Chapter 2.4
Olfactory Information Transfer During Recruitment in Honey Bees

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Abstract Honey bee colonies use a number of signals and information cues to coordinate collective foraging. The best known signal is the waggle dance by which dancers provide nest-mates with information about the location of a foraging or nest site. The efficiency of this nest-based recruitment strategy partly depends on olfactory information about food sources that is transferred from dancer to receivers in parallel to spatial information. Here we will address how the waggle dance facilitates the acquisition and the retrieval of food odor information and how olfactory memory affects the interaction patterns among nest-mates within the dancing and the food-unloading context. We further discuss how olfactory information affects the food preferences of foragers acquired directly from scented-food offered inside the hive. The discussed results show that odor learning in this context is an important component of the honey bee recruitment system that has long-term consequences for foraging decisions.

Abbreviations

LIO   Linalool
PER   Proboscis extension reflex
PHE   Phenylacetaldehyde
US   Unconditioned stimulus

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2.4.1 Background

Honey bees (*Apis mellifera*) are excellent models to study the formation and development of information networks in decentralized biological systems [39]. The different worker groups in honey bee colonies show a strong operational cohesion that emerges from the continuous interactions amongst nest-mates. In this chapter we discuss olfactory information transfer in this network, its role for the organization within worker groups and how olfactory learning leads to cohesion between worker groups in the context of food collection.

In honey bees, like in many other social insects, collective tasks such as foraging, nest-climate regulation, nest-building/repair or brood care constantly need to be adjusted in response to changes in the environment or within the nest. Food source locations, for example, are often stable only during some days or a few weeks [40]. Responses to these changes at a colony level are often the result of individuals responding to simple local information [39]. This local information is provided either by nest-mates, environmental cues or by modifications of the environment by nest-mates. Information from nest-mates is transferred via different sensory modalities (e.g. chemosensory, tactile), either inadvertently (cues) or based on traits specifically designed by selection to convey information (signals).

An example for inadvertent information transfer is the propagation of gustatory and olfactory information about the exploited resources during the distribution of liquid food within the hive ([12, 19, 21, 33, 34], see below). The frequent food sharing among workers connects different worker groups. It allows workers not directly involved in foraging, like nurse bees, to obtain information from bees that actively participate in resource exploitation and processing, i.e. foragers and food processor bees [19, 21, 33, 34].

The best known behavior in honey bees, the waggle dance, involves signal transmission [41] and provides nest-mates with information about the location of a foraging or nest site [9, 37, 41]. When foragers find highly-quality food sources, they perform waggle dances inside the nest to recruit other bees to the same location. The occurrence, duration and the rate of waggle-run production are tuned to the profitability of the feeding site, thereby allowing for an adaptive distribution of recruits among the various food sources ([26, 39, 41], see also Chaps. 2.1 and 2.3).

Honey bees are able to use floral scents as guiding cues for long-distance flights [42]. However, there are also some problems with using olfaction for long distance orientation because (1) floral bouquets can change in the air due to differences in volatility of the different compounds [24, 43] and (2) floral bouquets of some species change during the day [43]. Therefore, honey bees also strongly rely on visual information to find food sources, such as celestial and terrestrial references or familiar landmarks [7, 41]. Once a bee returns from collecting resources to the closed and dark environment of the hive cavity, other sensory modalities that are less relevant in the field become more important, e.g. acoustical signals and vibrations [8, 31].

When a successful forager returns with nectar, she brings back the food scent in the honey crop or clinging on her body. These odor cues act as attractant or orientation guide for nest mates while the forager walks or dances [5, 41]. Usually, several bees simultaneously follow a dancer for a few dance circuits. Most of these followers are foragers but also food-processing bees are attracted by dances [10]. Recruits are rarely able to find the precise location of the food source for landing with the vector information alone, but need additional information sources [37, 42]. These can be olfactory and visual cues from the flowers themselves or cues and signals provided by other bees on the food source [41]. Given the importance of olfactory cues for locating a food source, in-hive recruitment strategies involving not only the transfer of vector information of the waggle dance but also the transfer of olfactory cues are likely to have a positive effect on the foraging performance of honey bee colonies (review: [22]).

