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Vibrating the food receivers: a direct way of signal transmission in stingless bees (*Melipona seminigra*)

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Abstract An element common to the recruitment communication of eusocial bees (honey bees, stingless bees and bumble bees) are pulsed thorax vibrations generated by successful foragers within the nest. In stingless bees, foragers vibrate during the unloading of the collected food. In the present study on *Melipona seminigra* we demonstrate that during trophallactic contacts, the food receivers are directly vibrated by the foragers. As a consequence, both the temporal structure and the main frequency component of the forager's vibrations are directly passed on to the receiver. The vibrations are attenuated by about 17 dB on their way from the forager's thorax (velocity amplitude of the vibrations: ~70 mm/s) to the receiver's thorax (~10 mm/s), the main amount of attenuation (about 12 dB) occurring during transmission from the head of the forager to that of the receiver. Vibrations conducted through the substrate between the forager and food receiver are comparatively small with velocity amplitudes of 0.3 mm/s. Possible ways of perception and the advantages of vibration transmission by direct contact within the recruitment context are discussed.

Keywords Stingless bees · *Melipona* · Recruitment signals · Signal transmission · Vibratory communication

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Introduction

In social insects, the recruitment of unemployed hive mates to a food source often involves a complex interplay of various communication signals (Wilson 1971). Foragers of honey bees, stingless bees, and bumble bees generate pulsed thorax vibrations when they return from a valuable food source (Hrnčir et al. 2006). These have often been suspected to play an important role in the recruitment process. In stingless bees, the temporal pattern of the foragers' vibrations was shown to correlate with the sugar concentration of the collected solution (*M. costaricensis*: Aguilar and Briceño 2002; *M. mandacaia* and *M. bicolor*: Nieh et al. 2003) and with the more complex "net profitability" (energetic gains versus energetic costs) of the food source (*M. seminigra*: Hrnčir et al. 2004a, b). In some *Melipona* species, even a correlation between the duration of single pulses and the distance of a food source was found (*M. seminigra*, *M. quadrfasciata*: Esch 1967; *M. panamica*: Nieh and Roubik 1998; *M. mandacaia*, *M. bicolor*: Nieh et al. 2003). It is tempting to raise such correlations to the status of an "information" contained within the foragers' thorax vibrations, and claim them to be the cause of recruitment success. Yet, the sensory pathways of information transfer are still under debate, and due to the high variability of the temporal pattern in all cases studied the actual meaning of the forager vibrations for the hive bees remains speculative (Hrnčir et al. 2004b).

It is so far unclear whether the vibrations represent a mechanism of arousal, stimulating hive bees to forage, or whether the hive bees actually make use of the information potentially carried by the temporal pattern of the vibrations. In this regard it is important to know the details of signal transfer between the forager and the potential recipients. In the case of honey bees, substrate vibrations, airborne sounds, or airflow jets generated by the thorax vibrations have been suggested to carry the information to hive mates (Tautz 1996; Tautz and

Rohrseitz 1998; Kirchner 1997; Dyer 2002; Michelsen 2003; Hrnčir et al. 2006).

Stingless bees of the genus *Melipona* (Hymenoptera, Apidae, Meliponini) provide an excellent case to study the transmission of the thorax vibrations of foragers to nest mates during the recruitment process. In contrast to honey bees, foragers of *Melipona* do not embed these presumed signals into complex dance movements. Instead, they generate their pulsed thorax vibrations mainly when delivering food to hive bees (Lindauer and Kerr 1958; Esch 1967; Hrnčir et al. 2004a, b). During the trophallactic interactions (mouth-to-mouth contacts between bees; Korst and Velthuis 1982), hive bees learn about the sugar concentration, the nectar secretion rate, and the odor of a food source (Farina and Núñez 1991; de Marco and Farina 2003; Gil and Farina 2003). Also, along with these contacts, a direct transmission of the vibrations generated by foragers is to be expected (Hrnčir 2003) (Fig. 1).

The present study on the stingless bee *Melipona seminigra* clarifies to which extent the thorax vibrations of a forager are transmitted to food receiving bees during trophallactic contacts. Laser vibrometry allowed us to measure the attenuation of the vibrational signal on its way from the sender to the receiver and to see, how reliably its temporal pattern is transferred onto the receiving bees and the body parts carrying the most likely vibration receptor organs. We studied the vibration transmission through the substrate in order to judge the potential relevance of different transmission channels.

Methods

The experiments were performed on the campus of the University of São Paulo in Ribeirão Preto, Brazil

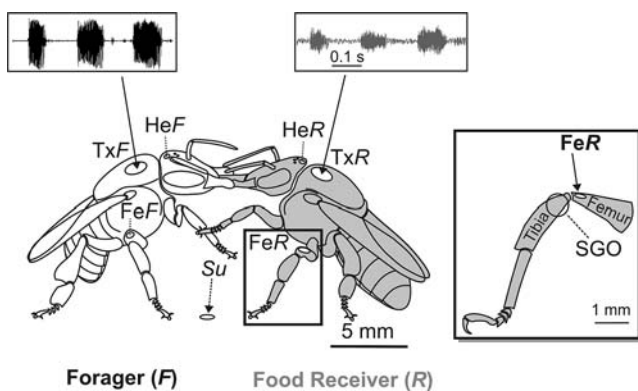


Fig. 1 Foragers (*F*) of stingless bees generate thorax vibrations which can also be measured on food receiving bees (*R*) during trophallactic contacts. Vibrations were simultaneously measured with two Laser Doppler Vibrometers on the thorax (*TxF*, *TxR*), on the head (*HeF*, *HeR*), on the femur of the middle leg (*FeF*, *FeR*) of forager and receiver, and on the substrate (*Su*) between the bees. *Inset* position of receiver's middle leg during food uptake and location of subgenital organ (*SGO*)

