# 10 Trophallaxis A Mechanism of Information Transfer

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# **INTRODUCTION**

Trophallaxis is the exchange of liquid material between individuals, mostly members of the same colony. Wheeler (1918) was the first to propose the term *trophallaxis* for describing these interactions between nestmates in ant colonies. He interpreted them as being "clearly cooperative and mutualistic relationships," and thereby separated his term from the term *trophobiosis*, which had been suggested earlier by Roubaud (1916) to indicate oral food transfers based on a "trophic exploitation" in social wasps (for review and historical background see Sleigh 2002).

There are two main kinds of intraspecific liquid food transfer in social insect nests: In the first one, adults exchange liquids with larvae (they imbibe larval saliva from the brood and transfer glandular secretions, honey, and pollen to the larvae). In the second one, the liquid is transferred between two adults. The stomodeal (or oral) trophallaxes are the most common ones. Here, donors regurgitate a drop of food from their crops while one or more receivers drink the liquid (Wilson 1971; Michener 1974). During these mouth-to-mouth contacts, intensive antennation (Montagner and Galliot 1982; Hölldobler 1985; Goyret and Farina 2003; Hrncir et al. 2006; McCabe et al. 2006), occasional foreleg movements of both partners (Hölldobler et al. 1974; McCabe et al. 2006), or as in stingless bees, the transmission of pulsed vibrations (Hrncir et al. 2006) accompany the oral contacts. Abdominal or anal trophallaxes are also used to distribute material such as intestinal symbionts for wood digestion in termite colonies (Grassé and Noirot 1945).

The evolutionary origin of trophallaxis might have been related to the regulation of aggression in group-living insects (Roubaud 1916). Indeed, aggressive behaviors often stimulate trophallaxis, and the aggression ceases after a food offering (Wilson 1971; Hölldobler 1977; Weislo and

González 2006). However, adult-adult food sharing may also enhance the chance of survival of a colony where unfavorable weather conditions prevent foraging over longer periods of time (Wcislo and González 2006).

The occurrence and high frequency of trophallaxes among adult individuals is a common characteristic of highly social insects (Michener 1969; Wilson 1971). While eusocial insects, such as honey bees and many other bee, ant, termite, and wasp species, engage in frequent oral interactions inside their nests, this form of contact is rare in communal insects (e.g., halictine bees, Kukuk and Crozier 1990).

During the course of evolution, trophallaxis probably became more important in species for which it considerably improved the efficiency of the performance of vital tasks like food collection or nest construction. The partitioning of tasks is assumed to increase overall colony task performance (Ratnieks and Anderson 1999). Once the material transfer became an important aspect of work organization, it offered an opportunity for both food donors and receivers to acquire information about internal and external environmental parameters via incidental cues, such as searching delays (Seeley 1995) and numbers of receivers (Farina 2000), and about olfactory (Gil and De Marco 2005; Farina et al. 2007) as well as gustatory (Pankiw et al. 2004; Martínez and Farina 2008) cues contained in the transferred material.

The frequency of trophallaxis varies greatly between the different social insect species. It is particularly high in honey bees (Michener 1974; Hölldobler 1977), where trophallaxes occur between bees of all castes and ages (Free 1957; Moritz and Hallmen 1986; Crailsheim 1998; Grüter and Farina 2007). In experimental hives, bees performing the trophallaxes are easily identified: the food donor opens her mandibles and regurgitates the food, whereas the recipients protrude the proboscis to contact the donor's prementum. Since the mechanism of food transfer in other social insects, such as ants and wasps, differs from that of the honey bees, the distinction between donors and receivers has to be made by differences in either the head position or the antennation between the trophallactic partners (Figure 10.1).

As central place foragers, honey bees perform successive feeding trips to a profitable food source, interrupted by hive stays. This allows the researcher to analyze their trophallactic behavior in observation hives in the context of foraging (von Frisch 1967; Núñez 1970; Seeley 1986, 1989; Farina 1996; De Marco and Farina 2001; Farina and Wainselboim 2001a). In this chapter we will discuss the role of trophallaxis for the transfer of information in the context of nectar foraging in honey bees. We will denote all mouth-to-mouth contacts as trophallaxes, because even short interactions with a low probability of an effective food transfer potentially provide important chemosensory information, such as the odor and taste of the exploited food source.



