information about the nutritional state of the colony (Farina 2000). Secondly, the dance seems to be relevant to transfer food odors (von Frisch 1923, 1967; Johnson 1967; Wenner et al. 1969; Wells and Wenner 1973). The particles of floral odors impregnated onto the foragers' body as well as the pollen loads carried on hind legs of the incoming foragers are enough to reactivate unemployed experienced foragers to resume collecting at known food sources (von Frisch 1923). While odors carried on the forager's body could be dissipated, the nectar odor preserved in the honey sac is maintained intact regardless of flight distance (von Frisch 1967). As a consequence, recruits can learn the nectar odor brought back by foragers (Farina et al. 2005; Gil and De Marco 2006; Grüter et al. 2006) via mouth-to-mouth trophallactic contacts (in lab experiments: Gil and De Marco 2005, in hive experiments: Farina et al. 2007).

Thus, a dancing bee can provide different kinds of information during the same behavior, and the dance, therefore, functions as a compound signal (Bradbury and Vehrencamp 1998). It is known that information cues can be transmitted in parallel or complementary to signal transmission. Contrary to the evolved signals, cues are provided inadvertently (Danchin et al. 2004; Dall et al. 2005). In this sense, the honeybee is an excellent model to study the role of these incidental cues during the performance of a conspicuous behavior that involves signal transmission such as the waggle dance.

Until now, follower behavior and distribution of hive bees around dancers have been explained in the context of spatial information acquisition (Michelsen et al. 1987; Rohrseitz and Tautz 1999). The fact that followers are

primarily positioned around the abdomen of a dancer, where the acoustic near field is most intense, has been explained by improved acquisition of information about the transmitted signal (Michelsen et al. 1987; Michelsen 2003). However, given the importance of odor cues and assuming that dancers provide olfactory information during this motor display, we hypothesized that hive bees located around the dancer may present behavioral patterns which particularly facilitate the acquisition of olfactory information. A quantitative study analyzing the distribution of hive bees around the dancer and its dependence on the presence of food odors was performed to address this hypothesis. By using video recording, we analyzed the distribution of hive mates around dancers foraging under natural situations (dancers returning from natural pollen and nectar sources) and in a controlled situation (dancers collecting scented or unscented sugar solution). Dancer behavior and trophallactic behavior during dancing were also measured for the controlled situation.

Materials and methods

The experiments were performed at the end of the nectar flow season (March–April of 2004) at the experimental field of University of Buenos Aires. We used a two-frame observation hive containing a colony of about 4,000 European honeybees (*A. mellifera ligustica*) with a queen, brood, and food reserves.

In-hive behavioral recordings

Dances of foragers coming from natural food sources, (natural situation) or coming from an artificial feeder of regulated rate (controlled situation) were video-recorded. In the natural situation, dances were divided in two groups, depending on the type of food source exploited: (a) Pollen foragers were distinguished from (b) non-pollen foragers by the pollen loads carried on the posterior legs (primarily nectar foragers).

In the controlled situation, we experimentally manipulated olfactory cues of a sucrose solution that was offered at an artificial feeder to a group of foragers. This group of bees from the experimental hive was previously trained to collect 0.5 M unscented sucrose solution at a feeder that was located 160 m from the hive and provided solution at a constant flow rate of 5 μ l/min during a period of 8 h daily.

A new group of five to eight trained foragers at the experimental feeder were individually marked each experimental day. The sucrose solution concentration and the flow rate were increased only for 3 h per day for data recording sessions. During a first period of 3 days, the groups of foragers collected 2.0 M unscented sucrose

solution with a constant flow rate of 40 $\mu\text{l}/\text{min}$ at the feeder. This period was followed by another 3 days, during which the trained foragers collected 2.0 M sucrose solution at the feeder scented with 50 μl of Linalool (LIO) per liter of sugar solution, with the same flow rate of 40 $\mu\text{l}/\text{min}$. These conditions of flow rate ensured the highest probability of dance to arrive to the hive (Cogorno et al. 1998).

