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Research article

The influence of the vibration signal on worker interactions with the nest and nest mates in established and newly founded colonies of the honey bee, *Apis mellifera*

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Abstract. Honey bees adjust cooperative activities to colony needs, based in part on information acquired through interactions with the nest and nest mates. We examined the role of the vibration signal in these interactions by investigating the influence of the signal on the movement rates, cell inspection activity, and trophallaxis behavior of workers in established and newly founded colonies of the honey bee, *Apis mellifera.* Compared to non-vibrated control bees, vibrated recipients in both colony types exhibited increased movement through the nest and greater cell inspection activity, which potentially increased contact with stimuli that enhanced task performance. Also, compared to controls, recipients in both colony types showed increased rates of trophallactic interactions and spent more time engaged in trophallaxis, which potentially further increased the acquisition of information about colony needs. The vibration signal may therefore help to organize labor in honey bees in part by increasing the rate at which workers obtain information about their colony. Vibrated recipients in the established and newly founded colonies did not differ in any aspect of behavior examined, suggesting that colony developmental state did not influence the degree to which individual workers responded to the signal. However, previous work has demonstrated that newly founded colonies have increased levels of vibration signal behavior. Thus, the vibration signal may help to adjust worker activity to colony conditions partly by stimulating greater numbers of bees to acquire information about colony needs, rather than by altering the level at which individual recipients react to the signal.

Keywords: Vibration signal, modulatory communication, information flow, communication signals, trophallaxis.

Introduction

In social insects, interactions with the nest and nest mates are primary means by which workers acquire information about colony needs (Seeley, 1995; Gordon, 1999; O'Donnell, 2006; Schafer et al., 2006). Mechanisms that influence the rates and patterns of these interactions are central to the organization of collaborative labor. In honey bees, one mechanism that may affect interaction rates is the vibration signal. The vibration signal functions as a modulatory communication signal (Schneider, 1987; Nieh, 1998), in that it causes a non-specific increase in activity that contributes to the performance of a greater total number of different tasks by individual bees, enhances the amount of time spent in brood care, food processing, and nest maintenance, and increases the likelihood of engaging in foraging (Schneider and Lewis, 2004; Hyland et al., 2007). Vibration signals are produced primarily by successful foragers, who often move through large areas of the nest while performing long series of signals that are preferentially directed toward less active bees of all ages (Lewis et al., 2002; Hyland et al., 2007). The modulatory effects of the signal may therefore influence an array of tasks that must be adjusted to changing colony food intake and energy needs (Hyland et al., 2007).

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The vibration signal may affect worker labor in part by increasing interactions with the nest and nest mates, and this may happen in three ways. First, vibrated workers respond with increased movement through the colony (Schneider et al., 1986; Nieh, 1998), which could increase contact with stimuli associated with the combs, brood, and nest mates that influence worker behavior (Fewell and Winston, 1992, 1996; Hyland et al., 2007). Secondly, recipients may increase their cell inspection activity (Schneider, 1987), which could provide a greater assessment of comb contents and alter task performance (Dreller and Tarpy, 2000; Pankiw, 2004). Finally, the vibration signal could alter trophallaxis behavior (mouth-to-mouth exchange of liquid food), which distributes food among nest mates and is an important means of information transfer that influences foraging and brood rearing activity (Crailsheim, 1998; Weidenmüller and Tautz, 2002; Leoncini et al., 2004; Grüter et al., 2006). Workers also frequently engage in brief trophallactic exchanges (typically less than 5 s in duration), which may involve little or no food transfer, but provide information about colony nutritional status and forage availability (Korst and Velthuis, 1982; De Marco and Farina, 2001; Farina and Wainselboim, 2005). Food-exchange interactions vary with colony condition (De Marco and Farina, 2001, 2003; De Marco, 2006). Thus, if the vibration signal influences the tendency to engage in these interactions, and if this tendency varies with colony state, this could alter the acquisition of information and help adjust labor to changing colony needs.

