

Past Experiences Affect Interaction Patterns Among Foragers and Hive-Mates in Honeybees

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Received: March 18, 2009

Initial acceptance: April 30, 2009

Final acceptance: May 11, 2009
(J. Schneide)

doi: 10.1111/j.1439-0310.2009.01670.x

Abstract

Social insect colonies face the challenge of adjusting the behavior of individuals performing various tasks to a changing environment. It has been shown in several species that characteristics of interaction patterns between nestmates provide social information that allows individuals to adjust their behavior in adaptive ways. A well-studied example is the modulation of recruitment by dancing in honeybees (*Apis mellifera*) in response to the time, the foragers have to search for unloading partners and the number of unloading bees. Here we tested if experiences that hive bees acquired during past social interactions affect interactions with the incoming foragers. Bees returning with food containing a floral scent that was familiar to the hive bees from previous interactions had more food receivers during unloading and more followers during dancing displays compared with foragers returning with food containing a novel scent or unscented food. We also confirm that the number of receivers during food unloading is positively related to the motivation to dance immediately after unloading. Our results show that prior social experiences affect the ways in which individuals interact in the context of honeybee nectar collection and, therefore, how learning in hive bees contributes to the organization of this collective task.

Introduction

Social insect colonies need to adjust the numbers and activity levels of individuals performing various tasks, such as foraging or brood care in response to changes in the environment or within the nest. These adjustments happen without central control (Gordon 1996, 1999). It has been shown in several insect species that colony level responses to a particular environmental situation can be the result of individuals responding to simple local information (Seeley 1995; Gordon 1999; O'Donnell & Bulova 2007). Nestmates are a rich source of such information. Individuals can respond either to signals, e.g. the vibration signal (Schneider & Lewis 2004; Cao et al. 2007) or to inadvertent social information cues

(Danchin et al. 2004; Dall et al. 2005). Interaction patterns provide the latter kind of information and facilitate individuals to adjust their behavior in ways that allow the colony to function efficiently in a variable environment.

For example, during nest construction in *Polybia occidentalis* wasps the optimal proportions of colony members performing the different tasks are maintained as individuals respond to the experienced time delays between interactions with each other (Jeanne 1986, 1999). In the red harvester ant (*Pogonomyrmex barbatus*), the interaction rate between foragers, and patrollers determines the forager's decision to leave the nest for foraging. If patrollers do not return safely, foragers will not leave the nest (Gordon 2002; Greene & Gordon 2003,

2007). In the ant *Temnothorax albipennis*, workers assess the suitability of a new nest site by assessing the rate of encounters with nestmates at potential new nest sites (Pratt 2005).

One of the best studied examples of how interaction patterns affect behaviors is nectar unloading and the subsequent waggle dancing in honeybees (*Apis mellifera*). When a forager returns from a profitable food source, she transfers her food to one or several food processor bees (von Frisch 1923, 1967; Park 1925) and may perform a waggle dance which provides information about food source characteristics such as the location to dance followers (von Frisch 1967).

Lindauer (1948, 1954) observed that the nectar abundance outside the nest correlates negatively with the time a returning forager has to wait until food processor bees start unloading nectar or water. If foraging conditions are good, more foragers collect food and as a consequence most of the food-processor bees are busy receiving and handling food. This increases the time-delay experienced by returning foragers. In times of poor foraging conditions only a few foragers collect food. It is therefore easy for them to find a food processor. In this way, searching time and the number of receiving food processors during unloading reflects the balance between the nectar collection rate and colony processing capacity (Seeley 1986; Seeley et al. 1991; Seeley & Tovey 1994). The waiting time (Lindauer 1948, 1954; Seeley 1989; Seeley et al. 1991; Seeley & Tovey 1994) and the number of receiver bees (Farina 2000; De Marco 2006) affect the motivation to dance after unloading: the longer a forager has to search and the fewer receiver bees unload her food, the less motivated she is to dance and as a consequence the less foragers she will recruit to her food patch. This social feedback mechanism facilitates colonies to keep an optimal balance between collection and processing (Seeley 1995).