**FIGURE 10.1** Trophallaxis in the honey bee *Apis mellifera* (a) and the carpenter ant *Camponotus mus* (b). In honey bees, the roles of the donor (D) and the receiver (R) of food are easily distinguishable. The receiver bee protrudes her proboscis and contacts the donor's prementum, which causes different head position of the trophallactic partners. In the carpenter ant *C. mus*, the position of the heads and differences in the antennation intensity provide information about the trophallactic roles. (Photographs by Christoph Grüter (a) and Sofia McCabe (b).)

# **RETURNING TO THE NEST AFTER FORAGING**

Division of labor, i.e., the formation of groups specialized in different tasks, is supposed to improve the efficiency of collective activities in a constantly changing environment (Wilson 1971; Michener 1974). In honey bees, young and middle-aged workers perform in-hive duties (e.g., cleaning cells, caring for brood, grooming, receiving and processing of nectar), while older workers forage outside (Rösch 1925; Lindauer 1952; Seeley 1982). Nectar foraging in honey bees is a partitioned task: for-agers collect nectar in the field and, inside the nest, transfer the food to bees of middle age (often called food processors, receivers, or food storers) in the delivery area close to the hive entrance (Park 1925; Lindauer 1954; von Frisch 1967; Seeley 1995). These bees of middle age are then mainly responsible for processing the nectar into honey and storing it in cells (Park 1925).

Foragers returning from a profitable food source sometimes display dance maneuvers (von Frisch 1967; Seeley 1995), which encode the location of a food source (von Frisch 1967; Riley et al. 2005). The dance also communicates the existence of an attractive food source and increases the attention and activity of bees in the dancer's vicinity and, subsequently, the disposition of inactive foragers to leave the hive and search for the food source (von Frisch 1923, 1967; Božič and Valentinčič 1991; Thom et al. 2007). However, the dance display attracts not only potential foragers but also food processor bees, which unload the forager (Farina 2000). Foragers not only provide information for other individuals, but also receive information during their interactions with hive bees. They seem to use both the time to find a bee for unloading and the number of unloading bees as cues to adjust their dance behavior after unloading (Lindauer 1954; Seeley 1992; Kirchner and Lindauer 1994; Seeley and Tovey 1994; Farina 2000). Thus, social interactions on the delivery area provide the foragers with information that helps them to adjust the dance levels according to the general interest of hive bees in a particular food source and the availability of food processor bees (Seeley 1995).

Waggle dances are often performed immediately after arrival, and prior to food unloading (Thom 2003). This shows that unloading delays depend not only on the availability of food processor bees but also on the motivation of the foragers themselves, which in turn depends, for example, on the recently experienced profitability of the food source (von Frisch 1967; Seeley 1986; Seeley et al. 2000; De Marco and Farina 2001). Laboratory studies similarly suggested an important role of the donor: the delays to initiate trophallaxis between worker pairs in experimental arenas increased when the crop load of donors was reduced (Farina and Núñez 1993) or when the sugar concentration decreased (Tezze and Farina 1999). Thus, the interplay between hive-internal and hive-external information available to the forager determines the amount of dancing (see also Seeley 1995).

Previous experiences of donors and receivers might be another factor affecting queuing delays and the social feedback inside the hive. 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 and Farina 2003). Similarly, food processor bees show a preference to unload foragers that had collected sugar solution with a previously experienced food scent (Goyret and Farina 2005a).

## THE OFFERING BEHAVIOR OF ACTIVE FORAGERS

Foragers often perform several food-offering contacts with a wide range of durations after returning from a nectar source (from milliseconds up to more than 60 s in some cases; De Marco and Farina 2001; Farina and Wainselboim 2001a, 2005) (Figure 10.2a). In general, nectar foragers perform one or two trophallaxes that last for more than 2–3 s per hive stay, and a much more variable number of shorter offering contacts (De Marco and Farina 2001). During the interactions with a duration of at least 2 s, food is effectively transferred between foragers and receivers (Farina and Wainselboim 2001a). Under constant reward conditions the frequency of food-offering contacts (short and long trophallaxes) is fairly constant between different foraging trips (De Marco and Farina 2001), and it is similar for different reward rates offered at the feeder (Fernández et al. 2003).



