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Source: *Behavioral Ecology and Sociobiology*, Vol. 18, No. 3 (1986), pp. 207-212

Published by: [Springer](#)

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Sound and vibrational signals in the dance language of the honeybee, *Apis mellifera*

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Received March 4, 1985 / Accepted June 10, 1985

Summary. Sound and vibrational signals exchanged by honeybees during the performance of wagging dances were simultaneously recorded by means of a microphone and a laser vibrometer. Previous descriptions of the 280-Hz sounds emitted by the dancing bee were confirmed, and no vibrational (substrate-borne) component could be detected. In contrast, the 320-Hz “begging signals” (emitted by bees following a dancer and used as a request for food samples from the dancer) do vibrate the comb with peak–peak displacement amplitudes up to 1.5 μm . Artificially-generated comb vibrations of sufficient amplitude cause bees standing on the comb to “freeze”. The threshold for obtaining a detectable freezing response was measured for frequencies between 100 Hz and 3 kHz. At 320 Hz it is just below the amplitude of the natural begging signals. Thus it seems likely that these signals are received by the bees as vibrations of the comb. The propagation velocity of waves, damping, and mechanical input impedance of honeybee combs were studied. These results, combined with the observed amplitudes of the begging signals, support the assumption that the begging signals are generated with the flight muscles. The begging signal propagates as a bending wave. The attenuation of the begging signal with distance is relatively small, so the amplitude of the signal probably needs to be carefully adjusted in order to restrict the range of the communication.

Introduction

In the wagging dance, honeybees (*Apis mellifera*) inform their nestmates of the distance and direction of food sources. The direction with respect to the sun’s azimuth is indicated by the direction

of the wagging run relative to gravity. Distance is indicated by the duration of the wagging run (von Frisch 1965). It is still not known how the bees following the dancer (the followers) detect the information in the wagging dance. Visual detection is unlikely since the bees normally dance in the dark. Because the followers seem to try to touch the dancer with their antennae, tactile detection seems a reasonable possibility (von Frisch 1923). Furthermore, silent dances are not successful in the recruitment of nestmates, which may suggest an acoustical component in the dance communication (Esch 1963). Towne (1985) recorded the dance sounds of three Asian honeybee species and found dance sounds similar to those of *Apis mellifera* only in *Apis cerana*, which is also a cavity nester; he concludes that sound is important in the cavity nesters because the dance communication takes place in the dark.

The dance sound might be received by followers as airborne sound or substrate-borne vibration. Attempts by von Frisch (1923) and Hansson (1945) to obtain behavioral reactions of bees to airborne sound were unsuccessful. On the other hand, the subgenual organs in the legs are highly sensitive to vibrations (Autrum and Schneider 1948), and bees readily react to artificial vibrations. They immediately stop and ‘freeze’ if the comb is vibrated (Hansson 1945; Frings and Little 1957; Gould 1975).

Communication by vibration has been reviewed by Markl (1983). In stingless bees (Meliponinae), Lindauer and Kerr (1958) showed that alerting sound signals emitted by returning foragers are effective only if transmitted through the substrate. Another acoustical signal in the dance language of honey bees is produced by the followers (Esch 1963). The “begging signal”, a short squeaking sound, may cause the dancer to inter-

rupt her dance, allowing the follower to approach the dancer for food (von Frisch 1965). Esch (1964) replayed begging sounds recorded on tape into the hive and observed that all the bees became motionless if the sound was of very high intensity or was transmitted through the substrate. This left open the possibility that airborne sound is also involved.

In the present study, the vibrations of the comb near dancing and begging bees and the concomitant airborne sounds were simultaneously recorded by means of a laser vibrometer and a pressure-sensitive microphone, respectively. In addition, artificially-generated vibrations were used to analyze the mechanical properties of combs and to measure the absolute thresholds for the freezing response over a wide range of frequencies.