Complete times foragers spent inside the hive from her arrival to the hive until her departure to the food source (hive stays) were recorded by using a Sony DCR-TRV520 video camera. Video recordings of the dances were analyzed with a resolution of 30 frames per second by using the Ulead Video Capture for Windows program (6.0 version).

Measurements

For both the natural and controlled situations, we recorded the position of hive bees around the body of the dancers during all the waggle phases of their hive stays. As the movements of the antennae (the insects' olfactory organs) could not be distinguished due to the temporal resolution of the video, the head contacts were quantified because their recordings guaranteed that the hive bee's antennae indeed contacted the dancer body. All the head contacts of hive bees with the dancers' body were recorded by using transparent acetate sheets, the medium position of the frontal part of the heads of the hive bees that contacted the dancer body were marked as points around a diagram of the dancer. Trophallactic interactions were not counted as head contacts. In this way, more than one contact per hive bee could have been recorded, as these bees were not individually marked. Each contact was recorded only once, although some lasted for more than one frame during the analysis. The space around the diagram (360°) was subdivided in 10° intervals (Fig. 1). The numbers of contacts in each of the intervals were registered. The contacts of the two corresponding intervals of both sides (e.g., $0\text{--}10^\circ$ and $350\text{--}360^\circ$) were added up for the analysis because we assumed that bees around dancers have no general preference for a particular dancer side. Henceforth, all angles are between 0 and 180° .

In the controlled situation, additionally, we measured (1) the duration of hive stays of experimental foragers, (2) the latency until the first waggle run began, (3) the number of waggle runs per hive stay, (4) the total time of trophallaxis, (5) the number of receivers per trophallaxis, and (6) the number of trophallactic contacts. For this last variable, we separated the trophallactic contacts that occurred during the dancing period (during the circle phases) from those that occurred in the absence of dancing (i.e., before and after the dancing period). If foragers stopped dancing for a period longer than 4 s, it was considered a period of absence of dancing (see Waddington 1982). Each contact was considered a mouth-to-mouth contact (trophallaxis) between the forager and the

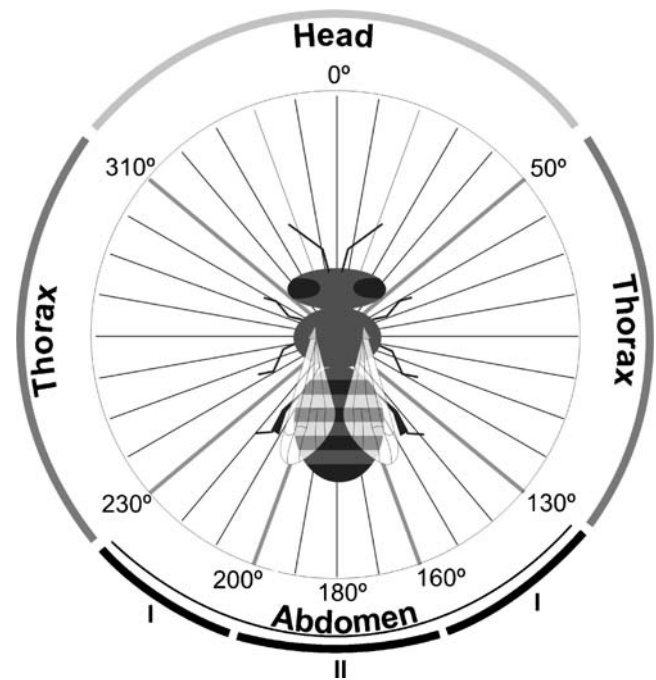


Fig. 1 Sketch of a bee with the intervals, in degree, representing the different body parts. Interval *I* represents the abdomen including the posterior legs; *II* the abdomen excluding the posterior legs

receiver when the receiver's head looked like a triangle, and its proboscis was extended towards the opened mandibles of the forager that offered the sucrose solution.