In these examples, individual decision rules are based on interaction patterns. The interaction patterns, on the other hand, depend on the number of individuals in groups (Gordon 1996, 1999; Anderson & Ratnieks 1999; Ratnieks & Anderson 1999a), their general activity level (Cao et al. 2007) and their spacing behavior (Gordon et al. 1993). However, prior experiences might be a factor affecting interaction patterns independent of the number of individuals in an area and the general activity level of individuals. This would be the case if certain individuals have an acquired preference to interact with a particular group of individuals, for example because the latter carry a familiar type of material such as food.

In honeybees, for example, food-receiving bees socially learn the food scent during food transfer (e.g. in experimental arenas: Gil & De Marco 2005; in hives: Farina et al. 2005, 2007; reviewed in Farina & Grüter 2009). Bees learn to associate a scent with the sweet food. As a consequence of extensive food sharing (Nixon & Ribbands 1952; Grüter & Farina 2007), large proportions of bees of all castes learn the food scent (Grüter et al. 2006). Food processor bees prefer to unload foragers if the offered food has a scent, which is known to the food processor from previous interactions (Goyret & Farina 2005). Therefore, the type of collected food could affect the reception of foragers by food processors, i.e. the interaction patterns experienced by foragers. Here, we tested if foragers returning with food containing a scent that is familiar to hive bees from previous interactions (1) find food processor bees faster, (2) are unloaded by more food processors and (3) are followed by more potential recruits during dancing.

Methods

Study Site and Animals

The experiment was conducted at the end of the nectar flow season (Aug.–Sept. 2006) at the Institute of Ecology and Evolution of the University of Bern, Switzerland. We used two two-frame observation hives containing a colony of about 2500 Buckfast honeybees (a cross between *Apis mellifera ligustica* and *A. m. mellifera*) each. Colonies had a queen, brood, and honey reserves.

Experimental Procedure

A group of bees (group 1) was trained to collect unscented sucrose solution of 15% w/w sucrose concentration at an *ad libitum* feeder (F1) located 5 m from the hive. Bees were marked individually and a number of about 10–15 foragers was maintained during 2 d of training. For the treatment of the nestmates, a second group (group 2) of foragers was simultaneously trained to collect 56% w/w sucrose concentration at an *ad libitum* feeder (F2) located 100 m from the hive. The group 2 (between 30 and 100 different foragers) was allowed to collect a total amount of 200 ml of solution scented with the treatment scent (known scent; KS) during the 2 d of training. This scented solution was then shared among hive bees, which causes many hive bees to learn the food odor (Grüter et al. 2006).

On day 3, individual foragers of group 1 were videotaped while they collected food at F1 (no food was offered at F2). One forager at a time was allowed to collect 56% w/w sucrose solution. The other foragers were held in cages for subsequent testing. We noticed no effect of keeping foragers in cages on their motivation to forage or dance. Each forager performed three foraging cycles with unscented solution (US), three cycles with solution containing the food scent collected by the group 2 (KS) and three cycles with solution containing a novel scent (NS) (a total of nine foraging cycles per forager). NS means that this odor has never been used as treatment odor before. We mostly were interested in the comparison between the KS situation and the NS situation and always started the sequence with US; afterwards we first offered the KS in half of the cases and the NS in the other half of the cases.

Because we wanted focal foragers to be equally motivated to collect both the KS and the NS, we fed these foragers at the end of training day 2 with small amounts of both scents at the feeding place (a few drops of both scents per forager). We planned this because we assumed that without this treatment, focal foragers would encounter and learn only the KS in the hive during mouth-to-mouth contacts (Grüter et al. 2006), which could cause differences in the motivation to collect solution containing the KS and the NS. So while the majority of all hive bees experienced only the KS, the focal foragers had experience with both the KS and the NS.