**FIGURE 10.2** Trophallactic offering behavior of active foragers. (a) Frequency of offering contacts performed by foragers in relation to the contact duration. The bees collected 50% w/w sucrose solution from a feeder, which provided a constant flow rate of 8.2  $\mu$ l/min. Given are the contacts without increase in the receiver's proboscis temperature (black bars) and contacts with an increase in proboscis temperature (white bars). A temperature increase represents an effective transfer of the liquid food among partners. Inset: Thermograms showing the surface temperatures of a donor forager (D) and a receiver (R) at three different times during one trophallaxis. The proboscis temperature of the receiver changed rapidly during the trophallactic interaction, whereas the donor's head and thorax temperature remained at 39.4°C. Grey-value scale indicates the measured temperature ranges. (After Farina and Wainselboim 2001b. With permission.) (b) The offering contacts by incoming foragers during their hive stays were categorized according to their length: contacts shorter than 2 s (filled circles) or longer than 2 s (empty circles), respectively. Given is the number of short and long offering contacts when foragers collected at a feeder with constant flow rate (5  $\mu$ l of sugar solution per minute) during twenty consecutive round-trips. The sucrose concentration (line above plot) changed after every fourth foraging bout. (After De Marco and Farina 2001. With permission.)

Under such conditions, most of the short offering contacts occur at the beginning of a hive stay (De Marco and Farina 2001). However, when reward conditions fluctuate, an adjustment of the number of short trophallactic contacts occurs (Farina 1996; De Marco and Farina 2001). An increase in profitability causes a rapid increase in the number of the short interactions (Figure 10.2b). In a changing environment, therefore, there is a clear and positive relation between the profitability of a food source (i.e., sugar concentration) and the number of short contacts as well as the dance duration (De Marco and Farina 2001).\*

In honey bees, short offering contacts can take place before, during, and after dancing (Park 1925; von Frisch 1967; De Marco and Farina 2001; Farina and Wainselboim 2005; Díaz et al. 2007), which leads to a rather equal distributing of contacts during hive stays, at least after an increase in food profitability (De Marco and Farina 2001). Hence, short offering contacts are not simply a failure to unload all the food at once due to the forager's high motivation for dancing. But why do foragers perform several short offering contacts if the chance to transfer food during these interactions is very low (Farina and Wainselboim 2001a)? Actually, the context in which they occur suggests that they might play a role in providing information about fluctuating resources, such as the taste and scent of the exploited food source (for more details see the "Odor Learning Through Trophallaxis" section below).

<sup>\*</sup> A correlation between offering contacts and spinning behaviors was also observed in the stingless bee *Melipona beecheii* (Hart and Ratnieks 2002). This study, however, did not investigate the effect of food quality (sugar concentration) on these behaviors.

While the number of short-offering contacts is highly variable, the number of long trophallaxes (longer than 2–3 s) is quite constant (Figure 10.2b) and does not seem to depend on the amount of food collected by the forager (Fernández et al. 2003) but rather on the colony's nectar influx (Huang and Seeley 2003; Gregson et al. 2003). In addition, a mismatch between the crop loads of foragers and the crop capacities of hive bees receiving the nectar seems to explain why foragers perform more than one long unloading trophallaxis (Gregson et al. 2003; Huang and Seeley 2003).

# **DYNAMICS OF FOOD TRANSFER**

Bees modulate their crop-loading behavior at the feeding place according to the food source profitability (Núñez 1966, 1970, 1982). Similarly, they adjust their crop-unloading behavior during the long trophallaxes according to a food source's profitability (Farina and Núñez 1991). In observation hives, the estimated transfer rate increased with higher crop loads, which in turn depended on the reward rates of the food source (Farina 1996; Farina and Wainselboim 2001a). In experiments using small interaction arenas, the transfer rate was further affected by the sugar concentration of the transferred food (Farina and Núñez 1991; Tezze and Farina 1999) and the reward rate experienced at a food source by a food donor (Wainselboim and Farina 2000a, 2000b). In addition, disturbances of foragers during food collection also affected the transfer rate. In summary, bees seem to evaluate the profitability of the food source by integrating an overall flow rate throughout the entire visit, instead of measuring only the current flow rate delivered at the feeder (Wainselboim et al. 2003; Wainselboim and Farina 2003). Furthermore, foragers also seem to be able to detect sudden changes in the delivered flow of solution within a single foraging bout, and subsequently adjust the transfer rate within the hive in relation to these changes (Wainselboim et al. 2002; Wainselboim and Farina 2003).