Methods

The experiments were performed with bees of the Italian race, *Apis mellifera ligustica*, in Odense, Denmark. A small colony was housed in an observation hive as described by von Frisch (1965). One of the glass windows of the hive was replaced by a wire lattice. To prevent overcooling, this side was illuminated by an infrared lamp. A group of marked forager bees was trained to visit a feeding station 120 m from the hive entrance.

The vibrational velocity of the comb surface was measured by means of a laser vibrometer, which detects Doppler shift in the light reflected from the vibrating surface (see Michelsen and Larsen 1978). The laser beam was focused to a diameter of 30 μm on a small amount of highly reflecting paint on the comb surface. A small cage attached to the wire lattice (but without contact with the comb) prevented the bees from passing through the laser beam. Airborne sound was recorded with a pressure microphone (Sennheiser MD 321 N) connected to an amplifier (Brüel & Kjaer 2604). Most of the signals were stored on a tape recorder (Hewlett Packard 3960) for further processing. A Fast Fourier Transform (FFT) spectrum analyzer (Hewlett Packard 3582) and a computer (HP 85) were used for further signal analysis.

For the analysis of the mechanical properties of the comb artificial vibrations were generated and analysed as described by Michelsen et al. (1982). A small magnet glued to the comb's surface was moved by an electromagnet 2 mm away. The force acting on the comb was estimated by measuring the force on the magnet when attached to a force transducer (DISA 51D17) and vibrated by the electromagnet at the same distance. Artificial vibrations simulating begging signals were transmitted to the comb in the observation hive through a short rod fastened to a vibration exciter (Brüel and Kjaer 4810). A pulse generator was used to simulate the pulsed nature of the natural begging signals. The vibrational stimuli were monitored as described above.

Results

Dance sounds and vibrations

The dance sounds consist of a train of 20 msec pulses, carried mainly by 250–300 Hz (Fig. 1). The peak sound pressure level at a distance of 1–2 cm

from the bee is about 73 dB (relative to 2×10^{-5} N/m²). In the simultaneously-recorded comb vibrations there is no sign of any vibrational components of the dance sounds in either in the time records (Fig. 1A) or the frequency spectra (Fig. 1B). Furthermore, we could not hear any dance sounds when listening to vibration recordings amplified and emitted from a loudspeaker as sound.

The begging signals emitted by the followers may last up to 100 ms (Fig. 2A). The amplitude spectra of both the airborne sounds and the comb-transmitted vibrations show peaks at the fundamental and higher harmonics of 320 Hz (Fig. 2B). The maximum (peak–peak) vibrational velocity amplitude is about 3 mm/s, corresponding to a 1.5 μm displacement amplitude at 320 Hz. In the frequency range 0–1,000 Hz, the amplitude of the vibrational background “noise” is a factor of 3–4 below the signal (Fig. 2A). Around 320 Hz, however, the background level is lower than the signal by at least a factor of 10 (= 20 dB, Fig. 2B).

Vibrations of the comb cause the bees immediately to “freeze”. If the amplitude is great enough, all the bees on the comb remain absolutely motionless as long as the comb is vibrated. The minimum response accepted as suprathreshold in this study was that some bees in a marked area (where the exact vibrational amplitude was known) froze when the vibrational pulse was given. The threshold curve in the frequency range from 200 to 3,000 Hz, measured within the hive against the background of the natural vibrational “noise”, is shown in Fig. 3. At 100 Hz, we tested vibrational displacements up to 90 μm without observing a freezing response (the only observable reaction was an audible wing beating). A preferred frequency is found at 300–400 Hz when the threshold curve is plotted as the vibrational acceleration (Fig. 3A). Above 400 Hz, the threshold increases about 20 dB per decade, i.e. the threshold remains constant in terms of vibrational velocity (Fig. 3B). The threshold decreases with frequency when plotted as vibrational displacement (Fig. 3C).