We filmed about 3–5 bees on a test day with a particular combination of treatment odor and novel odor. Hence, we used several different combinations of odors on different test days to reduce the effect of particular odors. Every odor was used only once as treatment odor (KS). We used orange, peppermint, anis, jasmine, lavender, eucalyptus (essential oils) and the pure odors linalool and phenylacetaldehyde (Sigma-Aldrich, Steinheim, Germany).

Behavioral Observations

We recorded the following forager behaviors and in-hive interactions with a digital camera: drinking time at the feeder, time of dancing, unloading duration, unloading delay (time between entering the hive and first food offering longer than 5 s), number of receivers during unloading, number of simultaneous dance followers [number of followers 10 s after the beginning of dancing; see Božič & Valentinčič (1991) for definition of 'following']. We measured the duration of dancing because this variable is strongly

related to the forager motivation (von Frisch 1967; Farina 1996). Furthermore, foragers sometimes interrupted drinking solution or left the feeder after a first approach. We recorded whether this happened and for how long foragers left the feeding place. The videotapes were analyzed with the JWATCHER 1.0 software (Blumstein et al. 2006).

Statistical Analysis

For data analysis, we used generalized linear mixed-effects models in R 2.6.0 (R Development Core Team 2006). Since we had more than one observation per bee, both bee and hive were used as random effects. Dependent variables had either a Poisson or a binomial distribution.

Treatment was used as a fixed effect. We tested the significance of the fixed effect by using a permutation (randomization) test (Manly 1997). This method estimates the probability of observing the value of the likelihood-ratio test (LRT) of the actual model or a higher value. Therefore, the LRT of the model is compared with a randomly generated LRT distribution obtained by 10 000 permutations of the model. The estimated probability corresponds to the p-value (Manly 1997). When the fixed effect had more than two levels, pair wise comparisons between levels were performed if a significant overall effect was found. We corrected for multiple testing of a data set and adjusted the significance level by using the sequential Bonferroni method (Sokal & Rohlf 1995). Values of $p < 0.05$ after correction are indicated with one asterisk (*) and p-values that are no longer significant after correction are indicated with (ns). The 'n' given in the text refers to the number of bees for which data were available. Descriptive statistics are given as $\bar{x} \pm SD$ (standard deviation).

Results

When approaching the feeder offering the food containing the KS for the first time, foragers often were reluctant to land on the feeder or they interrupted drinking for longer periods. If foragers left the feeder after an initial approach for at least 30 s or interrupted drinking for 30 s we considered them to be hesitating to accept the food. This 30-s limit was used as a conservative boundary since most bees hesitated to land or interrupted ingestion for several minutes. This was the case in 38% of the cases when foragers visited the KS-feeder for the first time, in 14% of the first visits of the NS-feeder and never with the US-feeder. This led to a significant

difference between the three situations (permutation test: $p < 0.001$). Comparisons between the treatments showed that foragers hesitated most when landing on the KS-feeder (KS vs. US: $n = 39/39$, $*p < 0.001$; KS vs. NS: $n = 39/39$, $*p < 0.001$). There was no significant difference between US and NS [$n = 39/39$, $p = 0.036$ (ns)].

Overall drinking time differed between treatments (Table 1). Foragers drank longer when collecting US solution. We found no difference between the KS and the NS situations (Table 1).

Unloading Delay and Dancing

In 30.1% (83 of 276) of all recorded hive stays, bees danced before unloading. Since we were interested in the relationship between unloading delay and the dance duration afterwards, we excluded these cases from this analysis. As expected, we found a negative relationship between unloading delay and the dance duration after unloading (permutation test: $n = 38$, $p = 0.009$).

Receiver Number and Dancing

We tested whether the number of receivers during unloading was related to the amount of dancing after unloading. Cases, in which bees danced before unloading were again excluded, because dancing attracts receivers (Farina 2000) and, therefore, including these cases would confound the outcome. Foragers had between one and nine receivers (2.51 ± 1.27) during unloading. We found a positive relationship between the total number of receivers and the probability of dancing ($n = 31$, $p = 0.007$) but no effect on dance duration was found (permutation test: $n = 31$, $p = 0.18$).

