

See discussions, stats, and author profiles for this publication at:
<https://www.researchgate.net/publication/248855164>

Acoustical communication in honeybees

Article in *Apidologie* · January 1993

DOI: 10.1051/apido:19930309

CITATIONS

31

READS

24

Review article

Acoustical communication in honeybees

WH Kirchner

*Theodor-Boveri-Institut für Biowissenschaften der Universität,
Lehrstuhl für Verhaltensphysiologie und Soziobiologie, D-9707 Würzburg, Germany*

(Received 14 December 1992; accepted 5 February 1993)

Summary — Airborne sound and vibrational signals play an important role in honeybee communication. Physiological mechanisms of production, transmission and perception of acoustical signals in honeybees as well as the biological significance of these communication systems are discussed.

acoustical communication / sensory physiology / vibration / sound / hearing

INTRODUCTION

Nearly all the social life of honeybees takes place in the darkness of the nest. Vision, which is of tremendous importance for orientation and navigation outside the nest, therefore does not play any role in interactions among bees inside the nest. For a long time, the world of the honeybee seemed almost exclusively to be a chemical world, in which pheromones are used to communicate. Recently, it has become increasingly evident that there is another world in which bees live, a world of sound and vibrations.

VIBRATIONAL COMMUNICATION AMONG QUEENS

Among the sounds made by bees there is one that has already been known for many

years. This is the sound made by young queens during the process of swarming. One of the first descriptions of this so-called queen piping was given by Charles Butler (1609) in his "feminine monarchy", the first scientific book on bee biology that we know about. Using musical notation, he documented 2 different types of sounds produced by bees. Some years later, Janscha (1774) studied swarming in bees and realized that the old queen leaves with part of her colony and that young queens are reared in special queen cells. Huber (1792) then discovered that the first of these young queens emerging from the cell in which she developed produces a sound signal called tooting, and that other young queens, which are still sitting in their cells, respond by quacking. Since then, a number of investigations have addressed both the question of the adaptive significance of the behavior; and on the other hand, questions

of signal production, signal transmission, perception, and discrimination. Some progress has been made during recent years in answering the second set of questions; however, most of what we find in the literature concerning the first question is highly speculative.

Honeybee queen piping (tooting and quacking) is broadcast in the bee's nest as vibrations of the combs (Michelsen *et al*, 1986a). Figure 1 shows the temporal patterns and a frequency spectrum of these signals which are more or less pure tones at low frequencies of ≈ 400 Hertz. They are produced by rapid contractions of the thoracic muscles, and transmitted directly to the substratum. The wings do not vibrate. The temporal structure of both signals can easily be distinguished: tooting starts with a first syllable, which lasts for more than 1 s, and rises in amplitude as well as frequency at the beginning. This sound is then followed by a variable number of syllables lasting for $\approx 1/4$ s each, which also show an initial rise in amplitude. Quacking consists of a number of syllables which are somewhat shorter, typically of < 200 ms duration, and which lack the initial rise in frequency and amplitude. The frequency is generally slightly lower in quacking compared to tooting signals but there is some overlap and also an age dependence of these frequencies. The signals are transmitted in the combs at amplitudes of $\approx 0.1\text{--}1\ \mu\text{m}$ displacement of the comb. The attenuation of the signals with distance is relatively low, *ie* ≈ 6 dB per 10 cm. Bees are able to pick up these vibrations (see below). Young queens can discriminate between tooting and quacking and respond to tooting more frequently than to quacking. They distinguish the 2 signals mainly by making use of the differences in temporal structure. Worker bees also react to queen piping. They immediately stop moving and freeze for the duration of the queen's song (see Michelsen *et al*, 1986a for more details).

What is the biological significance of queen piping? At first glance, it seems to be unwise for a young unemerged queen to make any sound at all in response to the tooting signals of an emerged young queen, for this queen is extremely aggressive, localizes the sound emitter and tries to open the cell in order to kill the occupant. The tooter gains information about the presence and location of quacking competitors. What is the quacker's benefit in quacking instead of waiting silently? It seems, but has never been experimentally proven, that quackers gain protection from worker bees which cluster around the queen cells and seem to chase the tooter away. They also feed the quacker through a small slit in the cell. After some days the first young queen eventually leaves with a second swarm. Then one or more of the former quackers emerge from their cells and become tooters and so on. Finally, the