We investigated the possible influence of the vibration signal on worker interactions under different colony conditions by comparing the movement rates, cell inspection activity, and food-exchange behavior of workers that received vibration signals in established and newly founded honey bee colonies. When a swarm of honey bees first occupies a new nest cavity, it must build all of its combs "from scratch" and rapidly initiate brood rearing and food storage to amass the honey reserves and worker population necessary for winter survival. In contrast, established colonies contain large worker populations, fully constructed combs, and large amounts of brood and food. Established and newly founded colonies therefore exhibit different allocations of resources and labor to brood production, foraging, and comb building (Eckert et al., 1994; Pratt, 2004; Hyland et al., 2007). Recently, we demonstrated that compared to established colonies, newly founded colonies have greater proportions of workers that perform vibration signals and increased signaling activity that is slightly, but significantly more focused on inactive recipients (Hyland et al., 2007). This, in turn, may help to adjust worker activity to the labor needs associated with the different stages of colony development, and this could occur partly by altering the rates at which workers obtain information about colony state.

Our study had two main objectives. First, we compared the behavior of vibrated recipients and non-vibrated controls within established and newly founded colonies to determine if the signal altered worker interactions with the nest and nest mates under both stages of colony development. Second, we compared the behavior of vibrated recipients between the two colony types to assess if colony developmental state influenced the extent to which the signal affected worker interactions. Because nest founding may require more carefully balanced allocations of labor among different cooperative activities (Hyland et al., 2007), we predicted that vibrated recipients in newly founded colonies would exhibit increased interactions with the nest and nest mates compared to recipients in established colonies.

Materials and methods

Colony set up and establishing populations of marked workers

The present study was part of a larger investigation of the effects of colony developmental state on vibration signal behavior (Hyland et al., 2007). The methods for colony set up and establishing populations of known age, marked workers have been previously reported in detail (Hyland et al., 2007) and are briefly summarized below. Our basic experimental plan was to examine the behavior of vibrated recipients in pairs of four-framed observation colonies, one of which was an established colony, whereas the other was a newly founded colony. The established colony was set up by transferring into an observation hive 6,000–8,000 workers, their queen, and four frames of fully constructed comb filled with food and brood in all stages of development. The newly founded colony was set up by transferring a swarm into an observation hive that contained four wooden frames, each of which was empty except for a 42 X 12 cm strip of wax foundation to ensure that combs were built with the proper orientation in the hive. The swarm was created by maintaining 6,000–8,000 workers and their queen in a 56 X 56 X 38 cm swarm cage and providing sucrose solution (50 % w/w) *ad libitum* until large numbers of wax scales were produced and the swarm was ready to initiate comb construction [methods for swarm creation as in Donahoe et al. (2003)]. After transfer into the observation hive, each newly founded colony had to build its complete complement of combs (except for the wax foundation strips) and initiate brood rearing and food storage, thereby simulating the conditions of nest founding.

The colonies used to create the established colony and the swarm for the newly founded colony were taken from pairs of field colonies maintained in five-frame box hives that were initially matched for population size and areas of brood and food comb. During a trial, both colonies were transferred into the observation hives simultaneously. The glass walls of the observation hives were marked off in a grid of 4 X 4 cm squares, to facilitate monitoring worker behavior.

We established in the study colonies populations of individually-recognizable, marked bees by gluing to the thorax of newly emerged workers plastic tags (Opalithplättchen, Chr. Graze, Endersbach, Germany), each with a unique number/color/paint mark combination. Tagged individuals were added in cohorts of 100 bees each day until a total of 1100–1300 had been introduced into each colony. Workers for tagging were collected from frames of comb maintained in an incubator (35 °C; 50 % RH). All workers added to the study colonies during a given trial emerged from combs taken from the same field colony, which was unrelated to the established and newly founded colonies. Workers were marked within 24 h of emergence, such that their exact age (in days) was known throughout the study.

We conducted four trials, which involved a total of four established and four newly founded colonies, during the spring and summer of 2004 and 2005 on the campus of the University of North Carolina at Charlotte. Each trial ran for three weeks, which corresponded to the first brood rearing cycle for the newly founded colony (Winston, 1987).

During the course of the trials, the newly founded colonies built larger amounts of comb, devoted greater proportions of comb space to brood rearing, had greater per capita foraging activity, but declined in population size by half compared to the established colonies (Hyland et al., 2007). Similar patterns of growth and activity have been previously reported for newly founded and established honey bee colonies, suggesting that our manipulations simulated the labor and energy demands associated with the different stages of colony development (Schneider and McNally, 1994; Hyland et al., 2007).

