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Honey bee workers generate low-frequency vibrations that are reliable indicators of their activity level

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Abstract

In social insects, the tuning of activity levels among different worker task groups, which constitutes a fundamental basis of colony organization, relies on the exchange of reliable information on the activity level of individuals. The underlying stimuli, however, have remained largely unexplored so far. In the present study, we describe low-frequency thoracic vibrations generated by honey bee workers (*Apis mellifera*) within the colony, whose velocity amplitudes and main frequency components significantly increased with the level of an individual's activity. The characteristics of these vibrations segregated three main activity level-groups: foragers, active hive bees, and inactive hive bees. Nectar foragers, moreover, modulated their low-frequency vibrations during trophallactic food unloading to nestmates according to the quality of the collected food. Owing to their clear association with the activity level of an individual and their potential perceptibility during direct contacts, these low-frequency thoracic vibrations are candidate stimuli for providing unambiguous local information on the motivational status of honey bee workers.

Keywords Social insects · *Apis mellifera* · Vibratory communication · Mechanical cues · Motivational state

Introduction

Social insect colonies are capable of quickly responding to changes in their environment, thereby reacting as a single, purposeful unit (Seeley 1989a). The underlying behavioural coordination of the colony members is the result of self-organized processes, in which collective decisions arise from individual responses to local stimuli, such as signals from nestmates or cues from the nest environment (Bonabeau et al. 1997; Moritz and Fuchs 1998; Seeley 1998; Camazine et al. 2003). The colony members adjust the level of work devoted to each task by responding to information stemming mainly from mechanical, chemical, and thermal stimuli, or from temporal cues (Stabentheiner and Hagmüller 1991; Seeley 1998; Farina and Wainselboim 2001; Hrncir et al. 2006a; Hunt and Richard 2013; Grüter and Keller 2016). Moreover, a colony can only function as a coherent unit if the activities of its members are coordinated (Johnson 2010a). This coordination among different worker groups is mediated through modulatory signals that are produced in a variety of behavioural contexts where they cause nonspecific shifts in task performance (Moritz and Fuchs 1998; Seeley 1998; Schneider and Lewis 2004; Moauro et al. 2018).

Many task regulation processes in social insect colonies depend on the perception of the activity levels of individuals. In honey bees, for instance, workers perform shaking signals predominantly on inactive nestmates, who respond to this signal with a general increase in activity, thereby facilitating cooperative interactions within and among task groups (Seeley et al. 1998; Lewis et al. 2002; Schneider and Lewis 2004; Slone et al. 2012). Moreover, information about the activity level of individuals nearby modulates the motivational states and attention levels of workers, eventually altering their behavioural thresholds, associative learning capacities, and stimulus responsiveness (Farina and Wainselboim 2001; Schneider and Lewis

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2004; Balbuena et al. 2012; Mc Cabe et al. 2015; Moauro et al. 2018). But how do colony members sense the activity levels of their nestmates?

In eusocial bees, the excitement level of individual foragers is encoded in the "liveliness" of their recruitment signals (Waddington and Kirchner 1992; Farina 1996; Seeley et al. 2000; De Marco and Farina 2001; Hrncir et al. 2004, 2006a, 2011). Many task regulation processes, however, rely on workers sensing activity-dependent cues, not signals, from their nestmates (Lindauer 1954; Farina 2000). A possible source of cue-based information about the activity level of worker honey bees is the irregular thoracic vibrations, generated by twitches of the asynchronous flight muscles, that have been attributed to pre-flight warm-up in bees (Esch et al. 1991). The frequency of the action potentials that trigger this "muscle shivering", and, consequently, the contraction of the flight muscles, increases with increasing metabolic activity of the bees (Esch and Bastian 1968; Bastian and Esch 1970; Kammer and Heinrich 1974). The resulting oscillations of the thorax (Esch et al. 1991) may be transmitted to the nestmates either directly during body contacts, or through substrate vibrations and/or air particle-oscillations in the close vicinity of the shivering bee (Michelsen et al. 1987; Sandeman et al. 1996; Hrncir et al. 2006b, 2008; Tsujiuchi et al. 2007).

In the present study, we wanted to determine whether thoracic vibrations produced by flight muscle shivering by a worker honey bee reveals an individual's activity status to its nestmates. For this to be the case, two conditions must be met: (1) differences among individuals in activity level result in measurable differences in their thoracic vibrations, and (2) the thoracic vibrations must be strong enough to be detected by the bees' mechanoreceptors.