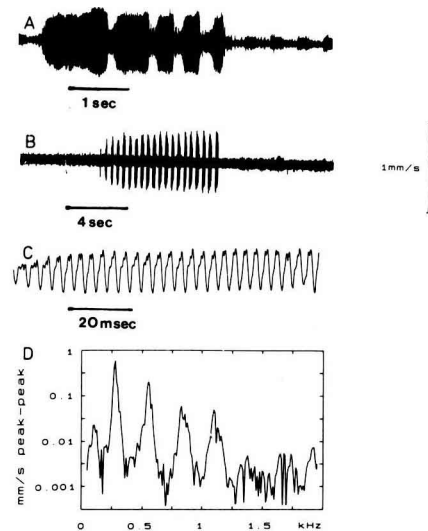


Fig 1. Queen piping signals. Time functions of tooting (A) and quacking (B) have been recorded as vibrations of the comb. Tooting is characterized by an initial rise in amplitude of each syllable (C). A typical amplitude spectrum of a quacking signal (D) shows a fundamental frequency of 300 Hz and some harmonics.

workers seem to allow one of the queens to kill all other queens. On the colony level theirs is a clear payout. Given that queens can only be produced by mated queens and that they need some time to develop, time which is expensive at that period of the year when swarming occurs, it appears to make sense that some spare queens for afterswarms and for the case that the first queen gets lost, *eg* during a mating flight, are kept for a while (Simpson and Cherry, 1969; Bruinsma *et al*, 1981; Michelsen *et al*, 1986a). But there is also an alternative model on how the system could work which was favored by Visscher (personal communication). If the tooting queen uses the quacking response to estimate the number and strength of the competitors, she may then calculate the risk of fighting with all these competitors and compare this risk and the benefit of making use of the nest resources, *ie* nesting site, food stores, the brood and the worker bees, at the risk of leaving the hive with a second swarm. She may then stay if the response is weak, but swarm if the response is strong. Even if there is no direct support for the idea that queen decides about swarming, it is an interesting hypothesis.

VIBRATIONAL SIGNALS OF WORKER BEES

Vibrational signals are also found in worker communication. Esch (1962) reported that bees attending the dances of their nest-mates from time to time make short squeaking sounds, which were at that time recorded as airborne sounds, but were later shown to be made and transmitted as vibrations of the comb (Michelsen *et al*, 1986b). The signals (fig 2) typically last for ≈ 100 ms at a frequency of ≈ 350 Hz and amplitudes of ≈ 1 μ m comb displacement. The emitters press the thorax against the comb and by doing so induce substrate vi-

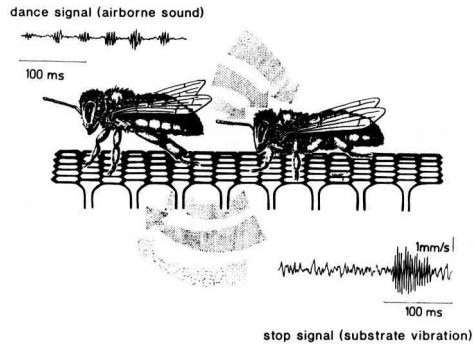


Fig 2. In the dance language dancing forager bees emit airborne sound signals by dorsoventral oscillations of the wings. Recruits produce substrate-borne vibrations, which propagate through the wax comb.

brations by contraction of the wing muscles. The dancers then sometimes but not always stop dancing and deliver small samples of the collected food to the dance attenders. The signal has therefore been called the begging signal (von Frisch, 1967) or stop signal (Gould, 1976).

Nieh (1993) showed that stop signals are also emitted by tremble dancers. The comb vibrations induced by the tremble dancers are indistinguishable in duration and frequency from those made by dance followers (Kirchner, 1993). The tremble dance is used to recruit more bees for the task of unloading the foragers (Seeley, 1992) and to reduce the recruitment of more forager bees, acting as a negative feedback system which counterbalances the positive feedback of the dance language (Kirchner, 1993).