Table 1: Treatment effect on the drinking duration, dancing duration and unloading duration

Comparison	Bees/ treatment	Duration (s)	p-Value
Drinking time overall	36/34/36		<0.001
US vs. KS	36/34	$101.9 \pm 40.2/89.6 \pm 37$	0.004*
US vs. NS	36/36	$101.9 \pm 40.2/85.3 \pm 34.4$	<0.001*
KS vs. NS	34/36	$89.6 \pm 37/85.3 \pm 34.4$	0.29
Dance duration overall	28/30/31		0.01
US vs. KS	28/30	$54.8 \pm 40.8/42 \pm 26.7$	0.012*
US vs. NS	28/31	$54.8 \pm 40.8/47.6 \pm 26$	0.11
KS vs. NS	30/31	$42 \pm 26.7/47.6 \pm 26$	0.23
Unloading duration overall	33/32/38	$22.6 \pm 8.1/24.7 \pm 8.2/22.3 \pm 8.4$	0.25

Number (n) of bees for which data were available. The three trips per treatment were averaged for this table ($\bar{x} \pm SD$).

US, no scent in solution; KS, a known scent in solution; NS, a novel scent in solution.

*Significant after sequential Bonferroni correction.

Unloading Delays in the Different Treatments

Our first hypothesis was, that foragers returning with a familiar food scent start unloading sooner because receiver bees in the hive are more interested in this food. Therefore, we tested if bees that did not dance before unloading started unloading sooner when collecting the familiarly scented food, but we found no significant effect of treatment (permutation test: $p = 0.77$; Fig. 1) on the unloading delay. Also the unloading duration did not differ between the different treatments (Table 1).

Number of Receivers in the Different Treatments

We hypothesized that more receivers unload foragers returning with a familiar food scent. There was a significant treatment effect on the number of receivers during unloading (overall treatment effect: permutation test: $p = 0.001$; Fig. 2a). When foragers collected food with the KS they had in total more receivers during unloading than when foragers collected US (permutation test: $*p = 0.001$) or solution with the NS (permutation test: $*p = 0.024$). Foragers also tended to have more receivers when they collected a novel scented food compared with the unscented situation (permutation test: $p = 0.074$).

Number of Followers in the Different Treatments

Our third hypothesis stated, that foragers returning with familiar scents have more followers (at an arbitrarily chosen moment) compared with instances when foragers collected US or solution with a NS. Treatment had a significant effect on the number of followers (permutation test: $p < 0.001$; Fig. 2b). As hypothesized foragers collecting food containing a

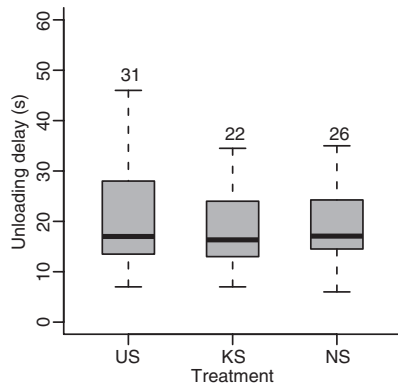


Fig. 1: Unloading delays in different treatments. US, no scent in solution; KS, a known scent in solution; NS, a novel scent in solution. The three trips per treatment were averaged for this figure. The boxplots show medians, quartiles, 5th and 95th percentiles. Numbers above bars represent the number of bees, for which data were available.

KS were followed by more bees than when they collected US (permutation test: $p < 0.001$) or solution containing a NS (permutation test: $p = 0.001$). There was no difference between the unscented situation and the NS situation (permutation test: $p = 0.16$).

Dance Probability and Duration in the Different Treatments

We compared the dance probability and duration in the different treatments. There was no treatment effect on dance probability before unloading (permutation test: $p = 0.071$), after unloading (no dancing before, permutation test: $p = 0.151$) and overall (permutation test: $p = 0.524$). However, we found that the overall dance duration differed significantly

between treatments (Table 1). Pair-wise comparisons showed that the dance duration was shorter when bees collected food with the KS compared with instances when collecting an US (Table 1). But there was no difference in dance duration between the KS and the NS treatment (Table 1).