But does the modulation of trophallactic behavior by donors actually modify the behavior of food-receiver bees? Infrared thermal analysis of foraging bees showed that if a feeder offered food with a higher reward rate, foragers initiated unloading inside the hive at higher thoracic temperatures, compared to low reward rates. During the food transfer, the receivers actively heat up their thoraxes. Their heating rate positively correlates with the foragers' thoracic temperatures and with the reward rate experienced by the donor at the feeder (Farina and Wainselboim 2001a; Figure 10.3a). These heating rates also depend on the orientation of the receiver toward the donor. Receivers positioned frontally to the donor forager warm up faster and attain higher proboscis temperatures than those positioned laterally (Farina and Wainselboim 2001a; Figure 10.4). These differences in proboscis temperature indicate that the unloading bees received different portions of sugar solution.

Receiving bees (mostly food processors) also adjust their nectar processing behavior in accordance to the profitability of the nectar source. After receiving nectar, food processors perform offering contacts or cell inspections, and often even both behaviors, prior to returning to the delivery area (Pírez and Farina 2004). When performing only one of these tasks, the occurrence of cell inspections increases or, alternatively, the amount of offering contacts decreases when the highest reward rate is offered to the donor forager (Pírez and Farina 2004). These results strongly suggest that first-order receivers acquire quantitative information about the nectar source exploited by foragers.

Another factor, which correlates with aspects of trophallaxis, is the intensive antennal contacts performed by trophallactic partners during food transfer (Montagner and Galliot 1982). In honey bees, the antennal movements of both donor and receiver, which are rapid during the food transfer (mean frequency of 13 Hz), vary according to the reward rate experienced by the food donor and show a positive correlation between both trophallactic partners (Goyret and Farina 2003; Figure 10.3b). In addition to information about the reward rate of the food source, information about the food supply of a colony might also be encoded in the tactile stimulation during trophallaxis, as has been suggested for the carpenter ant *Camponotus mus* (McCabe et al. 2006).



**FIGURE 10.3** Thermal behavior and antennation during trophallaxis in honey bees. (a) Thoracic temperature of food receivers in relation to the duration of the trophallactic contact with a forager that collected either 1.0 or 8.2  $\mu$ l of a 50% sucrose solution per minute at a feeding station. Different symbols represent different food-receiving bees. (After Farina and Wainselboim 2001a. With permission.) (b) Example of the antennal contacts (strokes, black bars) of a donor and a single receiver during a long trophallaxis inside the nest. The donor forager returned from a rate feeder offering either 1.0 or 8.2  $\mu$ l of a 50% sucrose solution per minute. Temporal resolution:5 ms. Grey bars indicate moments where the position of the antennae could not be precisely determined. Under these experimental conditions, the mean values of the thoracic temperature of the donor foragers at the beginning of the trophallaxis were 31.8°C for a reward rate of 1  $\mu$ l/min and 37.5°C for 8.2  $\mu$ l/min, respectively, and the estimated transfer rates of the donors for these reward rates were 1.1 and 2.1  $\mu$ l/s. (After Goyret and Farina 2003. With permission.)



**FIGURE 10.4** Trophallaxis with multiple food receivers. (a) Thermogram showing the food donor (D), which was an active forager trained to collect at a rate feeder that offered 8.2  $\mu$ l of a 50% sucrose solution per minute. Receivers in front of the donor (R1 and R2) attained higher proboscis temperatures (T<sub>pr</sub>) than receiver R3, which contacted the donor from its side. The heating of the frontal receivers was independent of the number of simultaneous receivers. (b) Mean differences between the receivers' proboscis temperatures and the maximum proboscis temperature (T<sub>pr</sub> Max) observed during trophallaxis with an incoming forager. Receivers in front of the donor had smaller temperature differences than receivers positioned laterally to the forager. (Farina, unpublished data.)

# CHANGING THE TROPHALLACTIC ROLE

After unloading their crop, foragers walk across the delivery area to the hive entrance, thereby often protruding their proboscis and touching the mouthparts of their nestmates. It has been suggested that these begging contacts are refueling events for the forthcoming foraging trip (Beutler 1950; von Frisch 1967). After leaving the hive, foragers carry more food if they do not know the feeding site well (Brandstetter et al. 1988) or if they collect far from the nest (Istomina-Tsvetkova 1960). This could be explained either by refueling inside the hive or by unloading only a part of the collected crop. However, begging behavior can also be observed in foragers that constantly collect food over a longer period of time at a feeder located close to the hive (Núñez 1970; Farina 1996; De Marco and Farina 2001). So, why do these bees beg for food? It would seem much more efficient if experienced bees simply retained the amount necessary for the flight to the food source during the unloading event.