In this chapter we will discuss how the waggle dance facilitates the acquisition and the retrieval of olfactory information about food sources and consider how this information affects the food preferences of foragers. Finally, we show that olfactory learning also has more subtle effects on honey bee foraging through its effects on perceived interaction patterns.

2.4.2   Floral Scents as Guiding Cues for Hive Mates

Apart from the transmission of spatial information mentioned in the previous section, the dance serves at least two other informational purposes: first, it increases the attention and activity of bees in the vicinity by communicating the presence of an attractive food source ([41], review: [22]). If a forager is performing a waggle dance, the increased attention of unemployed foragers facilitates the perception of the acoustic–vibratory signals emitted by the intensive movements of the wings that form the acoustic near field of the dancer ([8, 31], see also Chap. 2.2). Second, the honey bee dance is important to transfer food odor information [41, 42]. The molecules of floral odors clinging on the foragers' body as well as the pollen loads carried on hind legs can be perceived by other foragers. Dancing bees often shortly interrupt dancing and offer samples of food to surrounding bees ([41], review: [11]). These interactions are often brief (<2 s) which suggests that in these cases followers do not actually receive nectar but just probe it. There is good evidence, that these interactions play an important role in olfactory learning (see below).

Thus, a returning forager provides different kinds of information during dancing, which functions as a compound or multicomponent signal [22]. Information cues are transmitted in parallel or complementary to the signal. The transfer of floral odor information linked to the display of a stereotypic behavior can be seen in other social insects as well [27]. However, as far as we know only honey bees perform a nest-based signal that transmits location information [22, 41].
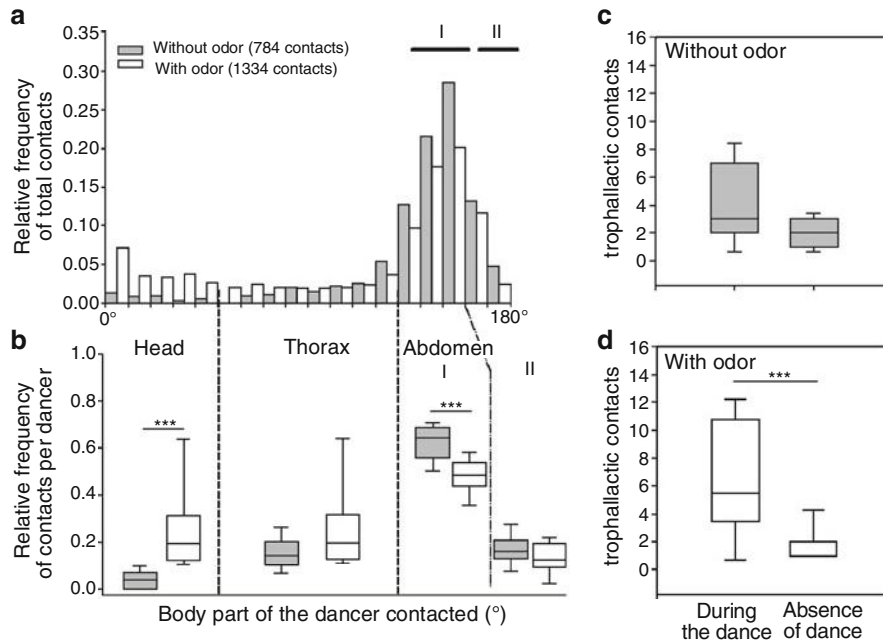
Fig. 2.4.1 Floral scents as guiding cues for dance followers. Distribution of the head contacts of hive bees onto the incoming foragers displaying waggles and the number of trophallactic contacts offered by the dancer inside the hive. (**a**) Head contacts onto the body of dancers. Comparisons were done between dancers that collected unscented 1.8 M sucrose solution (*gray bars*, without odor, N = 14) and dancers that foraged a scented (Linalool, LIO) sucrose solution (*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 (in relative frequencies) grouped according to the part of the dancer's body that was contacted. (**c**) and (**d**) The number of trophallactic contacts offered by dancers carrying either unscented (**c**, without odor, N = 15) or scented sucrose solution (**d**, with odor, N = 16). Trophallaxis events were grouped according to the period they occurred: during the dancing display, before the first waggle-run and/or after the last waggle-run phase observed. Medians, quartiles, and the 5 and 95° percentiles are shown. Asterisks indicate statistical differences (Mann–Whitney *U*-test in (**c**), Wilcoxon-test in (**d**), ***p < 0.001) (After [5]. With permission)