Hive odor

During the controlled situation, the entrance of the observation hive was scented with a different odor by putting an absorptive paper (diameter 3 cm) soaked with 50 μl of pure odorant, phenylacetaldehyde, inside a box connected to the entrance by a wire mesh. Returning foragers passed the box when entering the hive. This device was used to minimize the effect of food odors clinging on the forager bodies (von Frisch 1967; Farina et al. 2005). Hive and solution odors are pure natural flower components, and they were obtained from Sigma-Aldrich, Steinheim, Germany.

Statistic analysis

Because the assumptions of normality and homogeneity of variances were not met, nonparametric analyses were used. Mann–Whitney *U* tests were used to compare frequencies of hive bee contacts, and behavioral parameters of the experimental foragers such as the hive time, the latency, the number of waggle runs, the total trophallactic time, the total offering contacts, and the food receivers involved. Wilcoxon matched-pairs tests were used to compare the number of trophallaxis between stages of hive stays, i.e., during dancing period or in the absence of dancing (Zar 1999).

Descriptive statistics are given as medians and quartiles (in brackets). For the descriptive part, 24 dancers were analyzed; while for the experimental part, 31. Only 28 of these 31 bees could be recorded completely during their whole hive stays.

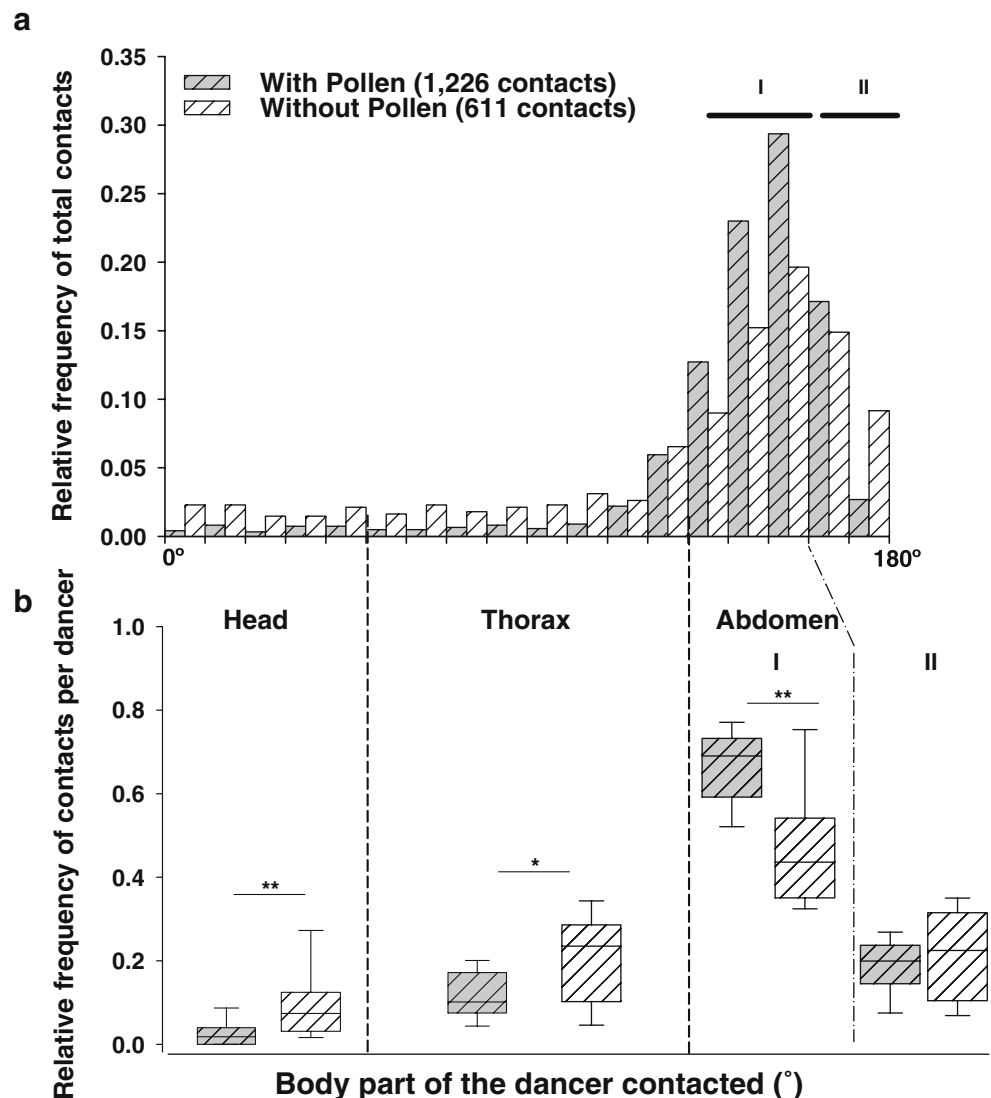
Results

Natural situation

The highest proportion of head contacts of hive bees around the dancers during the waggle-run phases was observed at the total area of abdomen of the dancers (more than 60% of all cases, Fig. 2). However, the distribution of head contacts around dancers foraging at natural food sources differed between the types of resources exploited (Fig. 2a). Head contacts around the hind legs were more frequent when hive

bees followed pollen dancers (with pollen loads in their hind legs) than when they followed non-pollen dancers (abdomen including posterior legs without pollen vs abdomen including posterior legs with pollen: $U=18, p=0.0018, N=24$, Mann–Whitney U test; Fig. 2b). Hive bees around non-pollen dancers presented a higher proportion of contacts with the anterior part of the dancer compared to hive bees around the pollen dancers (head without pollen vs head with pollen: $U=18, p=0.0018, N=24$; and thorax without pollen vs thorax with pollen: $U=33, p=0.024, N=24$, Mann–Whitney U test; Fig. 2b). When we analyzed the part of the abdomen that did not include posterior legs (range 160–200°), no differences were found between proportions of head contacts by hive bees comparing non-pollen dancers to pollen dancers (abdomen not including posterior legs without pollen vs abdomen not including posterior legs with pollen: $U=61, p=0.53, N=24$, Mann–Whitney U test; Fig. 2b).