between December 2004 and May 2005. The bees, *M. seminigra*, were kept in a wooden nest box inside a laboratory building and left/entered the nest via a plastic tube through the wall. A glass covered acrylic box (observation box: 10×5×4 cm³) was placed between the nest box and the exit/entrance tube. In most cases the returning foragers delivered the collected food to their nest mates inside this box. While recording the thorax vibrations, the glass cover was removed from the observation box, which did not affect the bees' unloading behavior (Hrnčir et al. 2004b).

Experiments and dual laser vibrometry

In 17 experiments we trained three bees each (foragers, marked with colored dots on thorax) to collect sugar solution (50% cane sugar weight/weight; verified with refractometer: HR 25/800 Krüss Optronic) at an artificial food source 10 m away from the nest entrance. When the foragers returned to the nest, their thorax vibrations and those of the food receiving hive bees were recorded simultaneously during food transfer (Fig. 1). The signal transmission (1) by direct contact, and (2) through the substrate were compared by simultaneously measuring vibrations at different points between the sender and receiver (Fig. 1). In honey bees, vibration sensitivity is predominantly attributed to the subgenital organ, a chordotonal organ in the proximal part of the tibia of each leg (Schön 1911; Autrum and Schneider 1948). The vibration characteristics of honey bee legs have been studied by measuring the substrate-vibration-induced vertical vibrations of the mesothoracic femur, close to the joint with the tibia (Rohrseitz and Kilpinen 1997). Because the legs are potentially important for vibration detection in *M. seminigra* and other stingless bees as well, we examined the vibration transmission to the food receivers' legs during direct vibration transfer (Fig. 1). Like Rohrseitz and Kilpinen (1997) we measured the vertical vibrations of the receiver's mesothoracic femur, close to the tibial joint.

For simultaneous recording, the beams of two identical Laser Doppler Vibrometers (Polytec, PDV100) were directed onto the bees' bodies using freely maneuverable mirrors (Fig. 2a). The output signals of both laser vibrometers were fed into a notebook (Gericom, Pentium IV, 2.4 GHz) using a 24 bit stereo-soundcard (Philips PSC 805) and the software Soundforge 7.0 (Sony Pictures Digital Inc.). Stereo recordings were made at a sampling rate of 44.100 Hz. The temporal pattern and frequency contents of the vibrations were analyzed using the software SpectraPro 3.32 (Sound Technology Inc.).

Due to the changing positions of the bees inside the recording box, the laser beams often were not oriented exactly at a right angle to the measured surface. However, the deviation was always less than 15° (Fig. 2a). In a control experiment the thorax vibrations of a bee were measured with two laser vibrometers at the same point

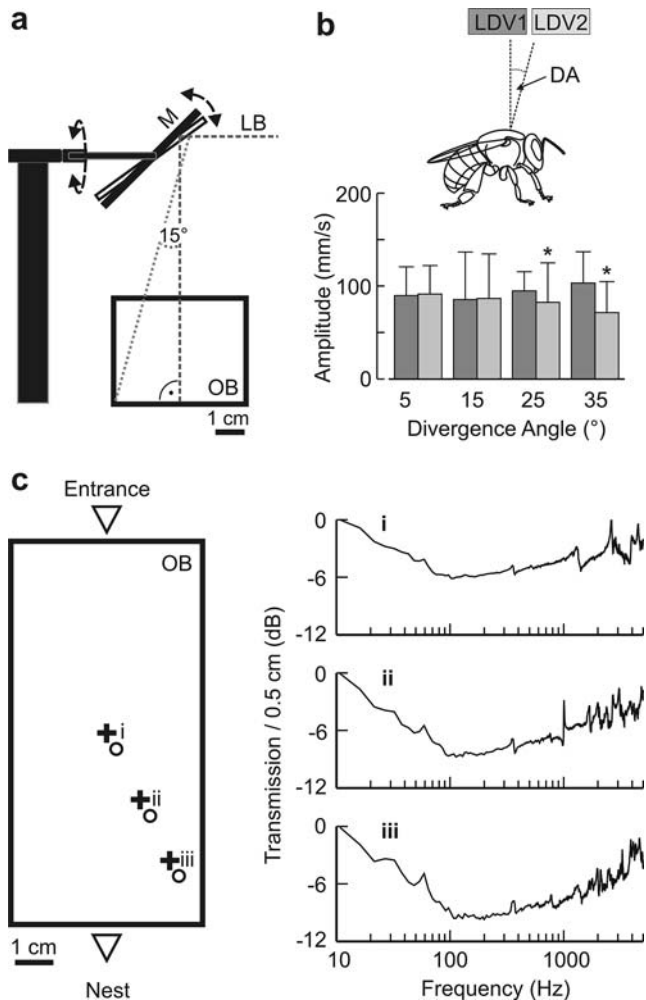


Fig. 2 Vibration recording in the observation box. **a** The beams (*LB* only one shown) of two Laser Doppler Vibrometers were directed onto the bees in the observation box (*OB*) using freely maneuverable mirrors (*M* only one shown). **b** Dark shaded bars velocity amplitudes (mean + SD) recorded with vertically oriented laser (LDV1); light shaded bars amplitudes recorded from same spot with slightly tilted laser beam (LDV2). *DA* divergence angle between laser beams; asterisks indicate significant difference between amplitudes (see text for statistics). **c** Vibration transmission by acrylic observation box (*OB*). Three examples (i–iii) measured at a distance of 0.5 cm (open circle) from the points where vibratory noise was introduced (cross). Attenuation values are 6–10 dB/0.5 cm for the frequencies relevant in the present study