PERCEPTION OF SUBSTRATE-BORNE SOUND

Hansson (1945), who tried (without success) to train bees to respond to airborne

sound, noticed that bees seem to pick up substrate-borne vibrations. When a platform in front of a feeding chamber was vibrated, the bees learned to associate this vibration with a food reward and moved into the feeding chamber only if the vibration was present. Autrum and Schneider (1948) studied the sense of vibrations in a variety of insects. They were able to record from the leg nerve of the honeybees and found thresholds for the sense of vibrations which varied somewhat for the different legs, but in the range of some 10 nm of displacement amplitude at the best frequencies of 2 500 Hz. Later, Frings and Little (1957) induced vibrations of the combs by loud airborne noise and made use of the freezing response of worker bees to estimate the frequency range to which the bees respond behaviorally. They found the highest sensitivity at 500 Hz. For a long time it remained unclear why the physiological threshold was lowest at 2.5 kHz, whereas the behavioral threshold was lowest at about 500 Hz. This was then clarified by Michelsen *et al* (1986b), who used the freezing response to vibrations of the combs of known amplitudes to study the behavioral thresholds. They showed that in fact both were correct: if we consider displacement amplitudes, the bees are most sensitive at high frequencies, but if the amplitude of the same vibrations is expressed as acceleration of the comb (which is proportional to the sound pressure used by Frings and Little (1957) as a measure of intensity), the best frequency is at 300–400 Hz (fig 3). These experiments were performed within the hive, with the background noise of thousands of bees walking around in that area. The data showed that bees are indeed able to pick up vibrations made by queens as well as by worker nestmates. Abramson and Bitterman (1986) used vibrational stimuli (amplitude not calibrated) for aversive conditioning experiments; bees learned to avoid

an electric shock by paying attention to vibrations of the ground. The sense organ used by insects to pick up vibrations is said to be the subgenual organ, a chordotonal organ which is found in the bee's tibia, distal from the knee (Autrum and Schneider, 1948).

AIRBORNE SOUND SIGNALS IN DANCE LANGUAGE

In dance language, successful forager bees inform their nestmates of the location of profitable food sources, as Karl von Frisch discovered in the 1940s (von Frisch, 1967). The direction of the food source relative to the direction of the sun is encoded in the orientation of the dance figure on the vertical comb relative to gravity. The distance to the food source is indicated by the speed of dancing: the closer the food source, the more dance circuits per time unit are performed. For a long time it remained unclear how the bees are able to pick up this information in the darkness of the bee hive.

Esch (1961) and Wenner (1962) independently discovered that dancing bees pro-

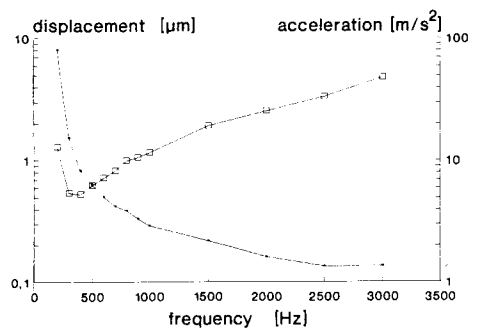


Fig 3. Perception of substrate vibrations in honeybees. Threshold amplitudes have been determined within the beehive using the spontaneous freezing response of worker bees to vibrations. The same set of data is plotted as displacement (solid symbols) and acceleration (open symbols) versus frequency.

duce sound in waggle dances. Kirchner *et al* (1988) found that dance sounds are also made in round dances. The dance sound signals (fig 2) are emitted as airborne sound by dorsoventral vibrations of the wings (Michelsen *et al*, 1987). The frequency is 200–300 Hz; the sound consists of short pulses at a repetition rate of ≈ 15 Hz. The amplitude, measured at a distance of few mm behind the dancer, is ≈ 94 dB sound pressure level. Whereas in normal so-called far field sound there is a certain fixed relationship between sound pressure and the corresponding air particle movement, these relationships are more complex in the near field of a sound emitter. In bees it has been shown in round dances (Kirchner *et al*, 1988) and waggle dances (Michelsen *et al*, 1987) that air particle oscillations are ≈ 200 times more intense than expected for the pressure amplitudes measured. The peak velocity of air particle movement close to a dancing bee was found to be ≈ 1 m/s. The vibrating wings act as dipole sound emitters: sound pressures below and above the wings are 180° out of phase and the corresponding large pressure gradients around the edge of the wings cause oscillating air currents around the abdomen of the dancer, which decrease rapidly with distance to the dancer. Most of the follower bees are found in the zone of maximum velocity of these air currents. The tail wagging movements of the dancer leads to a substantial modulation of the amplitude of the sound signals at the position of the dance followers (Michelsen *et al*, 1987).