Fig. 2 Distribution of the head contacts of hive bees around the incoming foragers during the display of the waggle-run phase. **a** Total head contacts (in relative frequencies) of hive mates performed around the body of 24 dancers returning from natural food sources. Dancers without pollen loads in the posterior legs were considered to be non-pollen foragers (white bordered bars, without pollen, $N=12$). Dancers with pollen loads in the posterior legs were considered to be pollen foragers (gray bordered bars, with pollen, $N=12$). 0° corresponds to the frontal part of the dancer’s head and 180° to the posterior extreme of its abdomen. **b** Total head contacts relative to each dancer and grouped according to the part of the dancer’s body that was contacted: head; thorax; posterior legs (I); the rest of dancer’s abdomen, (II). Medians, quartiles, and the 5 and 95° percentiles are represented. Asterisks indicate statistical differences (** $p<0.01$; * $p<0.05$; see “Results” for details)



Controlled situation

When the dancers collected scented sucrose solution from the controlled rate feeder, a higher proportion of hive bee contacts was observed during the waggle-run phase with the anterior part of the dancers' body compared to the situation in which dancers collected unscented solution (Fig. 3a). When contacts were grouped according to the same dancer body parts analyzed in natural situation, the differences were clear. For the head, the proportion of contacts was higher for the situation with odor (head without odor vs head with odor: $U=0.5, p<0.0001, N=28$, Mann–Whitney U test; Fig. 3b). At the abdomen, we also found differences but only for the part that included the posterior legs (abdomen including posterior legs without odor vs abdomen including posterior legs with odor: $U=11.5, p<0.0001, N=28$; abdomen not including posterior

legs without odor vs abdomen not including posterior legs with odor: $U=72.5, p=0.241, N=28$, Mann–Whitney U test; Fig. 3b). In this case, the higher proportion was found in the treatment without odor. Around the thorax, there were no differences between treatments (thorax without odor vs thorax with odor: $U=73, p=0.75, N=28$; Mann–Whitney U test, Fig. 3b).