of the thorax (3 bees, 108 vibration pulses). The beam of one laser vibrometer was oriented at 90°, whereas that of the other deviated from this angle by 5°, 15°, 25°, and 35°. The amplitudes of the two signals did not differ significantly as long as the divergence angle was smaller than 25° (divergence angle: 5°, paired *t* test: $t_{36} = -0.412$, $P = 0.683$; 15°, Wilcoxon signed-ranks test, $T_{36} = -73$, $P = 0.587$; 25°, $T_{22} = -134$, $P = 0.043$; 35°, $T_{10} = -62$, $P = 0.012$) (Fig. 2b). From this, we conclude that the velocity amplitudes of the vibrations recorded in the present study (laser beam divergence angles below 15°) can all be treated in the same way.

Analysis of vibration transmission

Vibrations at the measurement point closer to the source of vibration (thorax of a forager) are defined as “input”, whereas, those further along the transmission pathway are defined as “output”. To determine the transmission of the thorax vibrations the average amplitudes of simultaneously recorded vibrations were compared using either the paired *t* test (for normally distributed data) or the Wilcoxon signed-ranks test (not normally distributed data). The level of significance for differences was taken as $P \leq 0.05$. In the text, the data are presented as means \pm SD. Transmission in dB was calculated as $20 \times \log(\text{amplitude}_{\text{output}}/\text{amplitude}_{\text{input}})$. *N* refers to the number of trophallactic interactions, while *n* indicates the number of measured vibratory pulses.

To study potential changes in frequency transmission the spectra of simultaneously recorded signals were calculated using Fast Fourier Transformation (FFT). For each determined frequency within the spectrum, up to a frequency of 5 kHz, the transmission between the two simultaneously measured points was calculated (dB relative to the respective input).

To estimate the distortion of the foragers’ thorax vibrations along with its transmission through the substrate, we examined the transmission properties of the acrylic of the recording box. For this purpose, a vibratory noise containing frequencies between 10 Hz and 10 kHz (generated with software SpectraPro 3.32 on a second notebook, Pentium III, 800 MHz, 32-bit soundcard), was applied onto the observation box at different locations (Fig. 2c) using a vibrator (Ling Dynamic Systems, V101). The tip of the vibrator’s pestle was glued to the surface of the box with a drop of bees’ wax at a right angle. The vibrations were simultaneously registered directly beside the vibrator tip (input) and 0.5 cm away from it (output). A distance of 0.5 cm between input and output was chosen because of the measurement point on the substrate (*Su*) between the forager and the food receiver that was approximately 0.5 cm away from the legs (input) of the vibrating forager as well. In the range of particular interest (200–600 Hz, produced by foragers of *M. seminigra*) attenuation was more than 6 dB/0.5 cm by the acrylic of the observation box (Fig. 2c).

Temporal pattern of vibrations

To study the transmission of temporal patterns, the duration of single pulses (PD), the pulse sequence (PS), and the main frequency component (MFr) of the pulses were measured along the transmission channels (for details see: Hrncir et al. 2004a; Fig. 4). The degree of similarity between the two simultaneous recordings is indicated by the coefficient of correlation (Spearman rank correlation: $r_s = 0$, no similarity; $r_s = 1$, high similarity). *N* refers to the number of monitored trophallactic

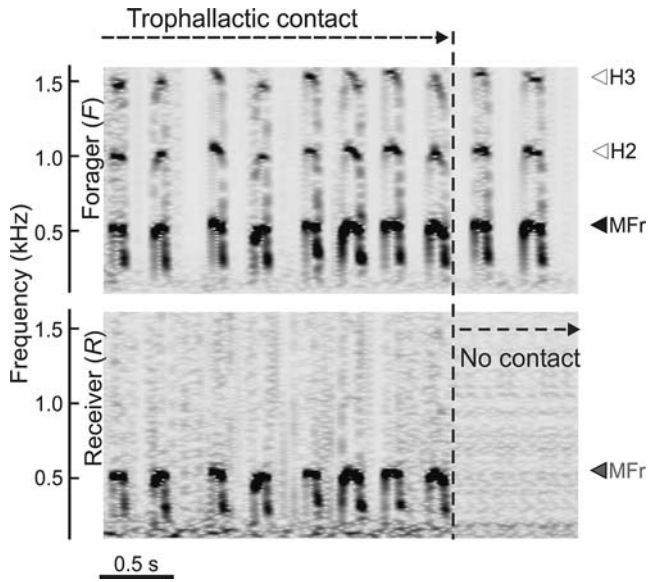


Fig. 3 Simultaneous recordings of thorax vibrations generated by a forager (*upper panel*) and of a food receiver (*lower panel*) during and shortly after a trophallactic contact. Note pulsed pattern in the forager’s “vibrogram”, typical of *Melipona* bees, the main frequency component (*MFr*) around 500 Hz and the first two harmonics (*H2*, *H3*).

interactions, while *n* indicates the number of measured vibratory pulses.