Materials and methods

Study site and setup of bee colonies

The study was performed at the experimental field of the University of Buenos Aires, Argentina (34°33′S; 58°26′W) with two queenright colonies of *Apis mellifera ligustica* Spinola, 1806. Both colonies (adult population between 2000 and 3500 individuals) were kept in observation hives set up inside a tent ($6 \times 3 \times 2$ m^3) covered with a translucent polyethylene cover (Arenas et al. 2008). The strongly reduced light intensities inside the tent allowed laser vibration-recordings through the glass panel of the observation hive (see below) without significant disturbance of intranidal colony activities. One lateral side of the flight chamber remained open so that foraging in the surrounding environment was not restricted.

Activity level-groups

For our study, we chose three bee groups with clearly distinct activity levels: (i) inactive hive bees (HI), (ii) active hive bees (HA), and (iii) nectar foragers (FO). (i) We considered hive bees as inactive (HI: $N = 12$ individuals) if they did not move for at least 15 min. (ii) Active hive bees included non-foraging individuals that were observed walking through the nest or engaged in any intranidal task such as comb manipulation, queen attendance, or food processing. We recorded the thoracic vibrations of twelve focal bees both during their respective activity (HA-A) and while standing still (HA-I), and of nineteen nectar receivers (HA-R) during trophallactic interactions with foragers. (iii) Nectar foragers returning from natural food sources (FO-N: $N = 19$) were identified through their dance behaviour after entering the nest and unloading their load to food receivers. In addition, we trained foragers to ad libitum sugar water feeders located at a distance of approximately 180 m from the nest (FO-T, $N = 23$). As food we offered unscented solutions containing 12.5%, 25%, or 50% sucrose weight on weight (w/w). Prior to each trial, we marked a single forager with nontoxic paint on her thorax while collecting at the feeding station. All non-marked foragers were captured with a plastic suction tube and released after the trial. To avoid pseudoreplications, the marked forager was killed by freezing after the trial. In total, 23 trained foragers participated in this experimental series. Twelve bees collected sucrose solution in a sequence of increasing concentrations (12.5% $-25\% -50\%$), and eleven bees in a sequence of decreasing concentrations (50% $-25\% -12.5\%$). Each sugar concentration was offered for at least 1 h. The thoracic vibrations of all investigated nectar foragers (FO-N, FO-T) were recorded during trophallactic interactions with food receivers. In addition to the investigated bees, we recorded vibrations from the combs (CO: $N = 12$) and the wooden frame of the observation hives (WF: $N = 12$) to control for possible artefacts in our recordings due to background noise.

Recording and analysis of thoracic vibrations

The thoracic vibrations generated by the bees and the background vibrations were recorded as velocities using a contactless portable Laser-Doppler-Vibrometer (PDV100: Polytec: Waldbronn, Germany). Recording the vibrations directly on the individuals´ thorax avoided interference by background noise like that produced by ventilating nestmates or other vibrating bees (Hrncir et al. 2004). The use of laser vibrometry kept the signal-to-noise ratio very

high, which allowed us to identify and measure the vibrations generated by the bees. The vibrations of the bees and the combs were picked up through the glass panel of the observation hive, which did not change the temporal or spectral characteristics of the vibrations (MH unpublished data).

The laser-vibrometer was connected to a portable microcomputer via a custom-made voltage-reducer (Insight Equipamentos: Ribeirão Preto, Brazil) and an external soundcard (PSC 805: Philips: Amsterdam, The Netherlands). The signals were recorded on the computer's hard-disc using the software Soundforge 7.0 at a sampling rate of 44,100 Hz and 16bits. Signal analysis was performed using the software SpectraPro 3.32 (Systat Software Inc., USA). Fast Fourier Transformation-analysis (FFT-analysis, SpectraPro 3.32) was performed at a frequency resolution of 2 Hz.