Discussion

We found that foragers collecting a solution containing a scent, which has previously been fed to the colony, did not initiate unloading faster than when collecting a food with unknown scent. However, they had more receivers during unloading and were followed by more bees when they performed recruitment dances. Given that there was no difference between the KS treatment and the NS treatment with respect to both drinking and unloading durations of foragers, our results suggest that hive bees were more motivated to unload foragers offering food with a KS compared with situations when foragers offered unscented food or food containing a NS. Accordingly, experiments with arenas demonstrated that if bees had prior odor information, new scents present in the crop of the donors negatively affected the occurrence of trophallaxis (Gil & Farina 2003). Similarly, food processor bees show a preference to unload foragers offering familiar scents (Goyret & Farina 2005). The result that foragers offering a familiar odor have more receivers is particularly interesting because there is a positive relationship between the number of receivers during unloading and the motivation to dance and recruit other bees to the food source immediately after unloading (Farina 2000; De Marco 2006).

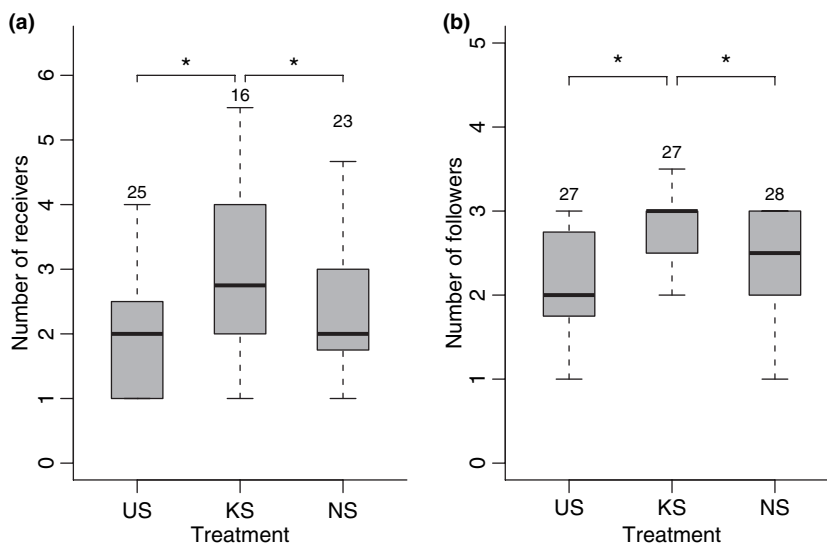


Fig. 2: Number of receivers and dance followers in the different treatments. (a) Number of receivers during unloading; (b) number of followers in case incoming foragers danced. *Significant differences. Boxplots as in Fig. 1.

Why was there no treatment effect on the unloading delay, i.e. the time between entering the hive and starting with the unloading contact? We predicted that the positive effect of our treatment on the motivation of hive bees to unload food containing KS would lead to a decrease of the unloading delay in cases when foragers returned with KS. However, the unloading delay not only depends on the availability and motivation of food processors but is also modulated by the motivation of the foragers themselves. This is obvious when a forager starts dancing before unloading. This was the case in 30.1% of all hive stays (see also Thom 2003). However, it has also been demonstrated in studies showing that unloading delays increase with decreasing food profitability (in hives: Seeley 1986; in experimental arenas: Tezze & Farina 1999). Since the presence of scents in the collected solution appeared to have an effect on the motivation of the collecting foragers (shorter drinking time and dancing duration), the unloading delay was probably confounded by these effects on foragers and, therefore, was not an appropriate measure for social feedbacks in our experiment.