Food source profitability affects the forager's begging behavior, just as it affects the short offering contacts, yet in the opposite direction: nectar foragers increase the frequency of begging contacts after food unloading when they return from a low-profit source (Farina 1996; De Marco and Farina 2001) or if the diversity of odor cues and food qualities encountered in the exploited food patch is high (De Marco and Farina 2003). These begging contacts often last less than 1 s (De Marco and Farina 2003), which indicates that the probability of an actual food transfer is very low (Farina and Wainselboim 2001b). Hence, it is unlikely that foragers are refueled during these begging interactions.

An alternative hypothesis proposes that begging might be a means of information acquisition (Núñez 1970; Farina 1996; De Marco and Farina 2001, 2003). Active foragers may direct their begging behavior toward other employed nectar foragers in order to obtain chemosensory information about other resources, which facilitates the reevaluation of their own food source. Consequently, employed foragers could decide whether to continue exploiting their food source, whether to switch

to a previously exploited one that reappeared again (indicated by the presence of its scent in the hive), or whether to stop foraging and stay in the hive. However, to date there is no evidence for these hypotheses, and begging contacts remain a puzzling phenomenon.

Experiments conducted under low-reward-rate conditions can help us to understand communication strategies in a more natural context. Natural flowers normally offer minute amounts of nectar with variable flow rates (Núñez, 1977; Vogel 1983), and bees often visit several hundred flowers per foraging trip (Ribbands 1949). Many of the modulatory effects described above become apparent only when bees collect food at a low reward rate.

# THE DISTRIBUTION OF THE NECTAR INSIDE THE HIVE

After receiving the nectar from foragers, a majority of processor bees offer it to other bees, sometimes large parts of their load, on their way to the honey cells (von Frisch 1923; Park 1925; Seeley 1989; Pírez and Farina 2004; Grüter and Farina 2007). Whereas workers that are not involved in food processing have only 0.25–0.75 trophallactic contacts per 10 mins (Istomina-Tsvetkova 1953a, 1953b, cited in Free 1959; Grüter and Farina 2007), food processor bees perform between 4.3 and 10.5 contacts during the same period of time (Seeley 1989), which highlights their role in the rapid distribution of the collected food among the hive bees. The workers that receive the food from processors (second-order receivers) are mainly nurse bees, but they can also be foragers and other food processors (Grüter and Farina 2007). These second-order receivers perform about four contacts per 10 min, most of them being offering contacts. As a consequence, the incoming nectar is rapidly distributed among bees of all ages. Nixon and Ribbands (1952) measured this food distribution within honey bee nests using a radioactive tracer in the sugar solution (<sup>32</sup>P). They fed between five and nine foragers belonging to colonies of different population sizes 10-20 ml of radioactive solution and found that within 4 h a majority of the hive bees had received samples of this food. Similarly, DeGrandi-Hoffman and Hagler (2000) found a rapid distribution of food among young hive bees by using a protein marker.

Several characteristics of food processing, like the rate of trophallactic events or the food storing behavior of the hive bees, depend on a variety of factors, such as the nutritional state of the colony, the amount of brood, the workers' genotype, the amount of incoming nectar, or the season (Free 1959; Kloft et al. 1976; Hillesheim 1986; Seeley 1989; Crailsheim 1998). Whereas experiments with caged bees also showed an effect of age on the trophallactic activity (Moritz and Hallmen 1986), the trophallactic activity of workers within beehives seems to depend on the performed task than on the bees' age (Free 1957).