For each bee, we analysed at least 3 s of recordings, measuring the velocity amplitude (VA, peak-to-peak, p-p) and the main frequency component (MF, peak frequency in spectrogram) of the vibrations (Fig. 1) in 0.5 s intervals (at least 6 measurements for each vibration parameter). In
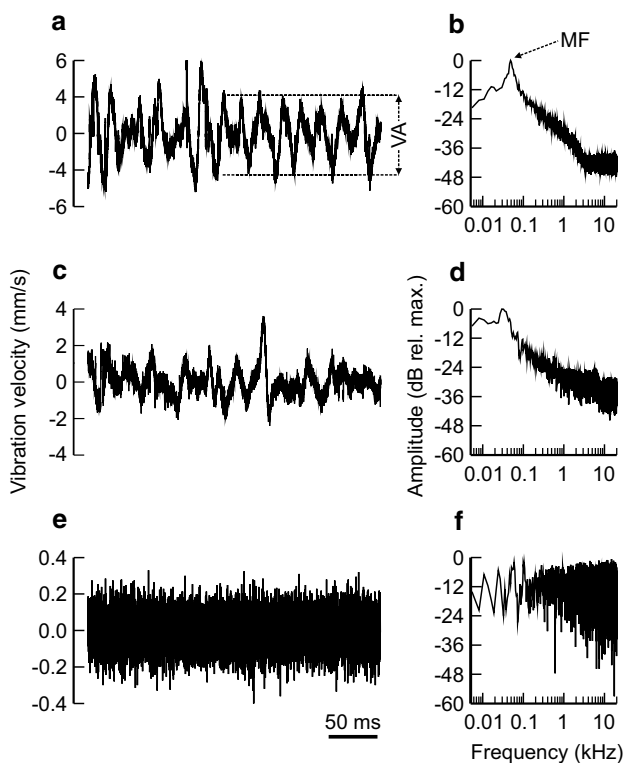
some cases, particularly when the VA of the vibrations was very low, we could not clearly determine the peak frequency in the spectrogram (Fig. 1e, f). In these cases, the vibrations were characterized only by their VA. For each bee and control recording (comb, wooden frame), we calculated the arithmetic means of the measured VA and MF as representative values for the respective individual or background noise sample (single VA and single MF for each bee and background noise recording). The statistical analysis was performed with these representative mean values to avoid different weightings in the analysis due to different sample sizes (Hrncir et al. 2004).

Statistical analyses

To identify whether bees of different activity level-groups produce different thoracic vibrations, and whether these responses differ from the background noise, we performed One-way analyses of variance (ANOVA; Tukey test for post hoc pairwise comparisons), comparing VA and MF (if available) of the vibrations picked up from inactive hive bees, active hive bees, nectar foragers from natural food sources, the combs, and the wooden frames of the observation hives. Foragers trained to artificial food sources collected food with either increasing or decreasing sugar content. Potential modulations in low-frequency vibrations (VA, MF) between experimental steps were investigated using One-way repeated measures ANOVA (Tukey Test for post hoc pairwise comparisons). Occasionally, trained foragers stopped producing waggle dances in the course of the experiment, albeit continuing their collecting activity for several foraging trips. We compared the thoracic vibrations (VA, MF) produced by these individuals during trophallactic food unloading between the situations with and without waggle dances using paired t tests. In case data did not meet the criteria for parametric tests, we performed logarithmic transformations to approximate normal distribution and equal variance (Zar 1999). All statistical tests were performed using the software SigmaPlot 13.0 (Systat Software Inc., USA). The level of significance for differences was $P \leq 0.05$. Throughout the text, average values are represented as arithmetic means $\pm$ SD. N refers to the number of recorded bees or background vibration takes.

Fig. 1 Samples of low-frequency thoracic vibrations generated by honey bee workers. Given are typical examples of recordings of the thoracic oscillations of a forager returning from natural food sources (**a, b**), an active hive bee (**c, d**), and an inactive hive bee (**e, f**). We analysed the velocity amplitude p-p (VA) of the vibrations (**a, c, e**), and the main frequency component (MF) from the frequency spectra (**b, d, f**). Note differences in velocity scaling between (**a**), (**c**), and (**e**)