Monitoring the behavior of vibrated recipients

Throughout a trial, tagged bees that received vibration signals were selected at random and monitored for 20 min each, or until they were lost in the colony or flew from the hive. For each vibrated recipient monitored, we also observed a non-vibrated control tagged bee. Each control bee was selected to be of the same age, in the same initial location of the nest, and exhibiting the same initial level of activity as her vibrated counterpart. Each control tagged bee was selected within one hour of monitoring the vibrated recipient and, whenever possible, was monitored by a separate observer simultaneously with her vibrated counterpart. If a control received a vibration signal during the observation period, observations were terminated and a new tagged control was selected. Each recipient and control was monitored only once.

We recorded the following data for each bee, using digital stopwatches when necessary: (1) number of grid squares crossed, (2) number of cell inspections performed (defined as a bee having at least her head inside a cell for less than 5 s), (3) number of brief trophallactic interactions (mouth-to-mouth contacts that lasted less than 5 s), (4) number of extended trophallactic exchanges (contacts lasting more than 5 s), and (5) the duration of each extended trophallactic exchange. Trophallaxis can transmit information to both recipients and donors of liquid food (Goyret and Farina, 2003; Wainselboim and Farina, 2003; Farina and Wainselboim, 2005). Thus, for each brief and extended trophallactic interaction observed, we noted if the focal bee was associated with receiving liquid food (e.g., extended her tongue between the spread mandibles of a bee to solicit or obtain food) or donating liquid food (spread her mandibles to offer or give food to a worker).

Subsequently, we determined for each vibrated recipient and non-vibrated control her movement rate (grid squares crossed/min) and inspection rate (cell inspections/min). With respect to the rates of trophallaxis, we determined for each bee her total number of brief and extended trophallactic interactions/min and the number of brief and extended interactions/min in which she received and donated food. We also determined for each bee the total proportion of observation time engaged in extended trophallaxis, and the proportion of time spent as a recipient and donor of trophallaxis.

Statistical analyses

We used three-way analysis of variance (ANOVA) with replication (SAS Institute, 1997) to compare recipients and controls within and between the established and newly founded colonies for: (1) movement rates (2) inspection rates, (3) trophallaxis rates, and (4) the proportion of time engaged in extended trophallactic exchanges. The main effect of bee type allowed us to assess if vibrated recipients and non-vibrated controls differed within each colony type. The first-order interaction of bee type X colony type was used to assess if the magnitude of the difference between recipients and controls (and thus the extent to which recipients responded to the vibration signal) varied between the established and newly founded colonies. The second-order interaction (trial X bee type X colony type) was used to determine if the effect of colony type on the difference between recipients and controls varied among trials. If significant interactions were found, we conducted post hoc paired comparisons using Tukey's HSD test (Sokal and Rohlf, 1995). All rates were square-root transformed and all proportional data were arcsine transformed before analysis to attain normality and homoscedasticity. The sequential Bonferroni adjustment (Rice, 1989) was used to determine significance levels for the multiple comparisons made between colonies and trials. All statistical tests were two-tailed; mean values are reported as ± one SE.

Results

We monitored a total of 894 recipient and control workers during the course of the study, consisting of 456 bees in the four established colonies (114.0 ± 3.1 bees per colony) and 438 bees in the four newly founded colonies (109.6 ± 3.9 bees per colony). On average, each bee was monitored for 17.9 ± 3.94 min, for a total of 267.3 h of observation over all trials combined. We found no trial X colony type interactions for any of the behaviors examined ($F_{3,878} < 1.85$ for all comparisons; $P > 0.12$). We therefore focused our results on the main effects of bee type (vibrated recipients versus non-vibrated controls) and colony type (established versus newly founded).

The vibration signal influenced how workers moved through the colony and interacted with the nest. Compared to non-vibrated controls, vibrated recipients exhibited greater rates of locomotion and cell inspection activity in both the established and newly founded colonies ($F_{1,878} > 66.60$; $P < 0.01$ for both comparisons; Table 1).

Table 1. Mean ± SE movement rates (grid squares crossed/min) and cell inspection rates for vibrated recipients and non-vibrated controls in the established (EST) and newly founded (NF) colonies.