Results

Two experiments (six different foragers, 28 trophallactic contacts) focused on the question whether the forager

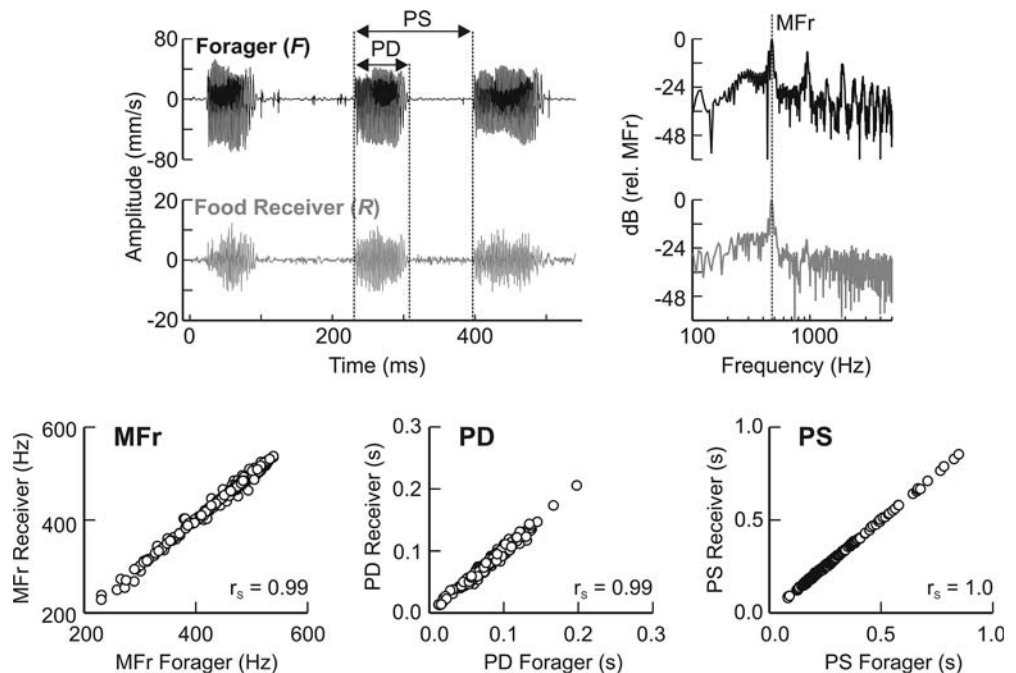
vibrations are transmitted directly onto the food receiving bees, and whether they are exclusively transmitted during the physical mouth-to-mouth contacts. Indeed, during the trophallactic contacts, the bodies of the foragers and of the respective food receivers vibrated synchronously. When the direct contact between the two bees broke up, vibrations could still be measured on the foragers’ thorax. The body of the food receivers, however, fell “silent” (Fig. 3). The vibrations generated by the foragers clearly induce vibrations of the food receivers’ bodies, but exclusively during mouth-to-mouth contacts, even if the food receiver remains close to the vibrating forager.

Vibration transmission by direct contact

On their way from the thorax of the forager (*TxF*) to that of the food receiver (*TxR*) vibrations were attenuated by about 17 dB (average velocity amplitude: *TxF*: 69.2 ± 19.1 mm/s, *TxR*: 9.75 ± 2.70 mm/s; Wilcoxon signed-ranks test: $T = -351$, $P < 0.001$; attenuation: 17.2 ± 2.63 dB; two different experiments, six foragers, $N = 26$, $n = 367$) (Fig. 5a). Whereas, frequencies above 180 Hz were attenuated by more than 6 dB (1/2 of the original value), those above 700 Hz were attenuated by more than 12 dB (1/4 of the original value) (Fig. 6a). However, the main frequency component as well as the temporal pattern of the pulsed vibrations did hardly change (main frequency: $r_s = 0.991$; pulse duration: $r_s = 0.986$; pulse sequence: $r_s = 0.998$; $N = 26$, $n = 367$) (Fig. 4).

To determine where the vibrational signal is attenuated most, we registered it simultaneously at various points along the pathway (Fig. 5). The comparison of

Fig 4 Vibration transmission by direct contact. *Top* Typical example of simultaneous recordings from the thorax of a forager and a receiver. *Bottom* Comparison of the vibrations recorded from the forager’s thorax and from the receiver’s thorax. Note similarity of main frequency component (*MFr*) and the temporal pattern of the vibrations (pulse duration *PD*; pulse sequence *PS*) (coefficient of correlation $r_s \sim 1$)



the vibrations simultaneously measured on a forager's thorax (Tx F) and its head (He F) showed that there was no difference in the amplitude between these points (velocity amplitude: Tx F : 78.5 ± 12.7 mm/s, He F : 84.4 ± 22.3 mm/s; paired t test: $t_6 = -0.676$, $P = 0.52$; amplification: 0.49 ± 2.10 dB; one experiment, three foragers, $N = 7$, $n = 99$) (Fig. 5b). As expected, the vibrations were strongly attenuated between the forager's head (He F) and the receiver's head (He R) by about 12 dB (velocity amplitude: He F : 71.9 ± 16.8 mm/s, He R : 18.9 ± 5.66 mm/s; paired t test: $t_5 = 7.649$, $P < 0.001$; attenuation: 12.0 ± 3.23 dB; one experiment, three foragers, $N = 6$, $n = 91$) (Fig. 5c). The frequency transmission between the bees' heads resembled the transmission between their thoraces. Frequencies above 180 Hz were attenuated by more than 6 dB, frequencies above 700 Hz were attenuated by more than 12 dB (Fig. 6b). This indicates that the low pass filtering observed between the thoraces of the sender and receiver bee actually occurred between the two bees' heads. The vibrational signal was further attenuated by about 5 dB between the receiver's head and its thorax (velocity amplitude: He R : 18.5 ± 5.03 mm/s, Tx R : 10.1 ± 2.12 mm/s; paired t test: $t_{11} = -7.627$, $P < 0.001$; attenuation: 5.14 ± 1.56 dB; one experiment, three foragers, $N = 12$, $n = 191$) (Fig. 5d).