2.4.2.1 Interactions During Scented Dances

The highest proportion of head contacts of hive bees around the dancers during the waggle-run phases is observed around the abdomen of the dancers (more than 60% of all cases, Fig. 2.4.1a, b). This can be expected if this position improves the acquisition of the transmitted signal [31] (see Chap. 2.2). However, the distribution of head contacts around dancers differs significantly for the different types of collected resources. Head contacts around the hind legs are more frequent when hive bees follow pollen dancers (with pollen loads on their hind legs) than when they follow non-pollen dancers [5]. Dancers that forage at natural nectar sources are contacted in

a higher proportion at their thorax and head (for details see [5]). These quantitative descriptions suggest that the general pattern of contacts depends on the type of the collected food source and the presence of odor in the collected food. Accordingly, a higher proportion of head-to-head contacts was found when dancers collected scented sugar solution at artificial feeders (Fig. 2.4.1a). Food odor effects seem to be stronger when odors are located on the dancers' mouthparts, probably due their persistency within the honey sac [41]. In the mentioned experiment (Fig. 2.4.1), the hive entrance was scented with a different odor in order to reduce the effect of the food odors clinging onto the foragers' body surface. The presence of odor in the collected solution does not seem to modify the number of trophallaxis events during hive stays [5], but it increases the proportion of these interactions during dancing (Fig. 2.4.1c, d). Hence, the dance acts as a congregating mechanism while the crop scent concentrated on the mouthparts helps other bees to orientate and taste the liquid food. Moreover, the higher proportion of the head-to-head contacts between "scented nectar" dancers and hive bees compared to the unscented situation might lead to a higher number of mouth-to-mouth contacts during the return phases of the waggle dance (Fig. 2.4.1c, d).

2.4.2.2   Associative Learning Within the Dancing Context

As mentioned above dance followers often receive or taste samples of the collected food during short interruptions of dancing. Dirschedl [6] showed that most of the recruits arriving at the food source (ca. 95%) received food samples collected by the recruiting foragers inside the hive. This might explain why von Frisch, during his pioneering study published in 1923, found that recruits had strong preferences for food containing odors that were brought back by the recruiting bee. These findings suggested that recruits learn the contingency odor-reward through these food offerings during the short interruptions of the dance. Only recently this idea has been tested using the proboscis extension reflex (PER) assay on recruited foragers [12].

The proboscis extension reflex (PER) assay offers a powerful method to test associations established between odor and sugar within a variety of behavioral contexts in honey bees (review: [29]). Bees reflexively extend their proboscis to drink solution when the antennae are touched with sucrose solution (unconditioned stimulus, US). In classical conditioning in the laboratory, an odor (conditioned stimulus, CS) is paired with the US, which causes the odor itself to become capable of eliciting the proboscis extension as a conditioned response [4]. The solution transferred or probed during trophallaxis events functions as an US, like the small samples of sugar solution applied in the laboratory during olfactory conditioning. The food odor functions as conditioned stimulus [17]. Farina et al. [12] used the PER assay to test whether foragers that were recruited by dancers to a food source 160 m from the hive learned the odor of the food source during interactions with a dancing bee. Once recruited bees arrived at a feeding platform they were captured

before drinking the solution offered by the feeder. In the laboratory, the PER of recruits for the food odor and a novel odor was evaluated. The proportion of bees that showed the proboscis extension after presenting the food odor linearly increased as increasing amounts of the scented food were carried into the hive by trained foragers. Four days after offering scented food to the foragers, the PER to the conditioned odor was still elevated but weaker than on previous days (see Fig. 2.4.1 in [12]).