Another interesting aspect of trophallaxis in honey bees is the fact that the transfer rates of subsequent trophallaxes are positively correlated (Goyret and Farina 2005b). In other words, trophallactic experiences of bees affect their trophallactic behavior in the immediate future in similar ways as nectar flow rates affect the unloading rate of foragers. Consequently, food receiver bees that are not directly unloading foragers might still be able to acquire information about the colony's foraging situation. Given the extensive sharing of food among bees of all ages, cues present in the collected food that convey information about food source characteristics can reach most hive members in a relatively short time. Information available to most or all individuals of a colony, or "global" information (Mitchell 2006), potentially affects the behavior of the majority of the nestmates, thereby causing a global response (Moritz and Southwick 1992; Pankiw et al. 2004). For example, the sugar concentration of incoming nectar affects the sugar response thresholds (SRTs) of nectar receivers (Martínez and Farina 2008) and even of young hive bees, which are not involved in foraging (Pankiw et al. 2004) and have little direct contact with engaged foragers (Seeley 1995). These results not only indicate a fine-tuning of sensory thresholds in hive bees, but also highlight the role of trophallaxis as a mechanism to transfer gustatory information in honey bees (Martínez and Farina 2008).

## ODOR LEARNING THROUGH TROPHALLAXIS

Bees are excellent learners and readily establish associations between odors (or other cues) and a reward, such as a sugar solution (e.g., von Frisch 1967; Koltermann 1969; Menzel 1999). During olfactory conditioning the sugar solution functions as an unconditioned stimulus (US), while the odor becomes the conditioned stimulus (CS).

Olfactory learning has a strong effect on foraging decisions (see Chapter 9). In a series of simple and elegant experiments, von Frisch (1923) showed that bees recruited by a forager showed a strong preference for food with the odor brought back by the recruiting bee. In the meantime, these findings have been confirmed in other social insects like bumble bees (Dornhaus and Chittka 1999), stingless bees (Lindauer and Kerr 1960; see also Chapter 12), wasps (Maschwitz et al. 1974; Jandt and Jeanne 2005), and ants (Roces 1990). It has been suggested that recruits learn food odors while receiving food samples from foragers, i.e., during trophallaxis (von Frisch 1967). Here, the transferred food samples could function as a reward for learning. Dirschedl (1960) found that more than 95% of all recruits arriving at a feeder that offered stained sugar solution had received small samples of this food inside the hive prior to leaving the colony.

The proboscis extension response (PER) test has been used with great success to study associative learning under controlled laboratory conditions, and to analyze the physiology and memory processes underlying learning in honey bees (Kuwabara 1957; Bitterman et al. 1983; reviewed in Menzel et al. 1993; Menzel 1999). Bees extend their proboscis when chemoreceptors on their antennae, tarsi, or proboscis are stimulated with sucrose solution (US). If an odor (CS) is presented simultaneously, it will subsequently elicit the proboscis extension (conditioned response, CR) if presented alone, often even after a single learning trial.

More recently, the PER assay was also used to investigate learning processes during trophallaxis. Honey bees associatively learn food odors while receiving food from other bees in a variety of behavioral contexts (e.g., within an experimental arena, Gil and De Marco 2005; within an observation hive, Farina et al. 2007). Several experiments have demonstrated that increasing the concentration of either the CS or the US results in better learning during trophallaxis (Gil and De Marco 2005). Interestingly, successful learning does not seem to depend much on the duration of the oral contact (e.g., trophallaxes as short as 1.2 s led to learning; Gil and De Marco 2005). For this kind of learning it should be of little importance whether the receivers perceive the odor in the solution or on the foragers' bodies. Most important, however, is the contiguity between CS and US (Rescorla 1988; Menzel et al. 1993).

Furthermore, PER assays revealed that bees that are recruited to a specific food source associatively learn the food's odors inside the colony (Farina et al. 2005; Grüter et al. 2006; Figure 10.5). Similarly, food processor bees show the PER for a particular scent with an elevated probability after having unloaded food containing this scent from foragers (Farina et al. 2007; Figure 10.5a). Grüter et al. (2006) fed scented sucrose solution to marked foragers for about a week and at the same time measured the PER of bees at the age of 4–9 days and 12–16 days, and of a sample of foragers (Figure 10.5b). During the feeding period, the proportion of bees extending their proboscises upon presentation of the solution's scent increased in all age groups, which indicates that olfactory information about the flower species exploited by foragers propagates within the entire colony as a consequence of food sharing. Potentially, this has long-term consequences, since olfactory information acquired inside the hive can be stored in the bees' long-term memory (LTM) (Farina et al. 2005; Gil and De Marco 2006; Arenas et al. 2007), a form of memory that affects the behavior of bees for several days (e.g., Menzel 1999).