Neither foragers coming from a scented sucrose solution nor those coming from unscented sucrose solution differed in their hive stay duration, the latency before dance, the number of waggle runs per hive stay, the total time of trophallaxis, the number of receivers per trophallaxis, and the total number of trophallaxis (see Table 1 for details). However, if we consider the trophallactic contacts according to the stage at which they occur (during dances, specifically during circle phases, or in the absence of it), the number of trophallactic-offering contacts was significantly higher

Fig. 3 Distribution of the head contacts of hive bees around the incoming foragers during the display of the waggle-run phases. **a** Total head contacts (in relative frequencies) of hive mates performed around the body of 28 dancers returning from a rate-feeder located 160 m from the hive. Dancers that collected unscented 1.8 M sucrose solution (*gray bars*, without odor, $N=14$) were compared with dances of another group foraging at a 1.8 M sucrose solution scented with *LIO* (*white bars*, with odor, $N=14$). 0° corresponds to the frontal part of the dancer's head and 180° to the posterior extreme of its abdomen. **b** Total head contacts relative to each dancer and grouped according to the part of the dancer's body that was contacted: head; thorax; posterior legs, *I*; the rest of dancer's abdomen, *II*. Medians, quartiles, and the 5 and 95° percentiles are shown. Asterisks indicate statistical differences ($***p<0.001$; see "Results" for details)