Some physical properties of the combs

Honeybee combs are very complicated structures. New combs consist only of wax, but old combs also contain several other materials (including faeces and cuticle from larvae and pupae). The geometry of the comb cells is surprisingly uniform, but different kinds of cells are made for workers and drones. Queen cells, holes and other irregularities may interrupt the uniform shape. Wild honeybees' combs are often attached to some solid

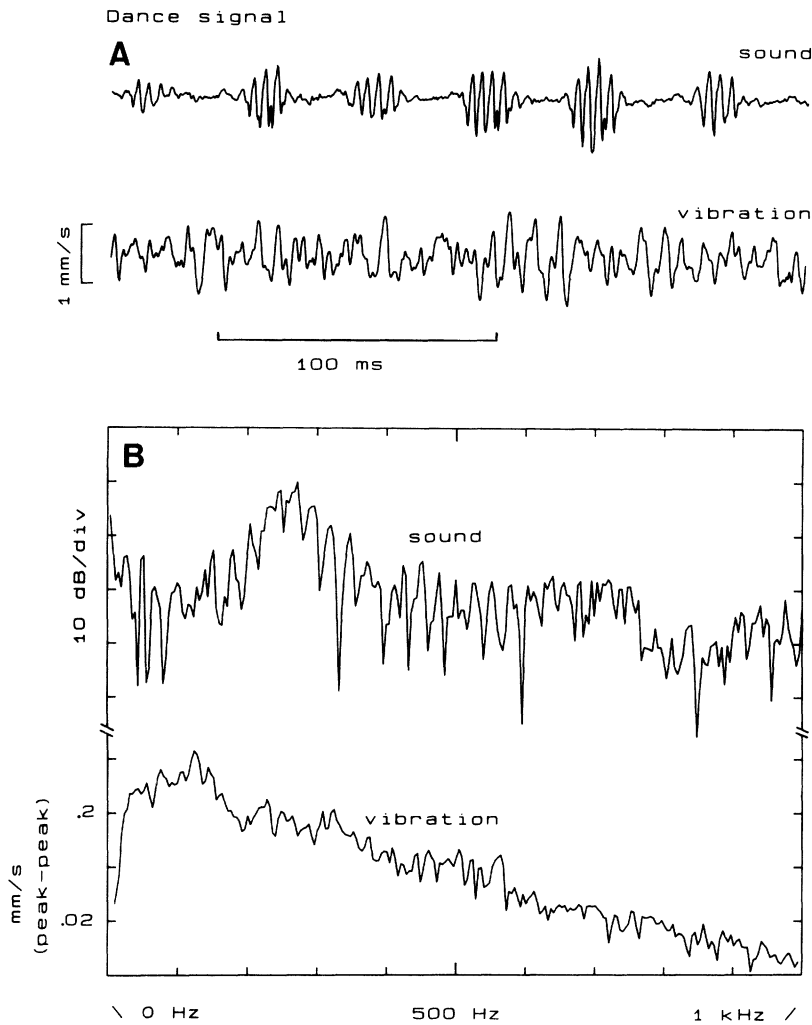


Fig. 1 A, B. Dance signal.

A Time-functions and **B** amplitude spectra of airborne sound pressure and comb vibration velocity measured a few cm from the dancing bee. The vibration spectrum shown is the average of several recordings during the emission of dance signals