The duration of the dance sounds is highly correlated with distance in waggle dances (Esch, 1964) as well as round dances (Kirchner *et al*, 1988) and is a suitable source of information on distance for the dance followers. Sound frequency also shows some negative correlation with distance (Spangler, 1991). The sounds are emitted during the tail wagging runs. There

is a strong correlation between tail wagging and sound production, but these 2 actions are not always strictly coupled as Griffin and Taft (1992) have shown. The orientation of the dancer's body while it is emitting the sound indicated the direction of the food source (Kirchner *et al*, 1988). There are also some correlates of profitability of food sources in the sound signals of round dancers, as Waddington and Kirchner (1992) have shown. The highest correlation was found between sound frequency and profitability. Thus, information about distance, direction and profitability is provided to the follower bees by the dance sounds.

The western honeybee, *Apis mellifera*, is not the only bee which makes dance sounds. Towne (1985) found that *Apis cerana* dancers emit similar dance sounds. This finding has been recently confirmed in *Apis cerana indica* as well as in *Apis cerana japonica* (Kirchner, unpublished observations). In *Apis dorsata*, Towne (1985) did not find any dance sounds. Recently, dance sounds similar to those of *Apis mellifera* but much lower in frequency, *ie* ≈ 100 Hz, have been found in *Apis dorsata* (Kirchner and Dreller, 1993). In *Apis florea*, no dance sound are emitted during the wagging runs (Towne, 1985; Kirchner, unpublished observations).

THE SIGNIFICANCE OF SOUND SIGNALS FOR DANCE COMMUNICATION

The hypothesis of an acoustical transfer of information in dance language has been tested by 2 different experimental approaches, one of which used an experimental manipulation of the sounds emitted by dancing bees and the other simulation of dance and dance sounds. To change the dance sounds in frequency and amplitude one can simply shorten the wings slightly. In higher insects the frequency of wing beat is determined by the mechanical

properties of the thorax and the wings. Shortening the wings increases the frequency of wing beat. The same is true for the dance sounds of honey-bees. In addition to the change in frequency the amplitude of the dance sound is much lower. It was shown by Kirchner and Sommer (1992) that bees with experimentally shortened wings did continue to forage and dance and that no changes in the dancers' behavior could be detected, but almost no recruitment by those dances could be found. The same is true for a mutant *diminutive wings*, which has wings of substantially smaller size compared to the wild-type. The dance language hardly works at all in the mutant. In a colony composed of 50% wild-type and 50% *diminutive wings* mutants it was shown that the dances of wild-type dancers recruited both groups equally well, whereas the dances of the mutants were equally ineffective for both groups. This result indicates that the changes in the dance sound made by the *diminutive wings* mutation cause reduced recruitment success. The second approach, simulation of the dance, had been tried several times (Steche, 1957; Esch, 1961; Gould, 1976). Based on recent findings on the acoustical signals in the dances, a new computer-controlled model bee has been used by Michelsen *et al* (1989, 1992). This model bee is made of brass covered with a thin layer of beeswax and is slightly larger than a worker honeybee. The wings are made by a piece of razor-blade connected to an electromagnet. A thin rod is affixed to the back of the model. A step motor attached to the far end of the rod rotates the model during the figure-eight path and also causes the model to waggle during the wagging run. An x-y plotter connected to a metal sleeve around the rod moves the model in a figure-eight path. A thin plastic tube, ending near the model's head, delivers small amounts of sucrose solution from a syringe under con-

trol of a second step motor. During the experimental sessions the model and the sucrose solution were given a faint floral scent, which was also added in minute amounts to baits placed in the field. At each of the baits, an observer noted the number of approaching bees. The experiments showed that the artificial dancer can indeed recruit nestmates to search for food in the indicated distance and direction, but completely fails to recruit as soon as the wings stop moving and therefore no sound is emitted. The 13–15 Hz tail wagging movements of the dancer, which produce infrasonic air oscillations as well as tactile signals for some of the dance followers (Bozic and Valentincic, 1991) seem to be as important as the wing movements: dances with sound but lacking the wagging were ineffective as well. Both, sounds made by wing vibrations as well as tail wagging, seem to be used to communicate distance and direction of feeding sites; and there seems to be some redundancy between those 2 signals (for more details see [Michelsen *et al*, 1992](#)).

PERCEPTION OF AIRBORNE SOUND

Bees, like other hymenopteran insects, were until recently generally assumed to be completely deaf. Several attempts to determine whether or not bees could hear had yielded negative results (von Frisch, 1923; Kröning, 1925; Hansson, 1945). The recent insights into the physical nature of the sound signals emitted by dancing bees led to a reinvestigation of the question of an auditory sense in bees, this time using near field signals similar to the sounds the dancing bees themselves produce.