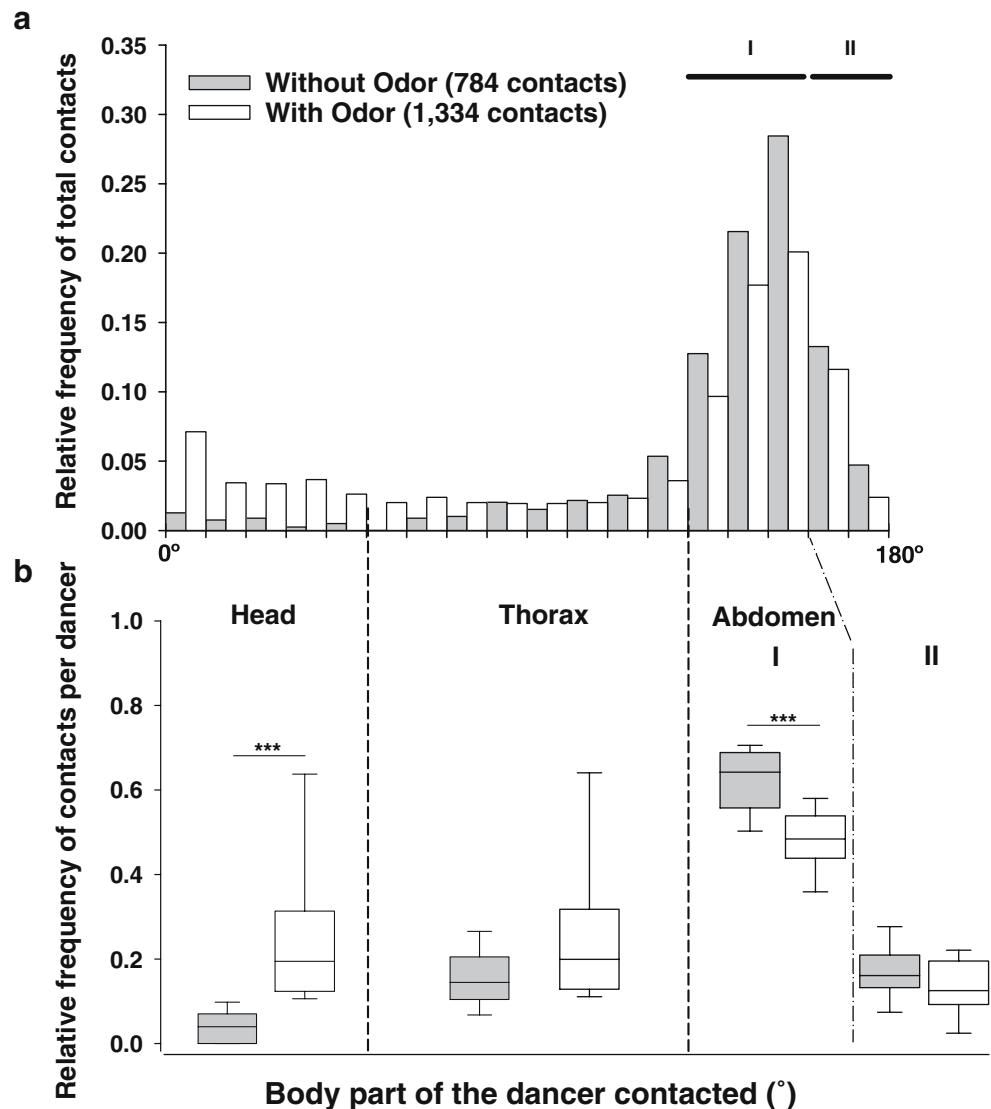


Table 1 In-hive behavioral parameters of the trained forager bees

	Without odor	With odor	<i>U</i>	<i>p</i>	<i>N</i>
Hive time (s)	102 (67, 139)	129 (87, 191)	84.5	0.16	31
Latency (s)	27 (11, 38)	23 (12, 34)	94.5	0.65	29
Number of waggle runs	24 (19,34)	41.5 (14,74)	101.5	0.46	31
Total trophallactic time (s)	36 (28, 42)	37 (25, 41)	93	0.82	28
Total offering contacts	5 (3, 8)	7.5 (5,12)	82.5	0.14	28
Food receivers involved	7.5 (4, 9)	9 (7, 12)	69.5	0.19	28

Behaviors of dancers collecting unscented sucrose solution were compared with dancers collecting scented sucrose solution. Medians and quartiles (in parentheses) and values for Mann–Whitney *U* test are shown

during the dancing period only for the situation with odor (for the unscented situation: $T=31.5$, $p=0.105$, $N=15$, Wilcoxon test, Fig. 3a; for the scented situation: $T=2$, $p=0.0009$, $N=16$, Wilcoxon test, Fig. 4b).

Discussion

The results show that odor cues of the food brought back by dancing foragers affect the distribution of hive mates around the dancers. We observed that these differences were not caused by conspicuous changes in the in-hive behaviors of the dancers, as all of the behavioral variables recorded in the trained foragers did not show differences between treatments. Therefore, the crop scent per se, specifically the odor concentrated on the mouthparts of the dancers, affected not only the head-to-head contacts between the dancer and hive mates but also the occurrence of trophallaxis amongst them.

Intensive interactions during scented dances

As expected, the highest proportion of hive bee contacts was observed around the hind legs of the dancers in all of the analyzed cases. This could be the result of bees trying to improve the acquisition of the transmitted signal (Michelsen et al. 1987), which supposedly is strongest at the rear part of the dancer or due to the body oscillation during the waggle runs, which presents the highest amplification at the abdomen. This could, incidentally, increase the probability of contacts with bees around her. Nevertheless, the general pattern of contacts also depended on the type of food source and the presence of odor in the food bees collected. We found a higher proportion of head-to-head contacts when dancers came from natural non-pollen sites and when foragers collected scented sugar solution at an artificial feeder. Food odor effects seem to be stronger when odors are located on the dancer mouthparts, while the fragrances of the pollen loads are probably less effectively transferred to other colony members (von Frisch 1943). Moreover, if we compare the proportion of head-to-head contacts between