This study suggests that associative learning does not seem to depend strongly on the duration of the oral contact. An excitatory motor display like the honey bee dance might be a particularly efficient context for olfactory learning where brief trophallactic interactions taking place within a context that increases arousal might increase the probability to establish olfactory memories [30].

2.4.2.3 The Extent of Information Propagation About Floral Odors

While information on distance and direction transferred during dance maneuvers is perceived only by the dance followers, olfactory and gustatory information about the discovered nectar source can be acquired by a much broader audience. It has been demonstrated that once the fresh nectar enters the hive its distribution can be rapid and extensive amongst colony members [19, 32–34]. Nixon and Ribbands [32], for example, found that 62% of all sampled foragers of a colony were in contact with sucrose solution collected by only six bees after 4 h. In this sense, chemosensory cues of nectars such as floral odors and food quality may provide the colony with global information about the available resources [33], which means that the information has the potential to affect most colony members [19, 21, 34].

Grüter et al. [19], for example, showed that the sharing of scented food within the hive leads to a propagation of olfactory information. Bees of different age/sub-caste groups learned the odor of relatively small amounts of liquid food that had been collected during 5 days by five to nine foragers. Furthermore, information propagation is more extensive, i.e. reaches more bees, as the food profitability (in this case sugar concentration) of the collected nectar increases (Fig. 2.4.2). The figure shows the proportion of nurse-aged bees (hive bees of 4–9 days old, N), receiver-aged bees (hive bees of 12–16 days old, R) and foragers (F) extending the proboscis after presenting a treatment odor. The PER levels for the solution odor were higher for all the age categories when the foragers of a colony collected 2 M sucrose solution versus 0.5 M sucrose solution. Apart from the positive relationship between learning and US strength [4], a higher level dancing in the 2 M treatment might have contributed to the increased propagation (e.g. due to arousal or a higher number of trophallaxis events). Hence, more bees learn the odor of high quality food sources than of food sources producing nectar of low sugar concentration.
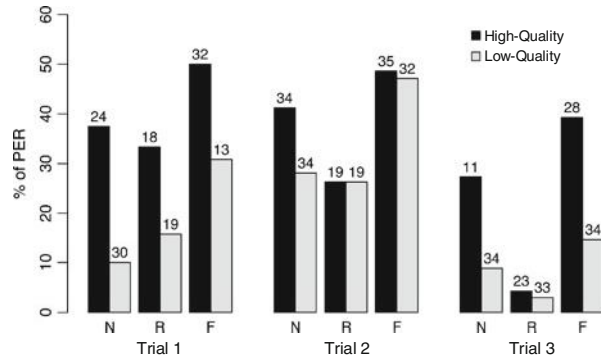
Fig. 2.4.2 Effect of food quality on information propagation. Proportion of nurse-aged bees (4/9-day-old bees, N), receiver-aged bees (12/16-day-old bees, R) and foragers (F) extending the proboscis (PER) after presenting a treatment odor to the antennae. Prior to the PER test, entire colonies were treated by feeding 8 foragers per colony with high-quality food (2 M sucrose solution) or with low-quality food (0.5 M sucrose solution) at an artificial feeding station. During 5 days, these eight foragers collected 14 ml of scented solution per day (totally 70 ml per colony). The scents were PHE (Trial 1, 3) and LIO (Trial 2). Two colonies were used in Trial 1, two other colonies in Trial 2. The two colonies used in Trial 2 were used again in Trial 3, but with reversed treatments. Overall, a higher proportion of bees responded to the treatment odor after treating colonies with 2 M sucrose solution compared to 0.5 M solution (For experimental procedure see [19]) (Grüter, Balbuena and Farina, unpublished results)