	Squares Crossed/min	Inspections/min
EST Colonies		
Recipients	2.50 ± 0.18	1.78 ± 0.13
Controls	1.43 ± 0.09	1.04 ± 0.08
NF Colonies		
Recipients	1.95 ± 0.19	1.49 ± 0.14
Controls	0.85 ± 0.11	0.64 ± 0.08

The vibration signal influenced all aspects of food exchange examined. Compared to non-vibrated controls, vibrated recipients in both colony types had greater total rates of brief and extended trophallactic interactions, and greater rates of interactions in which they were the recipient and donor of food exchange ($F_{1,878} > 6.80$ for all comparisons; $P < 0.01$; Fig. 1). Vibrated recipients spent a greater total proportion of time engaged in extended trophallaxis and spent significantly more time receiving trophallaxis than did controls ($F_{1,878} > 7.25$ for both comparisons; $P < 0.01$; Fig. 2). Vibrated recipients also spent a greater proportion of time as donors of trophallaxis than did non-vibrated controls, although this difference did not reach significance at the adjusted alpha level ($F_{1,878} = 2.80$; $P = 0.09$; Fig. 2).

Although the signal increased the locomotion rate, cell inspection activity, and food-exchange behavior of

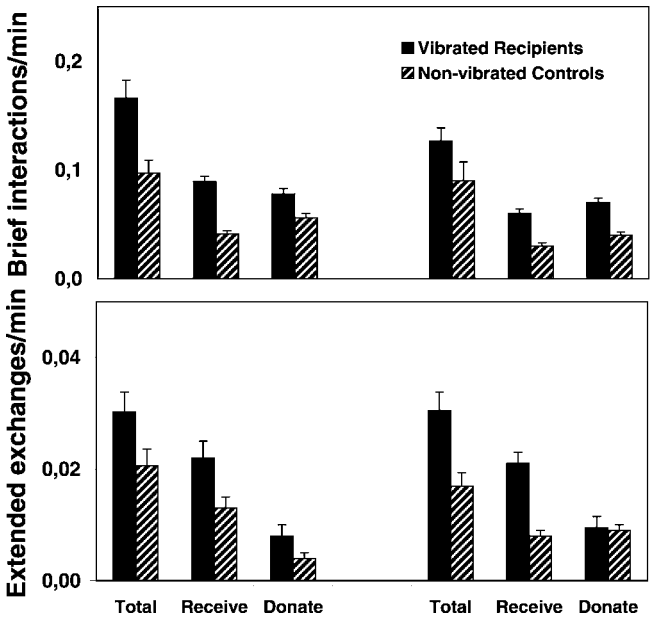

Fig. 1. Mean ± SE total rate of food-exchange contacts and the rate at which vibrated recipients and non-vibrated controls received and donated food during brief trophallactic interactions (upper) and extended trophallactic exchanges (lower) in the established (EST) and newly founded (NF) colonies.

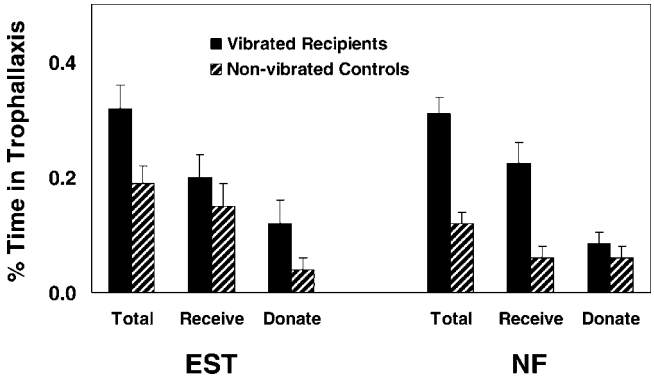

Fig. 2. Mean ± SE total proportion of time spent in extended trophallactic exchanges and the proportion of time spent as a recipient and donor of trophallaxis by vibrated recipients and non-vibrated controls in the established (EST) and newly founded (NF) colonies.

recipients relative to non-vibrated controls, we found no differences in the degree to which individual recipients in the two colony types performed the different activities monitored. The magnitude of the difference between vibrated recipients and controls in the established and newly founded colonies did not differ for movement rate ($F_{1,878} = 2.63$; $P = 0.106$) or cell inspection rate ($F_{1,878} = 1.32$; $P = 0.251$; Table 1). Likewise, the magnitude of difference between recipients and controls in the two colony types did not differ for any of the monitored rates of trophallaxis, or for the proportions of time engaged in extended trophallactic exchanges ($F_{1,878} < 3.32$ for all comparisons; $P > 0.07$; Figs. 1 and 2). Thus, contrary to our prediction, we found no evidence that individual vibrated recipients in the newly founded colonies increased their interaction rates relative to recipients in the established colonies.