Results

Active honey bees produced low-frequency thoracic vibrations

In all groups of active bees (foragers, FO-N, and active hive bees, HA-R, HA-A, HA-I), we detected weak thoracic vibrations characterized by low main frequencies (average MF
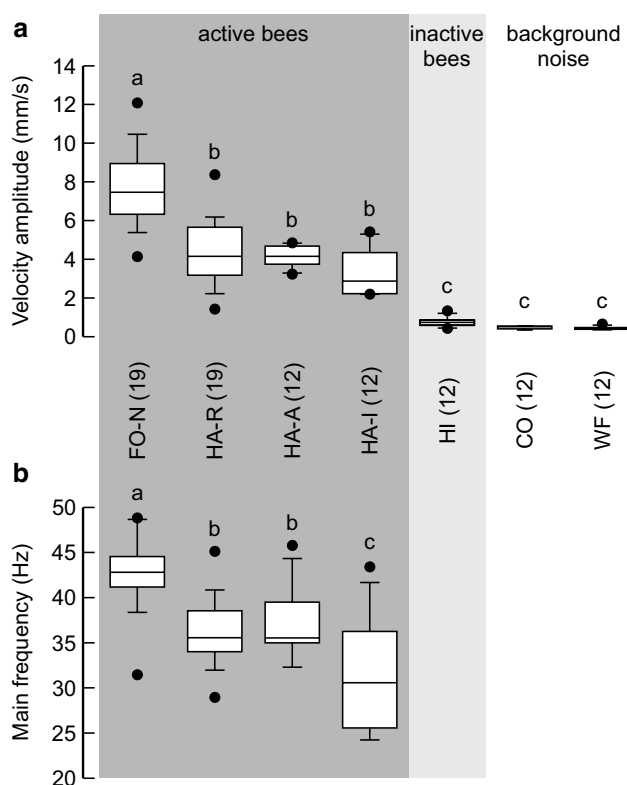
Fig. 2 Low-frequency thoracic vibrations by honey bee workers. Given are the velocity amplitudes (**a**) and main frequencies (**b**) of the thoracic oscillations picked up from foragers returning from natural food sources (FO-N), hive bees receiving food (HA-R), active hive bees while executing any other task (HA-A) or during brief interruptions of their activity (HA-I), and inactive hive bees (HI). Additionally, we measured background vibrations on the combs (CO) and the wooden hive-frame (WF). Owing to the low velocity amplitudes of the vibrations of inactive bees and the background, we could not identify their main frequency component (see Fig. 1). The numbers in the brackets refer to the numbers of recorded bees or background vibration takes. Box plots indicate inter-quartile range (box), the median value (horizontal line), 95% range (whiskers) and outliers of all data. Data were compared using One-way ANOVA. Different superscript letters in each graph indicate statistical differences between groups (Tukey Test: $P < 0.05$)

between 31.3 ± 1.77 and 42.7 ± 0.92 Hz; Figs. 1, 2). Both the mechanical and spectral characteristics of the thoracic vibrations differed significantly between the groups of active bees (VA: One-way ANOVA: $F_{6,91} = 170.9$, $P < 0.001$; Tukey Test: $P < 0.001$; MF: One-way ANOVA: $F_{3,57} = 17.2$, $P < 0.001$; Tukey test: $P < 0.01$; Fig. 2), separating, principally, foragers from the active hive bees ($VA_{FO-N} > VA_{HA}$). The main frequencies of the thoracic vibrations, additionally, segregated the standing active hive bees (HA-I) from the moving active hive bees (HA-R, HA-A) ($MF_{FO-N} > MF_{HA-R, HA-A} > MF_{HA-I}$; Fig. 2). Despite their reduced velocity amplitudes (average VA between 3.4 ± 0.35 and 7.5 ± 0.43 mm/s), these vibrations were clearly distinguishable from those of inactive hive bees (HI average

VA = 0.7 ± 0.07 mm/s) or the background (combs, CO, average VA = 0.5 ± 0.03 mm/s; wooden frame, WF, average VA = 0.4 ± 0.02 mm/s) (Tukey Test: $P < 0.001$; Fig. 2).

In contrast to active bees, the vibrations of inactive hive bees (HI) were not statistically discriminable from the background noise (CO, WF; Tukey Test: $P > 0.2$; Fig. 2). Due to extremely low velocity amplitudes (average VA ≤ 0.7 mm/s) and a reduced regularity compared to the oscillations picked up from active bees (Fig. 1e, f), we could not clearly identify the main frequency component of the vibrations of the inactive individuals or background noise.

Food unloading foragers tuned their low-frequency vibrations according to the collected sugar reward

The characteristics of the low-frequency vibrations generated by trained nectar foragers (FO-T) during trophallactic food unloading in the nest changed according to the sugar reward experienced at the feeding site. Both the velocity amplitude and the main frequency of the thoracic vibrations increased with increasing sugar concentrations (Fig. 3). The velocity amplitudes differed significantly between the different foraging conditions (One-way repeated measures ANOVA: $F_{2,10} = 23.6$, $P < 0.001$; Tukey test: $P < 0.05$; Fig. 3). The main frequency component of the vibrations, however, only increased significantly when foragers collected sugar solution containing sucrose at 50% w/w (One-way repeated measures ANOVA: $F_{2,10} = 13.0$, $P < 0.001$; Tukey test: $P < 0.05$). There was no significant difference between the main frequencies of the vibrations produced by the individuals when collecting 12.5 or 25% w/w sucrose solution (One-way repeated measures ANOVA: $F_{2,10} = 13.0$, $P < 0.001$; Tukey test: $P = 0.107$; Fig. 3).