In a first series of experiments (Towne and Kirchner, 1989) the bees were trained to associate a sound with a weak electric shock. Bees learned to avoid the shock by leaving a feeder when a sound signal was

given. It was thus concluded that they could hear airborne sound. More recently another training paradigm, in which the bees are trained to turn right or left as they enter the feeder, the correct way being towards the sound source, was used to determine the frequency range and amplitude thresholds of hearing in bees (Kirchner *et al*, 1991). It turned out that bees hear airborne sounds of low frequencies up to 500 Hz with sufficient sensitivity to pick up the sounds of a dancing nestmate (fig 4).

The same training technique has been used to find out which sensory structures are used to pick up the sound signals (Dreller and Kirchner, 1993a). Sensory structures suitable for perceiving near field sound signals are hair sensilla or the antennae. Bees which had learned to respond to sound were then manipulated by removing one or both antennae, or fixing a certain joint in the antenna or removing sensory hairs on the head. These behavioral experiments revealed that the sounds are picked up by Johnston's organ, a chordotonal organ located in the pedicel of the antennae, which is sensitive to vibrations of the antennal flagellum relative to the pedicel. The same sense organ is also used by flies and mosquitos to pick up airborne sound (Ewing, 1978). The data do

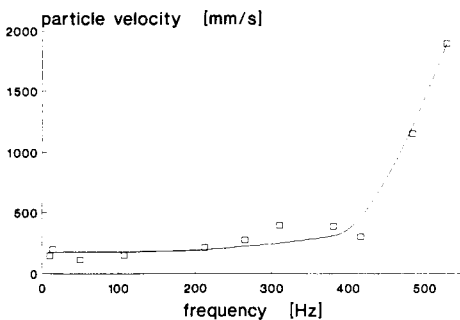


Fig 4. Perception of airborne sound in honeybees. Threshold amplitudes determined in an operant conditioning paradigm are expressed as air particle velocities and plotted *versus* sound frequency.

not support the hypothesis that sound is perceived by sensory hairs on the bee's head, which had been proposed by Es'kov (1975). Consequently, ablation of one antenna, but not removal of the sensory hairs on the head of bees attending dances of their nestmates reduces the chance of finding the advertized food source (Dreller and Kirchner, 1993b).

CONCLUSIONS

Acoustical signals have been found to be used for communication among bees in a number of behavioral contexts. Pheromones, on the other hand, are known to serve as a source of information in many other situations (Free, 1987). What are the advantages and disadvantages of these 2 channels? One of the differences between sound and smell is *speed*: the laws of diffusion generally limit pheromonal communication at any stage, *ie* emission, transmission, and perception, in temporal resolution. Acoustical signals can be produced for very short periods of time; they propagate fast and can be perceived and analyzed rapidly. This feature allows temporal coding of information in sound signals, while chemical information is exclusively coded spectrally by the blend of chemical compounds. As instantaneous change in the signal emitted, as found in emerging queens, which quack before and toot after hatching, seems therefore to be easier to implement in an acoustical than in a chemical communication system. The temporal properties of chemical communication, on the other hand, are much better suited for signals which are temporally integrated, the presence or absence of a laying queen, *eg*, should be reliably communicated without much noise by a system characterized by a long time constant, as found in the queen substance of bees. Another difference between sound and smell

is *reach*. Volatile chemical signals can be used to communicate throughout the nest, while airborne sounds emitted by bees are restricted to the close vicinity of the dancer and vibrations are mostly restricted to the single comb in which they are produced. The advantage of vibrations, however, is that they can be perceived throughout the comb, even in capped brood cells and queen cells, which is important for queen communication. The limited reach of the dance sounds may also be quite advantageous if we consider that sometimes hundreds of bees may return to the nest and advertise different food sources at the same time. There is a significant difference between pheromones and vibrations compared to near field airborne sound in the *gain*. Whereas pheromones and vibration signals emitted by a single individual can reach thousands of receivers, the sounds emitted by dancing bees are perceptible to a few dance followers. This low gain should not be seen as disadvantageous; in fact, it is not: given that there is a positive feedback in the dance language through the dances performed by those of the dance followers which fly out and find the food source, too high a gain would not only be unnecessary but even disadvantageous due to the cost of over-shooting recruitment. The last difference between sound and smell is *cost*. Production of vibrations and airborne sound by muscle contractions of high frequency is expensive. The pheromones of honeybees operate at such low concentrations that the energy consumption for producing these signals is low compared to acoustical signals. High energy expenditure, on the other hand, may sometimes also be advantageous: in queen communication by piping, it seems to be reasonable that the bees take the frequency and intensity of the vibrational signals as a measure of the fitness of young queens and demonstrate most support for the best pipers.