2.4.2.4 *Recalling Olfactory Memories While Following Dancers*

While bees forage they learn the odor of the food source and other characteristics like its location, color or shape [29, 30]. Active foragers rely on these memories to find particular locations when visiting food patches repeatedly [35, 36, 41]. Inside the hive the crop scent can cause a conditioned response in inactive foragers with knowledge about this scent from earlier foraging trips. After perceiving a familiar odor, these foragers often leave the nest and fly to the food sites where the odor was learned in the first place. Thus, inactive foragers use the odor of the floral type inside the nest as a prediction for the reappearance of their food source [35, 36, 41]. Most dance followers are experienced foragers [3] and the dance is the most frequent social interaction during this reactivation process to a profitable foraging site. They are attracted to dancers carrying familiar scents [20, 41]. However, the dancer to which an experienced forager is attracted to due to the familiarity with the odor does not necessarily advertise the foraging location where the dance follower learned the odor. As a consequence this follower has to decide whether to fly to the memorized location or whether to decode the vector information of the dance and follow its instructions. Hence, the waggle dance can create a conflict between the self-acquired navigational memory and the vector information of the waggle dance. Grüter et al. [20] found that in these situations

of informational conflict, followers with field experience mostly ignored the spatial information encoded by the waggle dance even if they followed a dance for several waggle runs. They relied on their own memory about food source locations in 93% of all cases (see Fig. 2.4.2 in [20]). This strategy is likely to be adaptive if nectar production of a plant species is synchronized so that the flowers of a species provide nectar at the same time of day at different locations and if finding familiar food patches is easier than finding novel patches advertised by dances ([22], see also Chap. 2.3). However, more research is needed to explore the role of flight distances, food quality or the amount of foraging experience on the use of self-acquired information against location information.

2.4.3 Outside Behavior After in-Hive Olfactory Learning

How does olfactory learning inside the hive affect food choice during foraging? Olfactory cues can be learned from the stores of the nest. Free [15] counted the number of visits (i.e. hovers and landings) either at a feeder scented with the odor of a currently collected food source or at a feeder scented with the odor of their stored food. He observed more visits for the currently collected food odor at the beginning of the test phase (during the first 10–30 min). After this period the bees' preferences shifted to the odor of the food stores. Hence, preferences are shaped by both the transfer of scented food from successful foragers and by the scent presented in the food stores but not communicated by mates.

Foraging preferences after offering scented sugar solution were evaluated recently in foragers that had to choose between two feeders either scented with a previously experienced odor or with a novel odor [1]. Scented food, obtained by mixing a pure odorant with a sugar solution was offered in an in-hive feeder that was left in the hive for a 4 day period. Honey bee foragers, trained to visit an unscented training feeder, were evaluated for their first landing choice when the feeder was removed and two similar feeders (testing feeders) were placed 6 m to the hive and 1.3 m from each other. A higher number of landings was recorded at the feeder scented with the solution odor compared to a novel odor. Thus, food odors learned within the hive were used to guide searching during short-range foraging flights [1]. Preferences for the solution odor were found to last for at least 4 days after all the scented stores of the hive were removed and replaced by combs that contained non-scented food (Fig. 2.4.3a). This implies that bees are able to retain olfactory memories established within the hive for several days and use this information for foraging decisions, though the time periods are slightly shorter than when associations are established outside the colony (13 days: [28], 10 days: [2]). In a study that allowed foragers to collect the scented solution rather than treating the colonies with in-hive feeders, in-hive olfactory memories analyzed via the PER paradigm showed high levels of responses to the food odor for up to 10–11 days after the end of offering food [21].
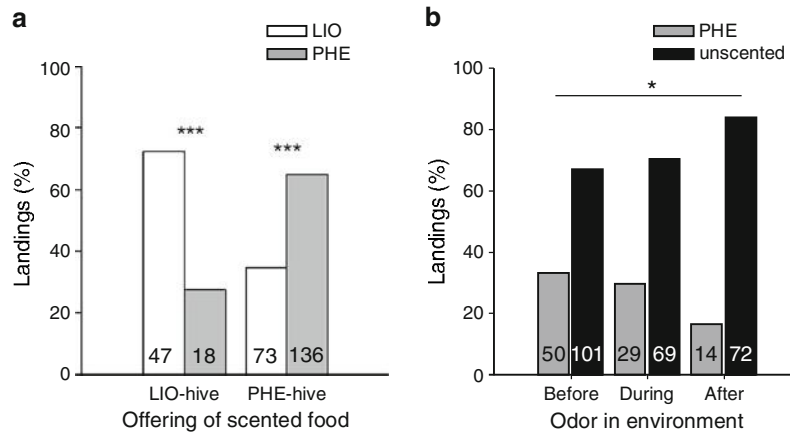
Fig. 2.4.3 Outside behavior after in-hive olfactory learning (**a**) Landings on a dual-choice device (PHE-feeder vs. LIO-feeder) 4 days after a scented food store was removed from within the hive. LIO-hive received sugar solution scented with LIO while PHE-hive received sugar solution scented with PHE. (**b**) Percentages of landings on a dual-choice device (PHE-feeder vs. unscented feeder) after PHE was presented in the hive environment as volatile for different times during the experiment: before (2 and 1 days before the test), during (2 and 4 days after initiating the odor experience), and after the odor experience (3 h and 2 days after removing the odor source and replacing all honeycombs). The number of bees landing on each feeder is shown at the *bottom* of each bar. *Asterisks* indicate statistical differences: *p<0.05, *** p<0.001, G-test (After [1]. With permission)