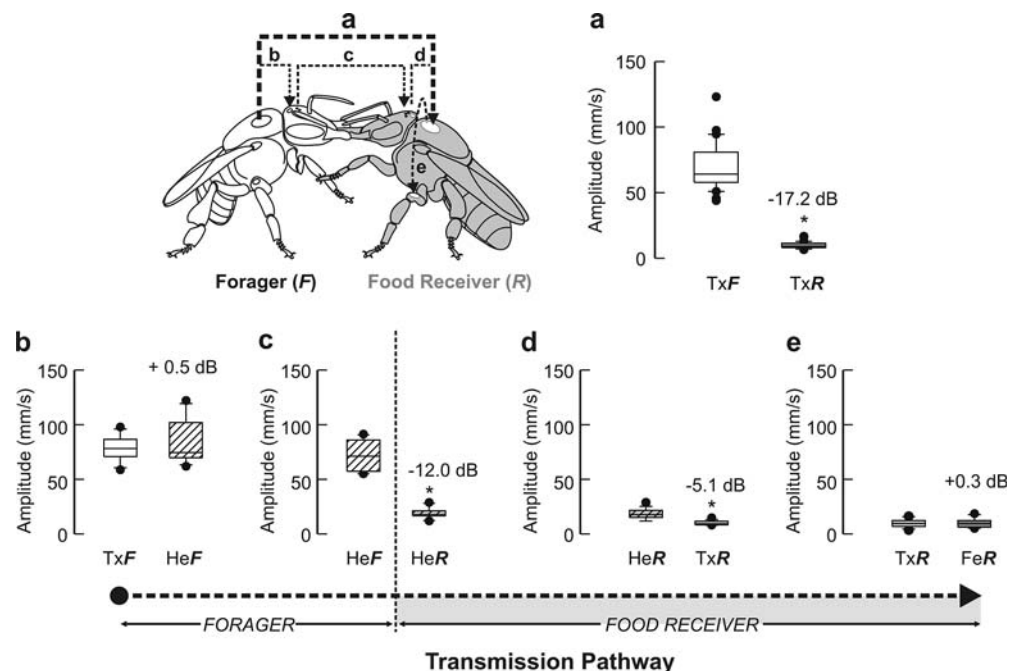
We compared the vibration of the food receiver's thorax (Tx R) and that of its femur (Fe R) in order to determine, how much of a forager's vibratory signal may reach the subgenual organ, which is likely to be the bee's most sensitive vibration receptor. Surprisingly, the vibrational signal did not change (average velocity amplitude: Tx R : 9.66 ± 3.91 mm/s, Fe R : 9.96 ± 4.54 mm/s; paired t test: $t_{11} = -0.373$, $P = 0.716$; amplification: 0.27 ± 3.05 dB; two experiments, six foragers, $N = 12$,

$n = 278$) (Fig. 5e). Accordingly, between the thorax of the forager (Tx F) and the femur of a receiver (Fe R) the vibrations were attenuated by a total of about 18 dB (velocity amplitude: Tx F : 70.3 ± 18.8 mm/s, Fe R : 9.40 ± 2.46 mm/s; paired t test: $t_{14} = 12.17$, $P < 0.001$; attenuation: 17.8 ± 4.40 dB; two experiments, six foragers, $N = 15$, $n = 292$).

Vibration transmission to the substrate

To estimate how much of the forager's thorax vibrations were transmitted to the food receivers through the substrate, we examined them at the forager's thorax (Tx F), the foragers' legs (measure point: femur, close to the tibial joint, Fe F) and on the substrate (Su) (Figs. 7, 8). Similar to the vibration transmission found between the food receiver's thorax and its legs (see above), the vibrational signal did not change in velocity amplitude on its way from the forager's thorax to its leg (average velocity amplitude: Tx F : 72.7 ± 16.0 mm/s, Fe F : 83.1 ± 30.3 mm/s; paired t test: $t_{17} = -1.535$, $P = 0.143$; amplification: 0.76 ± 3.17 dB; three experiments, nine foragers, $N = 18$, $n = 417$) (Fig. 8b). However, the vibrational signal was strongly attenuated when transmitted from the forager onto the substrate. Between the measurement point on the forager's femur (Fe F) and the substrate halfway between forager and food receiver (Su) attenuation was more than 48 dB (average velocity amplitude: Fe F : 82.4 ± 11.2 mm/s, Su : 0.40 ± 0.28 mm/s; paired t test: $t_{17} = 31.191$, $P < 0.001$; attenuation: -48.3 ± 6.18 dB; one experiment, three foragers, $N = 18$, $n = 126$) (Fig. 8c). Attenuation between the thorax of the forager (Tx F) and the substrate (measuring point: about halfway between forager and food receiver) amounted to