Thus, acoustical communication seems to be an alternative strategy to chemical communication, which was favored by natural selection in certain behavioral contexts and which is obviously favorable in these cases. Pheromones, tactile signals and acoustical signals interact in the social life of the honeybee colony in complex ways to ensure the exchange of information among individuals, which is necessary to maintain a high level of colony integration.

ACKNOWLEDGMENTS

The author's experimental work on acoustical communication in bees is currently supported by the German Research Council DFG (Ki-453/1-1). Financial support has also been provided by the Akademie der Wissenschaften und der Literatur, Mainz, and by Bert Hölldobler through the Leibniz award of the DFG.

Résumé — La communication acoustique chez l'abeille, *Apis mellifera* L. Il a été montré ces dernières années que, à côté des phéromones, les signaux sonores et vibratoires jouent un rôle important dans la communication des abeilles dans l'obscurité de la ruche. Le chant des jeunes reines (fig 1) est produit par la vibration du thorax et transmis par les rayons, qui présentent des oscillations de 0,1 à 1 μm . Les abeilles sont capables de percevoir de telles vibrations grâce à l'organe subgénéral situé sur le tibia (fig 2). Les ouvrières aussi produisent des signaux vibratoires. Les abeilles qui suivent les danses de leurs congénères se pressent parfois contre le rayon et produisent, également avec les muscles des ailes, un chant bref (fig 3), à la suite duquel la danseuse interrompt souvent sa danse et régurgite un peu de nourriture aux abeilles qui l'entourent. Ces signaux d'arrêt sont également utilisés dans la danse tremblée. La danse frétilante, qui

informe les congénères du nid sur la distance et la qualité des sources de nourriture, fait partie des systèmes de communication les plus développés du monde animal. Au cours de la danse sont émis des signaux sonores plus intenses transmis par l'air (fig 3). Ils véhiculent des informations sur la direction, la distance et la rentabilité des sources de nourriture. Les espèces *Apis cerana* et *Apis dorsata* produisent également ces sons, ce qui n'est pas le cas d'*Apis florea*.

Par des expériences utilisant des abeilles mutantes (mutation ailes raccourcies), qui émettent des sons de fréquence plus élevée et d'intensité sonore plus faible que le type sauvage, on a montré que les sons sont nécessaires à la communication. Et également, par des expériences utilisant une danseuse artificielle, on a pu montrer que les signaux acoustiques sont utilisés pour transmettre l'information de la danse concernant la direction et la distance des sources de nourriture. Si l'abeille robot dansait sans émettre de sons, les abeilles n'étaient pas attirées vers la source de nourriture. Mais si le signal sonore de la danseuse était simulé par une abeille robot contrôlée par un ordinateur, les abeilles allaient chercher la nourriture dans la direction et à la distance indiquées. L'ouïe de l'abeille a été étudiée à l'aide d'expériences de dressage. On a appris aux abeilles à associer un signal sonore à un choc électrique par une récompense ou une punition. Les abeilles peuvent percevoir des sons transmis par l'air grâce à l'organe de Johnston situé sur le pédicelle de l'antenne. La capacité d'audition de l'abeille est restreinte aux fréquences allant jusqu'à 500 Hz (fig 4). La sensibilité est suffisante pour percevoir les signaux sonores des danseuses. La communication acoustique et la communication chimique par les phéromones présentent toutes deux des avantages et des inconvénients spécifiques. La discussion porte sur le fait

de savoir pourquoi, dans certains cas précis, les signaux acoustiques sont plus appropriés à la communication.