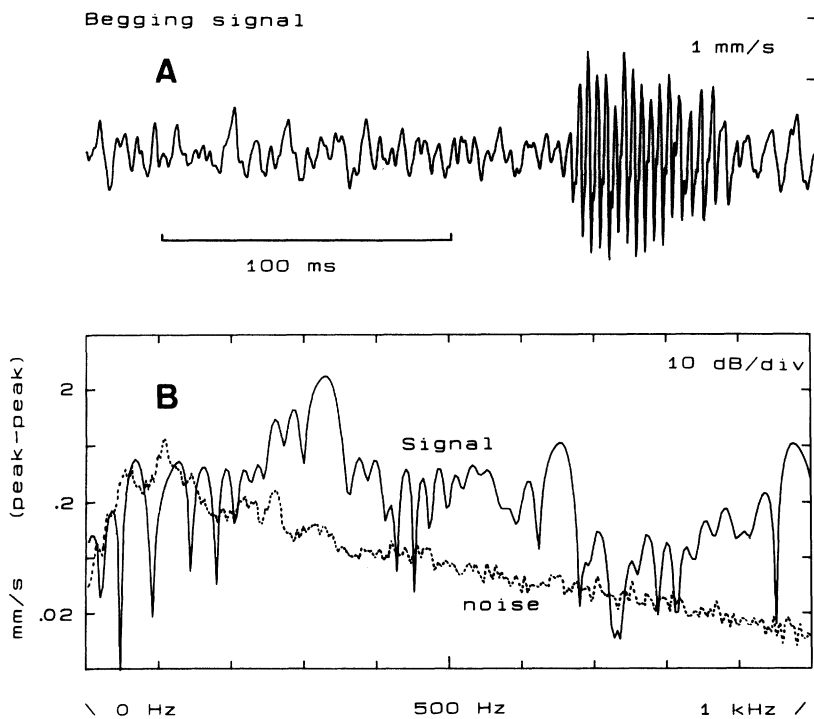


Fig. 2 A, B. Begging signal.

A Time-function and **B** amplitude spectrum of the comb vibration velocity measured a few cm from the begging bee. For comparison, the average background vibrational noise spectrum is indicated (dotted line). Time window for computation of spectra: 50 ms

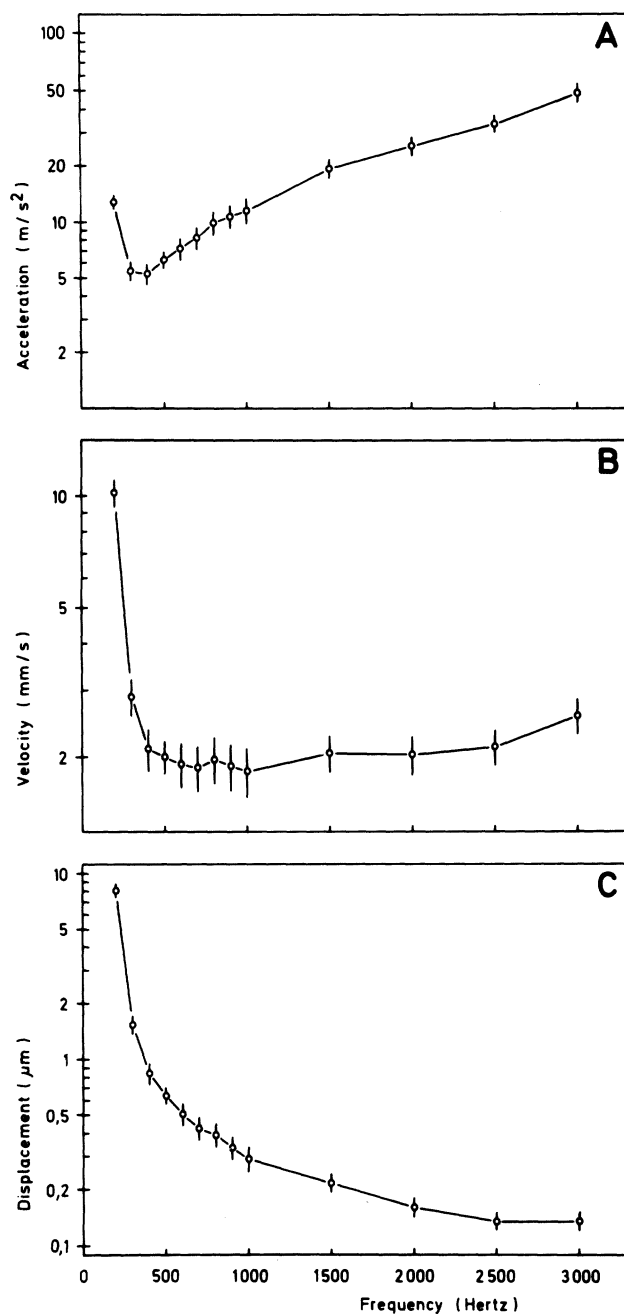


Fig. 3A–C. Freezing response. Threshold curves indicated as (peak–peak) A acceleration, B velocity, and C displacement of the comb