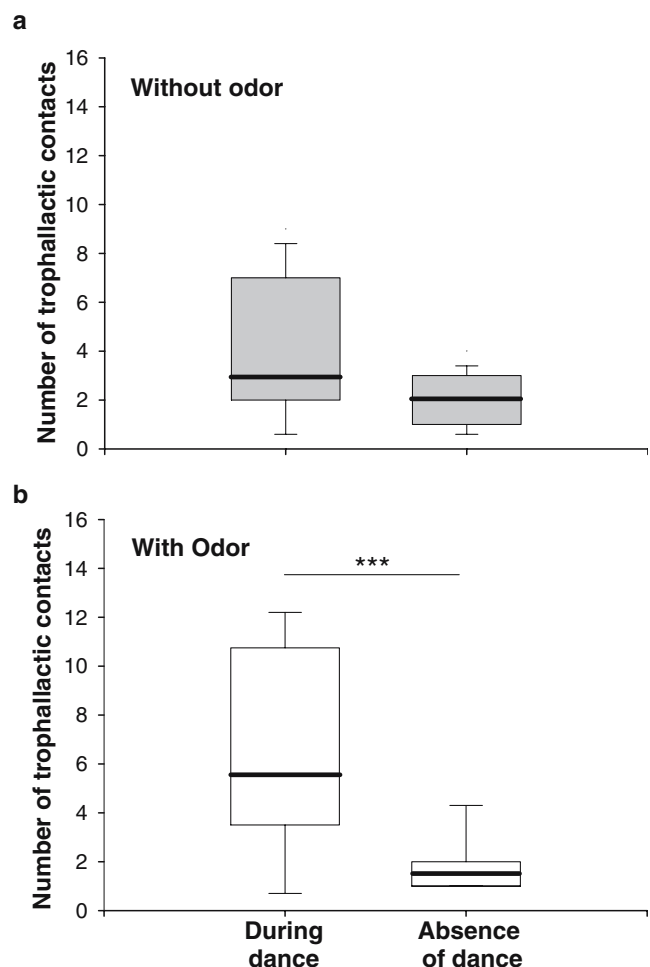


Fig. 4 Number of trophallactic-offering contacts performed by the trained foragers inside the hive. **a** Unscented sucrose solution (without odor, $N=15$), **b** scented sucrose solution (with odor, $N=16$) with *LIO*. The trophallactic contacts were grouped according to the period during which they occurred: during the dancing display (in-between waggle-run phases, i.e., during the circle phases) or before the first waggle-run and/or after the last waggle-run phase observed (absence of dancing). Medians, quartiles, and the 5 and 95° percentiles are shown. Asterisks indicate statistical differences (***) $p<0.001$; see “Results” for details)

non-pollen dances and scented solution dances, more contacts are observed for the dancers collecting scented solutions at the artificial feeder, which suggests a more salient response for this food odor compared with the natural odor. This could be a consequence of differences in odor concentration, odor identities, or both. Another reason may be that the hive entrance was scented only during the controlled situation, which reduces the putative effect of the food odors clinging on the forager bodies to the controlled situation. Therefore, while food odors brought back by the trained foragers were mainly concentrated onto their mouthparts, the dancers analyzed during the natural situation could have had food odors more equally distributed on the body surface. Oral contacts during dance performance have already been reported (von Frisch 1923, 1967; Park 1925). The occurrence of dance performance positively correlates with the number of nectar receivers, once the dancer stops its motor display (Farina 2000), which suggests that both behaviors, dance and trophallaxis, are coupled. Present results go beyond this, as we show that the presence of odor did not modify the number of trophallaxis during each forager's hive stay but increased the proportion of these trophallaxes while the active forager danced. Thus, honeybee dances, apart from encoding spatial information, function as a congregating mechanism, while the crop scent concentrated on the mouthparts would orientate the hive bees to obtain samples of the food recently collected. The higher proportion of the head-to-head contacts between "scented nectar" dancers and hive bees compared to the unscented situation could lead to a higher number of mouth-to-mouth contacts during the return phases of the waggle dance. During the trophallactic contacts, the food receivers can obtain information related to the odor and the profitability of the discovered nectar source (von Frisch 1967; Farina 1996; Crailsheim 1998; Gil and De Marco 2005; Farina et al. 2007). Thus, the performance of trophallactic contacts during dances might indicate that this display would facilitate the transfer of chemical cues about the new floral type found, while it encodes more complex information such as the food location.