The observation that many foragers were reluctant to land on a feeder offering solution with the KS during the first trip is surprising and puzzling. Particularly intriguing is the fact that the aversion to KS was greater than the aversion to NS. It is likely that focal foragers encountered the KS in the hive during mouth-to-mouth contacts during the 2 d of training (Grüter et al. 2006). This should cause a preference for this scent in the field, rather than an aversion (Arenas et al. 2007, 2008). On the other hand, focal foragers were collecting US during the two training days and they might have encountered the KS mostly passively on the bodies of other hive bees or in the hive atmosphere and only rarely associated with food. The permanent passive exposure to the odor can make the learning of the association between this odor and food more difficult, a phenomenon called latent inhibition (Chandra et al. 2000; Lubow & Moore 1959; Sandoz et al. 2000). However, it is not known whether LI could have inhibiting effects on landing and dancing behavior and more research on this question is needed.

The interaction pattern informs foragers about the balance between food collection and processing capacities (Seeley 1995). Social learning in hive bees alters this pattern, which might make the information about this balance less accurate. However, three reasons might explain, why food processor bees show a preference to interact with certain foragers based on olfactory cues. First, if many bees of a colony know a

particular floral odor, then this is likely to be a consequence of the high profitability of this plant species. It might be beneficial to enhance the dance motivation of foragers collecting at this plant species, compared with foragers returning from a plant species largely unknown to the colony. Second, this socially acquired preference to interact with a particular group of foragers can also be seen as a form of task specialization. Learning can contribute to task specialization and even lead to division of labor (Theraulaz et al. 1998; Ravary et al. 2007). Specialization to perform a task on the other hand is likely to affect working efficiency (Ratnieks & Anderson 1999b). The association between particular groups of food processors and groups of foragers, based on experience, could increase the efficiency of nectar collection compared with completely random interactions between foragers in food processors, e.g. by decreasing search delays (Goyret & Farina 2005). This, however, was not the case in our experiment. Third, it might simply be an inevitable side effect of associative learning. Once bees have learned the association between food and odor, the presence of the odor causes a conditioned response like the extension of the proboscis and the attempt to reach the food (Bitterman et al. 1983).

Foragers collecting the KS had also more simultaneous followers when they were dancing. These additional foragers could be bees that were attracted to scents emitted by these dances because they were already collecting this food type during the training phase (from the F2 group) at a different feeding location (von Frisch 1923; Grüter et al. 2008). At least some of these additional followers should become recruited to the advertised food source location under natural conditions. This would be an additional factor favoring the exploitation of plant species that are familiar to the colony.

Given the positive effect of the number of receivers during unloading on dance motivation and the positive effect of our treatment on receiver number, bees collecting the KS should also have danced more. This, however, was not the case. In our experiment, it was not possible to prevent foragers from being affected directly by our treatments (see above). Additionally, the presence of a scent in a sugar solution has complex concentration- and time-dependent effects on the dance motivation of foragers (Lindauer 1948; Kaschef 1957).

The learning of food odors during social interactions is relatively widespread. It has been found in ants (Roces 1990), stingless bees (Lindauer & Kerr 1960), bumblebees (Dornhaus & Chittka 1999) and wasps (Jandt & Jeanne 2005). Furthermore, insect

workers also transfer insect prey, leaves or seeds to other workers (reviewed in Ratnieks & Anderson 1999b). Workers handling these items might also acquire preferences for shapes, colors or odors. It remains to be seen whether the acquisition of preferences to interact with particular individuals because the latter carry a familiar type of material is a more widespread phenomenon.

In summary, our results demonstrate that past experiences, e.g. established during social interactions affect the ways in which honeybee foragers and food processors interact and, hence, how nectar collection is organized. Further research is needed to investigate if this kind of olfactory experiences in hive bees increases the processing capacity a colony or its nectar collection rate.

Acknowledgements

The authors thank Peter Stettler for technical help, Michael Taborsky for logistic support and Alain Jacob for statistical advice. CG was financed by the Janggen-Pöhn Stiftung and the Berner Hochschuls-tiftung. WMF was supported by funds from ANPCYT, CONICET and University of Buenos Aires. The present study complies with the current laws of the state country in which experiments were performed.

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