In the experiments with hive bees, the PER frequencies were lower than expected when comparing them to learning performances under controlled laboratory conditions, where a single learning trial often already leads to about 50% of bees responding to the odor (Menzel et al. 1993). However, there are several problems with such comparisons. First, in the experiments with hive bees, the individuals were tested in a context that differed from the context they had experienced when learning



**FIGURE 10.5** Olfactory memories formed within the hive during the sharing of scented food. (a) Percentage of food-receiver bees that extended the proboscis on the first presentation of an odor in a proboscis extension response (PER) assay. In the course of the experiment, foragers collected a 2.0 M sucrose solution that was either unscented (day 1), scented with phenylacetaldehyde (PHE) (day 2), or scented with nonanal (day 9). Responses for PHE (grey), nonanal (white), 2-octanol (dark grey), and for more than one test odor (black) are shown. Numbers of tested bees are given above the bars. (After Farina et al. 2007. With permission.) (b) PER on the first presentation of a treatment odor (linalool) and a novel odor (2-octanol) in 4- to 9-day-old bees, 12- to 16-day-old bees, foragers, and recruits. PER frequencies were measured on days 0, 2, 4, and 6 after starting to feed the colony with a linalool-scented sucrose solution. Bars indicate the percentage of bees showing a spontaneous PER to linalool (filled bars), or to both linalool and 2-octanol (hatched bars). The inset shows the daily quantity of the collected sucrose solution in milliliters (filled circles) and the number of trained foragers (empty circles). (After Grüter et al. 2006. With permission.)

the odor. This can cause a considerable reduction in performance (Bouton and Moody 2004), which, as a consequence, might lead to an underestimation of information acquisition. Second, within the hive, bees probably not always perceive an odor associated with a reward, but often without it, e.g., when attending or following a dancing bee without receiving a food sample. These CS-only experiences (retrieval trials after acquisition) often result in a reduction of the conditioned response (CR) (Stollhoff et al. 2005).

Given the rapid sharing of food among all bees of a colony (Farina et al. 2005, Grüter et al. 2006), the propagation of the information about the odor of a food source would be much more extensive if the scent was present in the nectar itself rather than just clinging to the forager's body. But are nectars scented at all? Unfortunately, very little is known about the presence of scents in nectars of most plant species visited by bees. Apparently, many types of nectars contain scents, but more systematic studies on the distribution of scented floral nectars (reviewed in Raguso 2004) are needed to evaluate their potential role as an information source in communication and learning processes in bees.

The propagation of olfactory information among hive bees has important behavioral and ecological implications (see also Chapter 9). Novice foragers without foraging experience leave the hive with socially acquired olfactory information about the food plants, which can help them to discover

new food patches of the same plant species (i.e., other patches than those exploited by the recruiting foragers). The bees' preference for odors they had experienced in the hive while searching for food in the field is also used for crop production: feeding honey bee colonies with sugar solution scented with crop plant odors is the basic principle of the attempts to guide bees to certain plant species in order to increase the visitation rates and seed production (von Frisch 1943, 1967).

As discussed above, olfactory memory also affects unloading decisions of food processor bees (Goyret and Farina 2005a). Consequently, the flower constancy observed in honey bee foragers (von Frisch 1967) can already be found in nectar processors during unloading, yet to a lesser degree. Thus, a forager returning with a new odor might be received with less interest by nectar processors, which, in turn, affects the forager's motivation to perform dances (Goyret and Farina 2005a). However, more studies are needed to investigate the consequences of olfactory experiences for these in-hive interactions. In addition, research should be extended to other social insect species in order to better understand the general importance of trophallaxis for learning in these organisms.

In the context of olfactory learning, the bee dance might have an amplifying effect. As mentioned earlier, dancers attract both foragers and food processors, and thereby increase the number of trophallactic interactions (Farina 2000). In this way, the dance creates an environment for the acquisition of olfactory information (von Frisch 1923, 1967; Díaz et al. 2007).

## CONCLUDING REMARKS

The attempt to understand how a honey bee colony coordinates the single individuals in order to efficiently obtain and process food in a system lacking central control is a fascinating challenge. Trophallaxis seems to be one of the means by which individuals that belong to worker groups carrying out different tasks are rapidly informed about characteristics of the collected resources. Hence, trophallaxis is an important mechanism not only to transfer food, but also to inform individuals about fluctuating foraging opportunities, to adjust in-hive tasks related to the foraging process, and to create information networks that connect different groups of workers.

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