Nectar foragers reduce the intensity of their low-frequency vibrations when abandoning food collection

Not all of the trained foragers completed the entire sugar sequence offered during our experiment. Of the 23 trained individuals, twelve abandoned foraging in the course of an ongoing trial. Initially, all these bees performed waggle dances when returning to the nest (recruitment state). Over time, however, they stopped dancing, yet continued to collect and deliver food to nestmates for a few more foraging trips (intermediate state) prior to abandoning completely their collecting activity. This decrease in foraging motivation was accompanied by a declining intensity of the bees' low-frequency vibrations produced during trophallactic food transfer to nectar receivers (recruitment state: VA = 8.2 ± 3.12 mm/s; MF = 37.9 ± 3.33 Hz; intermediate state: VA = 6.8 ± 2.51 mm/s; MF = 35.8 ± 3.78 Hz; VA,
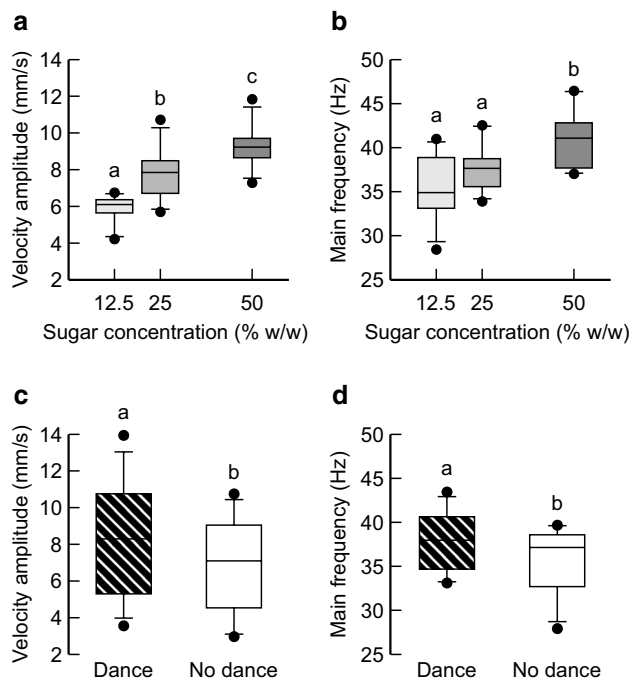
Fig. 3 Low-frequency thoracic vibrations of honey bee foragers during trophallactic unloading contacts. Given are the velocity amplitudes (**a**) and the main frequencies (**b**) of the thoracic vibrations during trophallactic food transfer generated by waggle-dancing foragers ($N = 11$ bees) trained to artificial food sources with varying sugar concentration (12.5, 25, or 50% w/w sucrose solution). Vibrations generated at the different concentrations were compared using One-way repeated measures ANOVA. Different superscript letters in each column indicate statistical differences between groups (Tukey test: $P < 0.05$). Several bees ($N = 12$) stopped dancing in the course of the experiment, albeit continuing food collection. We analysed the velocity amplitudes (**c**) and main frequencies (**d**) of their low-frequency vibrations generated during trophallactic interactions with hive bees before and after they stopped performing recruitment dances. Vibrations generated in these two behavioural states were compared using paired t tests. Different superscript letters indicate statistical differences between groups ($P < 0.05$). Box plots indicate inter-quartile range (box), the median value (horizontal line), 95% range (whiskers) and outliers of all data

Paired t test: $t = -2.78$, $P = 0.018$; MF, Paired t test: $t = -2.86$, $P = 0.016$; Fig. 3c).

Discussion

In the present study, we provide the first clear evidence that active honey bee workers produce weak low-frequency vibrations within the colony, whose mechanical and spectral characteristics change according to the individuals' activity level. The gain in acceleration of the thoracic oscillations (acceleration $\propto$ VA × MF) with increasing agitation of the bees is presumable related to an increasing specific power output of the indirect flight muscles associated with

higher muscle potential frequencies at higher metabolic rates (Esch and Bastian 1968; Heinrich and Kammer 1973; Kammer and Heinrich 1974; Esch et al. 1975; Pennycuick and Rezende 1984; Goller and Esch 1991). In addition to significant differences between active and inactive hive bees, foragers modulated their thoracic vibrations, generated during trophallactic interactions, according to both the sugar concentration of the visited food source and their foraging motivation. The observed association between the intensity of the low-frequency vibrations and an individual's activity level renders these mechanical stimuli potential local cues for bees to assess their nestmates' motivational state in different behavioural contexts.