Transfer of food odor information is an important mechanism of recruitment that has been observed also in other social insects (stingless bees: Lindauer and Kerr 1958; bumblebees: Dornhaus and Chittka 1999; wasps: Jandt and Jeanne 2005; and ants: Roces 1990). Additionally, many social bee species also show excitatory recruitment displays (Lindauer 1961; Hölldobler 1977; Nieh 1998; Dornhaus and Chittka 2001). It has been suggested that excitatory motor displays and the transfer of olfactory information during these behaviors represent more primitive recruitment mechanisms from which the waggle dance seems to have originated (Ribbands 1954; Hölldobler 1977; Nieh 2004). Therefore, the presence of odors might affect

behavioral patterns of potential recruits in similar ways in other social insect species that use socially transmitted food odor information.

Putative appetitive learning within the dancing context

Bee dances could be a suitable context for the acquisition of olfactory information through olfactory conditioning within the hive. This motor display may arouse the following bees and lead to better learning of the contingency between odor and reward. Indeed, honeybee recruits can be conditioned to the floral odor before arriving at a particular food source, which shows that olfactory memories for a specific odor can be formed during the recruitment displays inside the hive (von Frisch 1967; Farina et al. 2005; Grüter et al. 2006). This strongly suggests that recruits learn the contingency reward odor through mouth-to-mouth contacts while following dances. In this sense, Dirschedl (1960) showed that 96% of all recruits arriving at the food source received food samples from the recruiting foragers (i.e., carried dyed syrup collected by trained foragers).

The crop scent cannot only be learned within the hive, but it can also cause a conditioned response depending on the knowledge of the inactive forager about this floral odor. In fact, most dance followers are experienced foragers (Biesmeijer and Seeley 2005), and the dance is the most frequent social interaction during the reactivation process to a profitable food source (Gil and Farina 2002). Thus, inactive foragers can confirm the reappearance of their food source by only perceiving the odor of the floral type (von Frisch 1923, 1967; Ribbands 1954).

Although we have not identified the follower bees, it is known that the bees attending dancers often are recruits (Riley et al. 2005; Biesmeijer and Seeley 2005), reactivated foragers (Gil and Farina 2002; Biesmeijer and Seeley 2005), and also nectar processors (Farina 2000). The differences found in follower's behavior, depending on food source type, will not only affect the process of foraging activation (and reactivation) but also foraging-related tasks inside the nest such as nectar processing and storing. Floral odors are learnt inside the hive (Gil and De Marco 2006; Farina et al. 2007), they affect the occurrence of trophallaxes between foragers and nectar processors (Goyret and Farina 2005), and this food scent information is rapidly propagated amongst nestmates of all ages (Grüter et al. 2006).

Recent empirical and theoretical findings suggest that the benefits of the spatial information encoded in the waggle dance to foraging vary seasonally and with habitats (Sherman and Visscher 2002; Dornhaus and Chittka 2004; Dechaume-Moncharmont et al. 2005; Dornhaus et al. 2006). However, to understand the costs and benefits of dancing or of following dances and, therefore, the selection

pressures that act on this extraordinary behavior, we need to consider the fact that the waggle dance is a compound signal, providing different kinds of information. The role of the dance (waggle or round dance) as a mechanism for the amplification of olfactory information within the hive is likely to be relevant under any ecological circumstances of the honeybee hive.

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