The offering of scented food inside the hive as a method to increase the yield of honey or the production of seeds of a particular crop has been studied extensively during the 1940s and 1950s [41]. For instance, von Frisch [41] found positive effects of artificial feeding of scented food (increased yields of seed) in several floral species (e.g. red-clover, Swedish clover, rape). The fields to which bees were guided by the scent were visited by about 3–4 times more bees than control fields where hives were fed with unscented food. He concluded that round dances performed by foragers after finding the scented sugar solution recruited other bees to search for the food odor in the surrounding area. However, another study using a similar method did not succeed in guiding bees to the particular flower species [14].

Floral odors can also have inhibitory effects depending on how odors are exposed inside the hive. So far only a few works tested the effect of volatile odor exposure, i.e. not associated with a reward, in the hive environment on appetitive behaviors, both in the classical context of the PER [12, 13, 16, 38] or in an operant context in the field [15]. A recent study indeed found that honey bees avoided the odor while searching for food outside (Fig. 2.4.3b) after a 5-day-exposure period [1]. A reduced landing motivation was observed towards the previously experienced odor (PHE-scented feeder) against an unscented feeder. This bias might be related to forms of non-associative learning causing an avoidance response which might prevent the nectar foraging of a particular floral type in a context of searching for food (Fig. 2.4.3b). Note that differences between PHE and unscented choice before the

odor exposure (Fig 2.4.3b) might reside in the amount of information available in both testing feeders and their similarities with the immediately prior experience gained at this site. Because experimental bees were previously trained to an unscented feeder, to ensure a number of individuals approaching to the site, the unscented options of the choice device perfectly matched with the searching image obtained before.

2.4.4   Social Feedbacks During in-Hive Recruitment

Martin Lindauer observed that the dances of a forager did not only depend on the profitability of the food source itself but also on the amount of food collected by other foragers, i.e. the overall nectar (or water) influx [25]. He noted that on days of good foraging conditions when most foragers of the colony are active, returning foragers had to wait a long time until they found a receiver for their load. When foraging conditions were poor returning foragers usually quickly found several unloading receivers. This social feedback, the time a forager had to wait for a receiver bee, had a strong effect on the occurrence of dances [26, 39]. If the delay is short, a forager performs a waggle dance to recruit more foragers to work. If the delay is long, the forager does not perform waggle dances and her own foraging motivation decreases. We now know that also the number of unloading bees positively affects dancing [10]. The ability of foragers to adjust their recruitment behavior according to the availability of receiver bees enables the colony to keep a healthy balance between food collection and food processing [39].