material only at one end, whereas domestic honeybees are forced to use rectangular wooden frames. Furthermore, the cells may be empty or contain eggs, larvae, pupae, honey or pollen. In the present study, no attempts were made to investigate this complex situation in any detail. We measured the properties of only two combs: a 20×40 -cm rectangular comb framed in the usual manner with wood, which had been used in a

beehive for 2 years, and a new “wild” comb of more irregular shape (about 29×19 cm) attached at one of the shorter ends to a piece of wood. The latter comb contained only drone cells. Both combs had empty cells.

The physical properties of interest here are the approximate propagation velocity of substrate-borne waves, the attenuation with distance from the point of emission, and the mechanical input impedance of the comb. This impedance is the ratio between the force acting on the comb (the vibrational force from the calling bee) and the velocity of the emitted begging signal. Force, velocity, and impedance have complex values (i.e. they have both an amplitude and a phase angle), but in this analysis we calculate only the ratio between the amplitudes. We are interested in determining the impedance, because it can be used for estimating the amount of power needed by bees for emitting their substrate-borne signals.

The combs were vibrated with a small magnet so as to emit waves while interacting minimally with the comb's freedom to vibrate. The sinusoidal forces used were in the range 0.4–12 mN, (peak values). Both combs behaved as linear systems when activated with such forces, i.e. the velocities measured with the laser vibrometer and caused by 4 mN were about 10 times larger than those caused by 0.4 mN. Most measurements were done with a force of 1.2 mN. The vibrations observed with such a standard force varied greatly in amplitude, both with frequency and with the position of the magnet on the combs. The velocity amplitude is about five times smaller at 1–3 kHz than at 100–300 Hz, i.e. the impedance increases with frequency. (Note that we are comparing the velocity amplitudes; the displacement amplitudes vary by a factor of about 50, because the displacement amplitudes corresponding to a constant velocity amplitude decrease with frequency.)

At the middle of the wooden-framed comb, the input impedance for a 300-Hz vibration was about 20 Ns/m. At the end of the “wild” comb opposite the piece of wood the impedance was about ten times smaller. This is similar to the differences observed between plant stems and the ends of the branches or leaves (Michelsen et al. 1982). At such positions at the edge of a solid substrate the animals can make large amplitude vibrational signals with little muscular power, but the amplitudes decrease rapidly as the signals propagate to areas with higher impedance.

The “wild” comb was used to approximate the propagation velocity and attenuation at frequencies between 100 Hz and 3 kHz. The wild

comb is not ideal for such measurements since the impedance changes along the path of propagation. A normal wooden-framed comb would be worse, however, since the emitted waves would be reflected from all four sides of the frame, creating complicated vibrational patterns. A short pulse consisting of 2–3 sinusoids was emitted at the free end of the wild comb, and the amplitude and time of arrival of the reflected wave was measured. The distance to the wood was 29 cm, i.e. the total distance was 58 cm. The propagation velocity was found to be about 50 m/s at 300 Hz and to vary with frequency in the way expected for bending waves, that is the propagation velocity is proportional to the square root of frequency. At low frequencies (100–300 Hz) the reflected wave was not much smaller than the emitted wave, but at 1 and 3 kHz a substantial attenuation was evident.

The amplitude of vibration at a certain spot on a framed comb depends not only on the distance to the source, but also on the positions of the source and receiver relative to the frame. The positions of the nodes and antinodes also depend on frequency, and the attenuation with distance cannot be accurately determined. As an approximate rule, the amplitude of 300 Hz (begging) signals is about halved for each 10 cm of propagation (similar values were found by Fuchs and Koeniger 1974). A short signal consisting of a few sinusoids of 300 Hz may be followed by a “tail” of reflected waves, lasting 50 ms or more (see Fig. 7 in Michelsen et al. 1982).