communication acoustique / son / vibration / physiologie sensorielle / audition

Zusammenfassung — Akustische Verständigung bei Honigbienen. Bei der Verständigung der Bienen im dunklen Stock spielen, wie sich vor allem in den letzten Jahren gezeigt hat, neben Pheromonen Schall- und Vibrationssignale eine wichtige Rolle. Das «Tüten» und «Quaken» junger Bienenköniginnen (Abb 1), wird durch Vibration des Thorax erzeugt und durch die Waben ausgebreitet. Die Waben schwingen dabei um 0,1-1 μm . Bienen können solche Vibrationen mit den Subgenualorganen in den Bienen wahrnehmen (Abb 2). Auch Arbeiterinnen produzieren Vibrationssignale. Beinen, die die Tänze ihrer Nestgenossinnen verfolgen, pressen sich gelegentlich gegen die Wabe und erzeugen, ebenfalls mit den Flugmuskeln, ein kurzes Piepen (Abb 3), woraufhin die Tänzerin oft den Tanz unterbricht und Futterproben an die umstehenden Bienen abgibt. Auch im Zittertanz werden diese Stop-Signale benutzt. Der Schwänzeltanz, mit dem heimkehrende Sammelbienen ihre Nestgenossinnen über Lage und Qualität von Futterquellen informieren, gehört zu den höchstentwickelten Kommunikationssystemen im Tierreich. Im Bientanz werden Luftschallsignale von hoher Intensität abgestrahlt (Abb 3). Sie enthalten Informationen über Richtung, Entfernung und Rentabilität von Futterquellen.

Diese Tanzlaute werden auch von den asiatischen Honigbienenarten *Apis cerana* und *Apis dorsata* abgegeben, während die Zwerghonigbiene *Apis florea* keine Tanzöne produziert. In Experimenten mit der Honigbienenmutante *diminutive wings* (mit verkürzten Flügeln), die Töne höherer Fre-

quenz und geringerer Lautstärke als der Wildtyp abstrahlt, lies sich zeigen, daß die Töne notwendig für die Verständigung sind. Auch in Experimenten mit einer künstlichen Tänzerin konnte gezeigt werden, daß die akustischen Signale für die Weitergabe der Tanzinformation über Richtung und Entfernung von Futterquellen benutzt werden. Stumme Tänze der Roboterbiene können die Bienen nicht zu einer Futterstelle locken, wird jedoch auch das Schallsignal der Tänzerin von der durch einen Computer kontrollierten Roboterbiene simuliert, so suchen die Bienen in der angezeigten Richtung und Entfernung nach Futter. Das Gehör der Bienen wurde mithilfe von Dressurexperimenten untersucht. Bienen können lernen, ein Schallsignal mit einer Belohnung oder auch mit einer Bestrafung durch Elektroschock zu assoziieren. Die Bienen können luftgetragenen Schall mit dem Johnston'schen Organ im Pedicellus der Antenne wahrnehmen. Das Hörvermögen der Bienen ist auf Frequenzen bis 500 Hz beschränkt (Abb 4). Die Empfindlichkeit ist ausreichend, um die Schallsignale der Tänzerinnen wahrzunehmen.

Akustische Kommunikation und pheromonale Kommunikation haben jeweils spezifische Vor- und Nachteile. Es wird diskutiert, warum in bestimmten Fällen akustische Signale für die Verständigung geeigneter sind.

Akustische Kommunikation / Vibration / Schall / Gehör / Sinnesphysiologie

REFERENCES

- Abramson CL, Bitterman ME (1986) Latent inhibition in honey-bees. *Anim Learn Behav* 14, 184-189
- Autrum H, Schneider W (1948) Vergleichende Untersuchungen über den Erschütterungssinn der Insekten. *Z Vgl Physiol* 31, 77-88
- Bozic J, Valentincic T (1991) Attendants and followers of honey bee waggle dances. *J Apic Res* 30, 125-131
- Bruinsma O, Kruijt JP, Dusseldorp W van (1981) Delay of emergence of honey bee queens in response to tooting sounds. *Proc Kon Ned Akad Wet C* 84, 381-387
- Butler C (1609) *The Feminine Monarchy*. Barnes, Oxford, UK
- Dreller C, Kirchner WH (1993a) Hearing in honeybees: localization of the auditory sense organ. *J Comp Physiol A* (in press)
- Dreller C, Kirchner WH (1993b) How bees perceive the information of the dance language. *Naturwissenschaften* 80 (in press)
- Esch H (1961) Über die Schallerzeugung beim Werbetanz der Honigbiene. *Z Vgl Physiol* 45, 1-11
- Esch H (1962) Über die Auswirkung der Futterplatzqualität auf die Schallerzeugung im Werbetanz der Honigbiene (*Apis mellifera*). *Verh Dtsch Zool Ges* 1962, 302-309
- Esch H (1964) Beiträge zum Problem der Entfernungsweisung in den Schwänzeltänzen der Honigbiene. *Z Vgl Physiol* 48, 534-546
- Es'kov EK (1975) Phonoreceptors of honey bees. *Biofizika* 20, 646-651 (in Russian)
- Ewing AW (1978) The antenna of *Drosophila* as a love song receptor. *Physiol Entomol* 3, 33-36
- Free JB (1987) *Pheromones of Social Bees*. Cornell Univ Press, Ithaca, NY
- Frings H, Little F (1957) Reactions of honey bees in the hive to simple sounds. *Science* 125, 122
- Frisch K von (1923) Über die "Sprache" der Bienen, eine tierpsychologische Untersuchung. *Zool Jahrb (Physiol)* 40, 1-186
- Frisch K von (1967) *The Dance Language and Orientation of Bees*. Harvard Univ Press, Cambridge, MA
- Gould JL (1976) The dance language controversy. *Q Rev Biol* 51, 211-244
- Griffin DR, Taft LD (1992) Temporal separation of honeybee dance sounds from waggle movements. *Anim Behav* 44, 594-595
- Hansson A (1945) Lauterzeugung und Lautauffassungsvermögen der Bienen. *Opusc Entomol suppl* 6, 1-124