Fig 5 a–e Vibration transmission during trophallaxis. **a** Comparison of velocity amplitudes (boxplot) of the vibrations recorded from both the forager's thorax (Tx F) and the receiver's thorax (Tx R). **b–e** Transmission pathway in more detail: Boxplots of velocity amplitudes simultaneously measured on the forager's thorax (Tx F) and its head (He F), from the forager's head and the food receiver's head (He R), from the food receiver's head and its thorax (Tx R), and from the food receiver's thorax and its femur (Fe R). Asterisks indicate significant differences (see text for details on statistics)



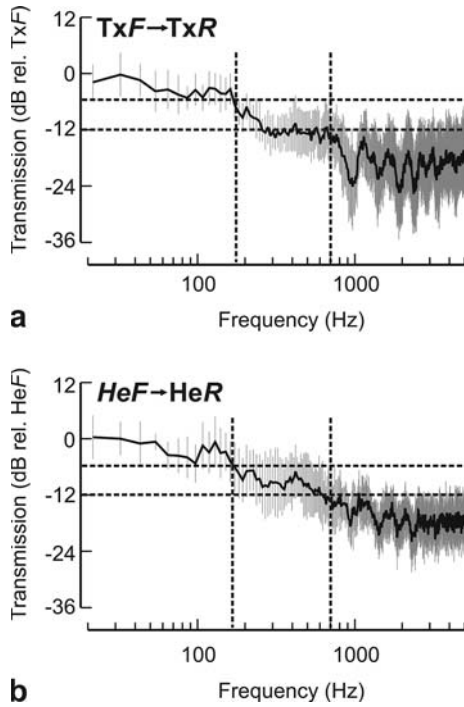


Fig. 6 Low pass filtering mainly occurred between the head of the forager and the head of the food receiver. **a** Transmission between the forager’s thorax (*TxF*) and the receiver’s thorax (*TxR*), **b** transmission between the forager’s head (*HeF*) and the receiver’s head (*HeR*). Graphs each represent mean \pm SD of ten trophallactic interactions

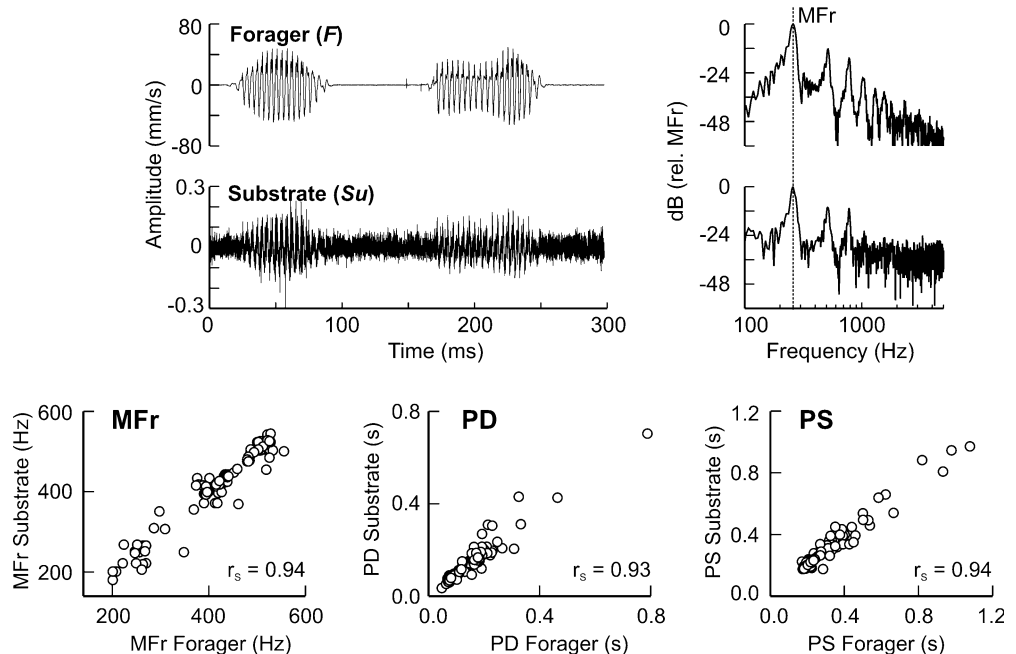
about 47 dB (average velocity amplitude: *TxF*: 70.9 ± 12.5 mm/s, *Su*: 0.34 ± 0.13 mm/s; paired *t* test: $t_{17} = 24.043$, $P < 0.001$; attenuation: 47.3 ± 3.69 dB; two experiments, six foragers, $N = 18$, $n = 193$) (Fig. 8a). The analysis of frequency transmission between the forager’s

thorax and the substrate showed that the strongest attenuation occurred at frequencies between 200 and 900 Hz (Fig. 9a). The main frequency component and the temporal pattern of the vibrations measured on the substrate were very similar to those simultaneously generated by the forager’s thorax (main frequency: $r_s = 0.940$; pulse duration: $r_s = 0.933$; pulse sequence: $r_s = 0.935$; $N = 7$, $n = 108$) (Fig. 7).