Discussion

No substrate-borne components were found in the dance sounds. Of course, we cannot exclude the possibility that some vibration is transmitted in the comb, but it is very unlikely that the follower bees can detect such a signal buried in the background noise. Our ears are narrowly tuned both in frequency and time, yet our ears are unable to detect any dance sounds when we listen to the vibration records. It therefore seems safe to conclude that the dance sounds are carried exclusively through the air.

In contrast, the begging signal produced by the followers is transmitted as vibrations through the comb. A few centimetres from the begging bee (i.e., at the distance of the dancer) the vibration amplitude is well above the background vibration (Fig. 2). Further, the threshold curve for the “freeze reaction” (Fig. 3) and the observed vibrational amplitude of the begging signals suggest that the bees should be able to detect the begging sig-

nals against the normal background vibration in the beehive. The reaction can be induced over a broad frequency range. Although some role for an airborne component can still not be ruled out entirely, these data indicate that the comb vibrations are probably sufficient to explain the freezing reactions elicited by the natural begging signals.

The attenuation with distance at the begging signal's fundamental frequency (320 Hz) is small compared to the size of the comb, so the amplitude of the begging signal should be limited if only neighbouring bees are to receive the message. This may explain why the amplitude of the signals is just barely above the response threshold at 320 Hz. Since the higher frequency components of the begging signals are less intense than the fundamental (Fig. 2) and attenuate more with distance, the higher frequencies can probably be neglected in this regard.

From the measured input impedance of the comb and the observed vibrational amplitude of the begging signal, one can calculate the power needed for emitting these vibrations (for details see Michelsen et al. 1982). The power input P is given by the equation: $P = Z \times v^2$ where Z is the input impedance of the comb and v the (root mean square) velocity of movement. Inserting our values we find a power input of about 0.02 mW, which corresponds to the power produced by about 0.3 mg of muscles (assuming a power of 70 W/kg muscle at 30° C, see Jensen 1956). Some energy is probably lost in the process of converting muscular energy to vibrations of the comb. Furthermore, in combs filled with e.g. larvae or honey more energy would be needed for producing begging signals with amplitudes above the threshold for the freeze reaction. It therefore seems likely that only the flight muscles (total weight about 20 mg) are large enough to produce the begging signal. Simpson (1964) found that another acoustical signal produced by honeybees, queen piping, is also produced by the flight muscles. The piping queen probably transmits the vibrations to the substrate by pressing her thorax against the comb.

The sound pressure recorded in the air about 2 cm from the comb surface during the begging signals is about the same as during the dance sounds. On the other hand, a human observer at a distance of 30 cm is hardly able to hear the dance sound, but clearly hears the begging signal. The reason for this difference is that a dancing bee is a much less efficient sound emitter than the much larger vibrating comb.

Frings and Little (1957) used airborne sound to induce vibrations in combs and found minimum

thresholds for the “freezing response” below 1,000 Hz. These results are in agreement with the frequency dependence of the mechanical input impedance of the combs observed in our study. Our observation of a minimum threshold for the “freezing response” at 2,500–3,000 Hz when the vibrations are measured as displacement amplitudes is in accordance with the electrophysiological data for the vibration sense determined by Autrum and Schneider (1948) and with the behavioral data of Gould (1975), who determined the threshold of the freezing response while measuring the stimulation amplitude with an accelerometer.

The freezing response is said to have a function in queen communication. The queens probably use the comb as transmission channel for their piping, and the freezing of the worker bees may reduce the background noise level. The begging signal is also transmitted through the substrate, and the same reaction thus seems to be used in two different communicational situations.

Acknowledgements. This study has been supported by the Akademie der Wissenschaften und der Literatur, Mainz, and by the Danish Natural Science Research Council. We thank Richard Fay for the reflecting paint, Lee Miller, Ole N. Larsen, Michael Neumann, and an anonymous referee for comments on the manuscript; and Henning and Tove Nielsen for helping us with the bees.

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