Receiver bees that have experienced a certain odor during unloading contacts show a preference to receive food containing the same odor from foragers during subsequent unloading [18]. In this experiment, receiver bees had a 78% chance of unloading a forager returning with a particular odor if the receiver bee experienced the same odor during unloading contacts in the past. Only 12% of all receivers unloaded an unfamiliar odor (10% unloaded both odors). This finding challenges the assumption of random unloading made in many theoretical studies on the informational value of transfer delays and the causes of multiple unloading contacts in honey bees [39]. Rather, foragers returning with odors that are well known to most receiver bees of a colony experience a stronger social feedback than foragers returning with a new food odor. A food odor could be well-known to receiver bees if a particular plant species has been exploited intensively in the past. This idea was tested by treating entire colonies with scented food. A group of ca. 30–100 foragers collected 200 ml scented food at an artificial feeder (Fig. 2.4.4, see details in [23]). The authors tested how foragers returning with a familiar food scent were unloaded. Interestingly, no effect on the unloading delay was found (Fig. 2.4.4a). As discussed by [23], latent inhibition effects on foragers caused by the treatment might have made the experimental design unsuitable to test this particular question. On the other hand, foragers returning with the familiar odor were unloaded by more receivers than when returning with a novel odor (Fig. 2.4.4b). During dancing they were also attended by more follower bees (Fig. 2.4.4c). Hence, the social feedback experienced by foragers that collect from apple might depend on the availability of receivers that
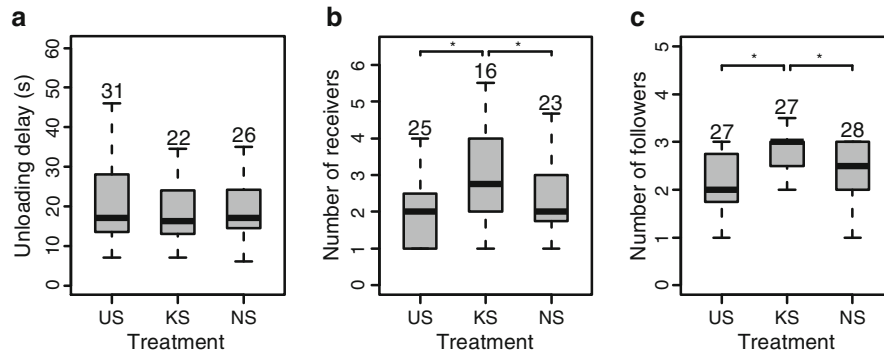
Fig. 2.4.4 Social feedbacks during in-hive recruitment. (**a**) Unloading delays for foragers coming back with nectar solution US, no scent in solution; KS, a known scent in solution; NS, a novel scent in solution. (**b**) Number of receivers during unloading. (**c**) Number of followers in case incoming foragers danced. The boxplots show medians, quartiles, 5th and 95th percentiles. The number of bees are presented above the bars. Asterisks indicate statistical differences (*$P < 0.05$, permutation test) (After [23]. With permission)

unload apple, and not on the total number of available receivers. Having these associations between foragers and processor bees based on odors could be seen as a form of team formation and one might speculate that it increases the efficiency of nectar collection compared to completely random interactions. However, more research is needed to confirm or refute this idea.

2.4.5   Concluding Remarks

Food odors learned inside the colony lead to a preference for these odors and help foraging workers to find a particular food source in the surrounding area. Odor information can have an effect on foraging decisions even if it is not acquired within a recruitment context. This effect persists for several days which suggests that olfactory learning in young bees not directly involved in foraging-related tasks might affect their food preferences at forager age. Moreover, previously acquired olfactory information seems to play a significant role within the hive in that it leads to non-random interactions within the dancing and the food-unloading context. Known odors affect interaction patterns between foragers and followers and between foragers and receivers. This might have consequences for the operational balance between food collection and processing capacities. However, more empirical and theoretical research is needed to explore the consequences of non-random unloading for the efficiency of food collection and processing. The discussed results show that odor learning inside the hive is an important component of the recruitment system of honey bees (and other insects) with long-term consequences for foraging decisions. Future directions in this research field should consider precocious olfactory experiences and their role related to resource exploitation.

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