- Huber F (1792) *Nouvelles Observations sur les Abeilles*. Paschoud, Geneva
- Janscha A (1774) *Abhandlung vom Schwärmen der Bienen*. Kurzbock, Vienna
- Kirchner WH (1993) Vibrational signals in the tremble dance of the honeybee, *Apis mellifera*. *Behav Ecol Sociobiol* (in press)
- Kirchner WH, Sommer K (1992) The dance language of the honey-bee mutant diminutive wings. *Behav Ecol Sociobiol* 30, 181-184
- Kirchner WH, Dreller C (1993) The dance language of the giant honeybee, *Apis dorsata*. *Behav Ecol Sociobiol* (in press)
- Kirchner WH, Lindauer M, Michelsen A (1988) Honeybee dance communication: acoustical indication of direction in round dances. *Naturwissenschaften* 75, 629-630
- Kirchner WH, Dreller C, Towne WF (1991) Hearing in honeybees: operant conditioning and spontaneous reactions to airborne sound. *J Comp Physiol A* 168, 85-89
- Kröning F (1925) Über die Dressur der Biene auf Töne. *Biol Zbl* 45, 496-507
- Michelsen A, Kirchner WH, Andersen BB, Lindauer M (1986a) The tooting and quacking vibration signals of honeybee queens: a quantitative analysis. *J Comp Physiol A* 158, 605-611
- Michelsen A, Kirchner WH, Lindauer M (1986b) Sound and vibrational signals in the dance language of the honeybee, *Apis mellifera*. *Behav Ecol Sociobiol* 18, 207-212
- Michelsen A, Towne WF, Kirchner WH, Kryger P (1987) The acoustic near field of a dancing honeybee. *J Comp Physiol A* 161, 633-643
- Michelsen A, Andersen BB, Kirchner WH, Lindauer M (1989) Honeybees can be recruited by a mechanical model of a dancing bee. *Naturwissenschaften* 76, 277-280
- Michelsen A, Andersen BB, Storm J, Kirchner WH, Lindauer M (1992) How honeybees perceive communication dances, studied by means of a mechanical model. *Behav Ecol Sociobiol* 30, 143-150
- Nieh JC (1993) The stop signal of honey bees: reconsidering its message. *Behav Ecol Sociobiol* (in press)
- Seeley TD (1992) The tremble dance of the honey bee: message and meanings. *Behav Ecol Sociobiol* 31, 375-383
- Simpson J, Cherry SM (1969) Queen confinement, queen piping and swarming in *Apis mellifera* colonies. *Anim Behav* 17, 271-278
- Spangler HG (1991) Do honeybees encode distance information into wing vibrations of the waggle dance? *J Insect Behav* 4, 15-20
- Steche W (1957) Gelenkter Bienenflug durch Attrappentänze. *Naturwissenschaften* 22, 598
- Towne WF (1985) Acoustical and visual cues in the dances of four honey bee species. *Behav Ecol Sociobiol* 16, 185-187
- Towne WF, Kirchner WH (1989) Hearing in honey bees: detection of air-particle oscillations. *Science* 244, 686-688
- Waddington, Kirchner WH (1992) Acoustical and behavioral correlates of profitability of food sources in honey bee round dances. *Ethology* 92, 1-6
- Wenner AM (1962) Sound production during the waggle dance of the honey bee. *Anim Behav* 10, 79-95