Discussion

In the present study, we describe a highly efficient way to transmit forager vibrations onto hive bees during trophallactic contacts in stingless bees (Figs. 3–5; Table 1). Judging from the data for honey bees, the food receivers are indeed capable of perceiving the forager’s thorax vibrations. In honey bees, the reception of substrate vibrations has been predominantly attributed to the subgenual organ (Autrum and Schneider 1948). When studied electrophysiologically, its sensory cells showed the highest sensitivity to vertical vibrations of the leg at frequencies between 150 and 900 Hz, with an average response threshold between 0.06 and 0.15 mm/s peak-peak (Kilpinen and Storm 1997; Rohrseitz and Kilpinen 1997). Assuming similar properties for the subgenual organ in stingless bees, the vibrations of the food receivers during trophallaxis measured in the present study (~ 10 mm/s) were well above the threshold of their subgenual organs. Essentially, these vibrations did not result from substrate vibrations. Thorax vibrations of the foragers (~ 70 mm/s) were attenuated by almost 50 dB on the way to the substrate (~ 0.3 mm/s). An additional attenuation by 5 dB on the way back from the substrate to the receiver’s femur (honey bees:

Fig 7 Vibration transmission through the substrate. *Top* Typical example of simultaneous recording from the thorax of a forager and the substrate close to the forager’s leg. Note difference of velocity scales. *Bottom* Comparison of the vibrations of the forager’s thorax and of the substrate. *MFr* Main frequency component; *PD* pulse duration; *PS* pulse sequence



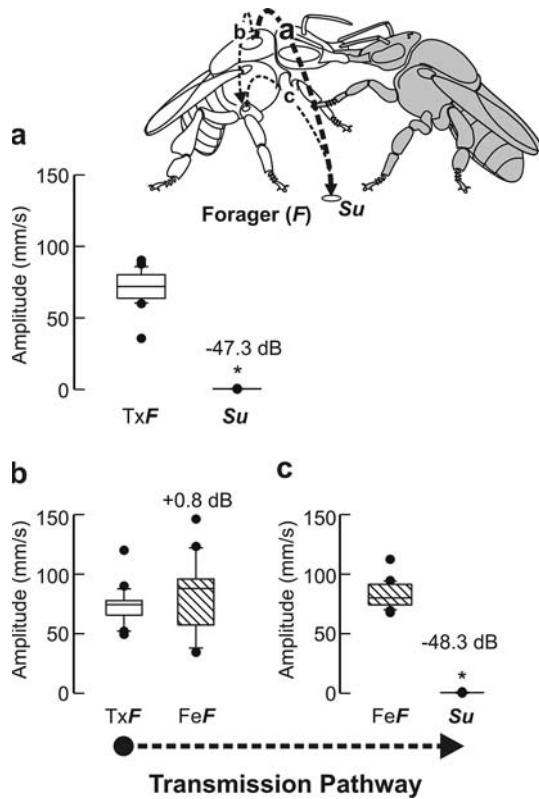


Fig. 8 Vibration transmission to the substrate. **a** Comparison of the velocity amplitudes (*boxplot*) of the forager's thorax (*TxF*) and of the substrate (*Su*) close to the forager's leg. **b, c** Details of the vibration transmission from the forager's thorax (*TxF*) to its femur (*FeF*) and from there to the substrate (*Su*). Data from simultaneous recordings are presented as *boxplots*; *asterisks* indicate significant differences between the measurements (see text for details on statistics)

Rohrseitz and Kilpinen 1997) would result in oscillation amplitudes of about 0.2 mm/s only. This is much less than the value actually measured during trophallaxis (~10 mm/s).

The subgenual organs are not the only vibration receptors in bees (Sandeman et al. 1996). An additional receptor had its highest sensitivity at low vibration frequencies between 20 Hz and 100 Hz, with a displacement threshold of about 2 μm (corresponding to a velocity threshold between 0.5 and 1.5 mm/s at these frequencies; calculated from Sandeman et al. 1996). The receptor organ has not been identified yet but was suggested to be one of the other three chordotonal organs found in the femur, tibia, and tarsus of each leg (Snodgrass 1956). In addition, a pair of small fusiform chordotonal organs in the head of honey bees as well as campaniform sensilla on the legs and head potentially serve as vibration detectors (Snodgrass 1956).

Likewise, the food receivers' antennae may detect the vibrations directly transmitted during trophallaxis. Honey bee antennal flagella resonate at frequencies close to 300 Hz when the head of the bee is moved dorso-ventrally (Heran 1959). Johnston's organ in the antennal

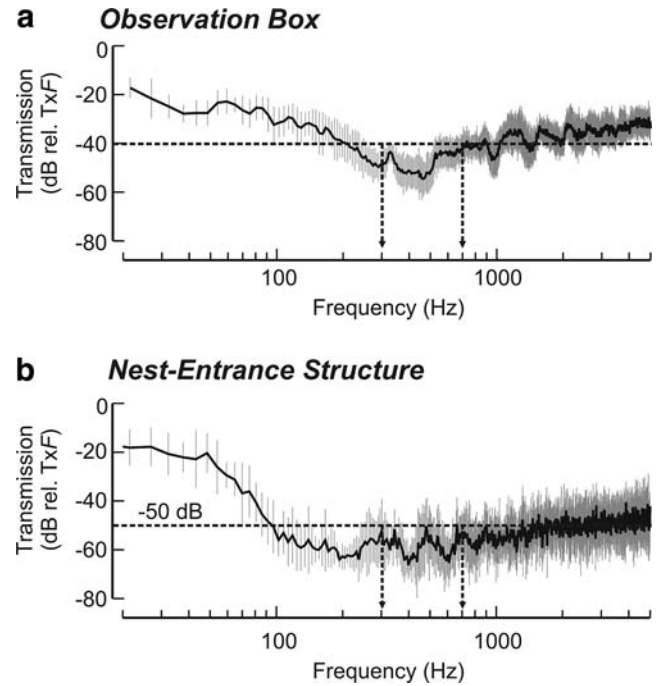


Fig. 9 Frequency transmission between the thorax of the forager and the substrate close to the forager's leg. **a** Acrylic material of the observation box; note attenuation by more than 40 dB (mean \pm SD of 10 different trophallactic events) between 200 and 600 Hz. **b** Batumen of a nest-entrance; note attenuation by more than 50 dB (mean \pm SD of 12 vibrating bees) between 200 and 600 Hz