In analogy to our findings for low-frequency vibrations, honey bee workers tune their thoracic temperatures to their activity level. The temperatures of inactive hive bees are similar to those of the nest environment (Esch 1960), yet they increase with increasing activity level of the individuals (Stabentheiner et al. 2003). Furthermore, as well in compliance with the results of our study, body temperatures of returning foragers exceed those of active hive bees and are modulated according to the sugar concentration of the collected food (Stabentheiner and Hagmüller 1991; Stabentheiner et al. 1995) and the individuals' recruitment motivation (Sadler and Nieh 2011). These concordant tendencies indicate a tight link between low-frequency thoracic vibrations and thoracic temperatures, and, ultimately, the association of both with the bees' metabolic rate (Heinrich and Kammer 1973; Kammer and Heinrich 1974; Goller and Esch 1991). Yet, although both thermal and vibrational stimuli can be detected by honey bees (thermal stimuli: Heran 1952, 1959; Lacher 1964; vibrational stimuli:; Autrum and Schneider 1948; Sandeman et al. 1996; Tsujiuchi et al. 2007), their potential communicative value as indicator of an individual's activity remains to be investigated.

The low-frequency thoracic vibrations recorded in the present study are probably too weak to generate detectable substrate vibrations or air particle-movements. However, during direct contacts like the shaking signal or trophallactic food transfer (Farina 1996; Seeley et al. 1998; Schneider and Lewis 2004), workers presumably pick up the thoracic vibrations of their nestmates with vibration-sensitive mechanoreceptors in their legs and antennae (Heran 1959; Sandeman et al. 1996; Staudacher et al. 2005). In *Melipona quadrifasciata*, a South-American stingless bee species (Apidae, Meliponini), the amount of thoracic vibrations produced by nectar foragers during trophallaxis influenced the food receivers' posterior learning performance (Mc Cabe et al. 2015). This finding clearly demonstrates that bees not only are capable of perceiving thoracic vibrations of nestmates during direct contacts, but also modulate their behaviour according to the intensity of the received vibrations. Thus, it can be speculated that the low-frequency thoracic vibrations

described in our study may indeed provide local information about a worker's motivational state in the darkness of the hive.

Key function of such motivation-related stimuli could be the tuning of activity levels among different worker task groups, such as foragers and potential recruits. However, despite the increase of the foragers' body temperature with food quality (Stabentheiner and Hagmüller 1991; Stabentheiner et al. 1995), no correlation between dancing temperature and recruitment success could be found in honey bees (Germ et al. 1997). Maybe, motivational changes of receivers manifest themselves on a less evident level, like the bees' physiological state. During trophallactic interactions, for instance, food unloaders tune their activity level according to that of the food donors (Farina and Wainselboim 2001; Pírez and Farina 2004; Martinez and Farina 2008). Concomitant changes in the bees' gustatory sensitivity, attention level, and learning performance facilitate the acquisition of additional local information, such as the floral odours carried by returning foragers or other nestmates (Scheiner et al. 2001; Pankiw et al. 2004; Farina et al. 2007; Martinez and Farina 2008; Mc Cabe et al. 2015; Moauro et al. 2018). Moreover, given the bi-directionality of information transmission during trophallaxis, food donors, as well, receive stimuli associated with the motivational state of the trophallactic partners. In case the food receivers are nectar processors, information on their activity level provides an important feedback cue for foragers, influencing their decision to continue or abort food collection (Lindauer 1954; Seeley 1989b; Farina 2000).

An important first step for a more detailed understanding of the proximate mechanisms underlying this tuning of activity levels among different worker task groups is the identification of cues that provide reliable information about the motivational state of individuals. Potential candidate stimuli are the low-frequency vibrations, discovered in our study, as well as thoracic temperatures, chemical cues related to task group-identity (Kather et al. 2011) and activity level (Thom et al. 2007), and temporal cues like queuing delays (Seeley 1989b, 1998; Anderson and Ratnieks 1999). Future research shall investigate which of these cues the bees use to identify the motivational state of their nestmates, or whether they act synergistically in colony task organization.

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