Discussion

Our results suggest that the greater task performance elicited by the vibration signal occurs in conjunction with increased rates of contact with the nest and nest mates. Compared to non-vibrated control bees, vibrated recipients exhibited greater movement through the nest, increased cell inspection activity, and greater food-exchange behavior. Such behavior patterns can increase exposure to a wide variety of cues and signals, and have been suggested to influence information flow and task decisions in honey bees and many other social insects (Biesmeijer and Slaa, 2004; De Marco, 2006; Dornhaus and Chittka, 2004; Greene and Gordon, 2003; Gordon, 2002; Hyland et al., 2007). Although we did not monitor information acquisition by vibrated recipients *per se*, our results suggest that the vibration signal may contribute to the organization of labor in honey bees partly by increasing the rate at which workers obtain information about their colony.

However, the precise manner in which the vibration signal influences worker behavior is unclear. We do not know if vibrated recipients show greater task performance because of increased exposure to stimuli, or if the signal elicits task performance which subsequently affects interaction rates and contact with signals and cues. However, given the non-specific effect of the signal on worker activity and the strong role of context in determining the responses of individual recipients (Schneider and Lewis, 2004), it seem likely that the vibration signal often influences worker behavior by altering exposure to stimuli that affect subsequent labor decisions. The greater movement, cell inspection activity, and food-exchange behavior elicited by the signal may result in recipients more quickly reaching the threshold of stimulation necessary to elicit particular tasks. Additionally, the signal may lower response thresholds, so that less stimulation is required to trigger a specific behavior. Titers of juvenile hormone (JH) show slight, significant increases in workers that receive vibration signals (Schneider et al., 2004), which may alter metabolic rate and influence response thresholds for a number of different stimuli (Elekonich et al., 2001; Sullivan et al., 2003). The vibration signal may therefore exert behavioral and physiological effects that increase the likelihood that workers will contact and respond to stimuli that influence a wide array of tasks.

Although the signal caused increased locomotion, cell inspections, and food-exchange behavior by vibrated workers relative to non-vibrated controls, colony developmental state did not influence the extent to which recipients exhibited these responses. Thus, we found no evidence that recipients in the newly founded colonies

increased their individual rates of contact with the nest and nest mates relative to recipients in the established colonies. Similarly, Hyland et al. (2007) found that recipients in the established and newly founded colonies did not differ in the amount of time spent performing the tasks of brood care, food processing, or comb manipulation. However, compared to established colonies, newly founded colonies have greater numbers of vibrators that perform signals on larger proportions of the inactive bees they contact, resulting in significantly higher per capita rates of signaling and potentially the activation of a greater portion of the workforce (Hyland et al., 2007). Taken together, these results suggest that any contribution of the vibration signal to adjusting labor to colony developmental state may occur primarily by stimulating greater numbers of less occupied bees to acquire and respond to information about colony needs, rather than by altering the extent to which individual recipients react to the signal.

In a number of species of social insects, contact rates vary with colony condition and help to adjust task allocations to changing colony needs (Hölldobler and Wilson, 1990; Seeley, 1995; Gordon, 1999; 2002; O'Donnell, 2006; Schafer et al., 2006). By operating in a non-specific, modulatory manner, the vibration signal of the honey bee may contribute to the coordination of worker labor with colony needs by altering exposure to stimuli that affect task performance. Vibration-like modulatory signals are widespread in the highly social insects and are often involved in the multi-component signaling processes that regulate collective activities (Hölldobler, 1999; Partan and Marler, 1999). This raises the possibility that tactile modulatory signals may be a common mechanism for influencing the acquisition of information and organizing information flow in many insect societies.

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