pedicel (McIndoo 1922; Snodgrass 1956) is most sensitive at oscillation frequencies around 350 Hz with a displacement threshold of the tip of the flagellum of about 13 μm (~29 mm/s at 350 Hz); (Heran 1959). During trophallactic food transfers in honeybees, both donor and receiver bees show rapid antennal movements with a stroke frequency of about 13 Hz once the oral contact is established (Goyret and Farina 2003). Due to similar movements in *M. seminigra* it was impossible to properly monitor the antennal vibrations during trophallaxis in the present study. However, if we assume that Johnston's organ of stingless bees has physiological properties similar to those in honey bees, the perception of the food receiver's vibration with this organ is a reasonable possibility.

Although all measurements of the present study were made in an acrylic observation box, the vibration transmission under natural conditions within the nest seems to be very similar. In preliminary experiments on the vibration transmission properties of stingless bee nests we found that vibrations in the biologically relevant frequency range (200–600 Hz) are attenuated by the nest material as much or even more than by the acrylic material of the observation box. Specifically, close to the entrance of a nest of *M. seminigra*, where most of the trophallactic interactions between foragers and hive bees occur on particular structures made of batumen, attenuation was found to exceed 50 dB

Table 1 Vibration transmission during trophallaxis

	Forager			Food Receiver		Substrate	
	TxF	HeF	FeF	HeR	TxR	Su	
Direct Transmission	69.2 ± 19.1			→		9.75 ± 2.70	
	78.5 ± 12.7		▶	84.4 ± 22.3			
			71.9 ± 16.8	→		18.9 ± 5.66	
				18.5 ± 5.03		▶	10.1 ± 2.12
						9.66 ± 3.91	▶
	70.3 ± 18.8			→		9.40 ± 2.46	
Transmission to Substrate				82.4 ± 11.2		→	0.40 ± 0.28
	70.9 ± 12.5			→			0.34 ± 0.13
Total	73.1 ± 22.3	78.6 ± 20.2	82.4 ± 11.2	18.6 ± 5.07	9.72 ± 3.11	9.60 ± 4.03	0.37 ± 0.18

Given are mean ± SD of simultaneously measured velocity amplitudes (mm/s) (one pair per line), as well as total mean ± SD of each point calculated from all data. Points of measurement were: *TxF* thorax of forager; *HeF* head of forager; *FeF* femur of forager; *HeR* head of food receiver; *TxR* thorax of receiver; *FeR* femur of receiver; *Su* substrate between forager and receiver

between the thorax of the bee and the substrate less than 1 cm away from the bee (Fig. 9b).

Advantages of vibration transmission by direct contact

In the recruitment process of honey bees, trophallactic food transfer is an important means of communication between individuals (Farina 1996; Hart and Ratnieks 2001). During the food exchange, hive bees receive information about the sugar concentration, the nectar secretion rate, and the odor of a food source (Farina and Núñez 1991; de Marco and Farina 2003; Gil and Farina 2003). In stingless bees, trophallaxis is poorly investigated, but has been proposed to serve similar purposes as in honey bees (Hart and Ratnieks 2002).

The advantages of receiving vibratory signals that potentially contain information on the net profitability or perhaps even on the distance of a food source during trophallaxis are the following. (1) The vibratory input received during direct contact with the forager by far exceeds the vibratory stimulation through the substrate (compare Figs. 5 and 8; Table 1). Bees in the immediate vicinity of the vibrating forager but not touching it will be able to detect these substrate vibrations despite their small amplitude. Assuming the threshold of their subgenital organ to be similar to that of the honey bee (0.06–0.15 mm/s) the range of a just noticeable forager vibration would be between 10 and 15 mm. However, it will be difficult for receiver bees to extract information from these substrate vibrations as soon as two or more foragers returning from different food sources are within

the perceptive range. As soon as a hive bee has direct trophallactic contact with the forager, the vibratory input it receives will drastically exceed stimulation through the substrate. Any information about a single food source will then be easily recognized by its strength. (2) Food receivers get multiple information about the food source during trophallaxis. In addition to the gustatory input, which reflects the sugar concentration, and the odor of the collected food (Gil and Farina 2003), the receiver bee simultaneously gains information on the profitability (Hrnčir et al. 2004a, b) of this very food source through direct vibration transfer. As has been proposed for meliponine bees (*M. fasciata*, *M. beecheii*: Biesmeijer et al. 1998), information about the profitability of a food source greatly influences the decision of potential recruits whether to forage or not.

A crucial question pertaining to the information transmission during trophallaxis is, whether potential recruits do indeed have trophallactic contacts with the foragers, or whether this is restricted to hive bees with food unloading and storing tasks only. It has been shown in *M. quadrifasciata* and *M. seminigra* that prospective recruits indeed engage in trophallactic contacts with the foragers before they leave the nest to collect at an advertised food source (Hrnčir et al. 2000; Kronberger 2000). The number of such food transfers even increased shortly before the prospective recruits left the nest (*M. quadrifasciata*: Hrnčir et al. 2000; *M. seminigra*: Kronberger 2000).

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