Illustrations and Adittional information:
http://www.beesource.com/point-of-view/adrian-wenner/sound-communication-in-honey-bees/

Sound Communication in Honeybees

[1964 Wenner, A.M. Sound communication in honey bees. *Sci. Amer.* 210:116-124.]

It has been known for some time that bees perform an intricate dance in directing their hivemates to a source of food. Now it appears that they also transmit information by means of sound

by Adrian M. Wenner

(1. Effect of sound on bees in a hive)

Can we ever fully understand how the members of another species communicate with one another? The question has been given a new implication by the recent proposals that we listen for messages from the planets of other stars. Whether we ever detect such messages or not, we can investigate the question here on earth. We now know of many forms of communication in other species. None is subtler or more interesting than the "language" of the honeybee.

It is no accident that Karl von Frisch of the University of Munich chose the bee for his now famous investigations of animal communication. A honeybee colony is a marvelously compact community of some 50,000 individuals; it takes care of itself and usually ignores its human investigator; its members are highly social and could not survive without constant intercommunication, and the more one looks into their methods of conversation, the more remarkable they are found to be.

The obvious features of honeybee communication have been reported widely and are now a familiar story. When a foraging bee finds a source of food, it flies back to the hive and conveys to its fellows the distance and direction of the source. In the course of doing so it performs on the vertical surface of the comb a waggling "dance" in which its abdomen traces a figure eight. The orientation and rate of the dance, it has been supposed, tells the location of the food source.
This hypothesis runs into an awkward difficulty: the interior of most hives is so dark that the bees probably cannot see the dance. Investigators of the phenomenon have found, however, that the bees follow the dance by means of their antennae,
which touch the dancer's body.

Robert C. King of Servomechanisms, Inc., and I, working in my laboratory at the University of California at Santa Barbara, looked into the question further. The dancing bee traces the figure eight with the tip of its abdomen. That is not, however, the part of the body on which the observing bees usually concentrate their attention: their antennae tend to rest on the dancer's thorax. Does the thorax also describe a figure eight during the dance? We marked foraging bees with a spot of white paint on the thorax and later photographed its movement during the course of the dance in the hive by means of a series of rapid-flash exposures. The pictures showed that the thorax did not describe a figure-eight pattern (*2. see illustration*).

The dance pattern itself, then, can hardly convey an unequivocal message. What can? Using a tape recorder, I had discovered that during the dance the bee emitted a peculiar sound at the low frequency of 250 cycles per second. This sound was made while the bee was waggling along in the straight run of its dance. It suggested a surprising new outlook on the whole problem. Perhaps the honeybee communicated with its fellows not only by the dance movement but also by sound signals!

To test this possibility I made tape recordings of the sounds made by dancing bees after they had visited dishes of sugar syrup placed at different distances from the hive. Would the sound patterns show a relation to the distance traveled? In other words, did the foraging bee tell its hivemates the distance by means of a sound language?

Analyzed with the (3. sound spectrograph), the sounds proved to be made up of trains, each train being further broken into pulses with a frequency of about 32 per second *(4. see illustration*). The bee emitted a train of sound during each straight run of its waggling dance. A careful analysis showed that the average length of the sound trains during a given dance (and also the average number of pulses in a train) was directly proportional to the distance the bee had traveled to the food source (*5. see illustration*). The correlation was so good that it seems altogether likely – certainly as likely as any other proposed mechanism – that the bee reports the distance by means of this sound language.

How is the sound produced? The first and most obvious guess was that the bee might create the pulses of sound with the waggling of its abdomen. To resolve this question I attached a small piece of cellophane to a microphone and placed the microphone so that with each waggle the dancing bee would tap the cellophane. The sound pulses proved to be about two and a half times more frequent than the waggling taps, so it became clear that the sound could not be arising from the waggling. Harald Esch, now at the University of Munich, who independently had discovered the honeybee's dance sound at about the same time as I had, also demonstrated that it was not produced by the waggling. Instead of a cellophane- and-microphone device, he used the ingenious method of attaching a small magnet to the bee's abdomen; as the bee moved the magnet it generated a fluctuating electric voltage that was recorded simultaneously with the pulsed sound, so that the waggle and pulse rates could be compared.

The function of the sound train was illuminated by considering the question of whether or not the bee's judgment of distances is affected by the wind. Analysis of the sound-train records showed that it is to some extent. When a bee flies to a source of food against the wind, the sound trains indicating the distance tend to be a little longer than when it does not buck a wind. The deviation from the true distance is not nearly so much, however as one might expect on the basis of the wind velocity. A possible explanation is that the bee adjusts its flying efforts to the wind so that it always flies at about the same ground speed; thus, whatever the wind velocity it can still use the elapsed time of travel to a goal as the measure of its distance. I measured the flight speed of bees under various wind conditions and found that they do tend to fly at a constant ground speed. For example, flying against a wind of five meters per second (about 11 miles per hour) bees are slowed by only about a fourth of that amount. They minimize the wind effect by flying closer to the ground. When the wind is too strong (more than 13 miles per hour), the bees simply stay in the hive.

We may conclude, then, that the foraging bee's communication to its fellows in the hive is made up of two elements: (6. the dance) and the accompanying sounds. The angle of the dance from the vertical is correlated with the angle between the food source and the overhead sun, and the length of the train of sound during the straight run of the dance tells the distance. This may not be the whole story, however. Some current experiments indicate, for instance, a strong correlation between the rate of pulse production and the strength of the sugar concentration in a food source. It may conceivably turn out that the foraging bee's entire message is carried by sound signals.

(7. Transmittal of information by foraging bees)

The sound spectrograph's indication of regularity and precision in the bee's dance sounds naturally drew attention to other forms of bee "talk." As everyone knows, the bee is a rather noisy animal. Even its buzz in flight, however, is not just noise. The buzz has modulations and variations. When bees begin to swarm, an experienced beekeeper can detect the event by the sound alone, even though he may be surrounded by other buzzing bees from hundreds of hives. When an individual bee is aroused to attack, its buzz rises in pitch and fluctuates in intensity. And recordings within the hive show that bees in the hive make at least 10 distinctly different sounds, some of which have already been related to specific activities.

Two of these sounds are particularly noticeable. One, known as the characteristic hum of a beehive, is produced by the "ventilating" worker bees: bees that stand anchored on the comb or some other structure in the hive and create currents of air by beating their wings. This sound, varying in intensity, has a basic frequency of 250 cycles per second and often has strong overtones. It is usually much louder than the buzz of a flying bee, undoubtedly because the sound emitted by the ventilating bee is enhanced by the resonant vibration of the structure on which it is standing.

The other type of loud sound in the hive is heard (8. when the hive is disturbed). When an intruder – for example an ant – approaches, the bees guarding the hive rock forward on their legs and issue a short burst of sound; they may go on repeating these warning bursts every two or three seconds for 10 minutes or more. When the hive is jarred, the collective reaction of hundreds of guarding bees is heard as a sharp, loud buzz. This is followed shortly by a "piping" of workers throughout the hive, which consists of faint beeps at half-second intervals, the sound being a complex one with a fundamental frequency of 500 cycles per second. The piping goes on for several minutes. Apparently it serves to soothe the hive; it has been found that a recording of such piping, played to the hive, will quickly quiet the disturbed bees.

The most interesting of all the hive sounds, however, is the piping of the queen. Naturalists have long known that queens inside the hive emit two kinds of sound, called “tooting” and “quacking.” A close analysis of these sounds and the circumstances of their emission now provides the strongest evidence that bees use sound to convey specific messages.

Tooting is the regal identification of a virgin queen soon after she has emerged from the cell in which she developed. A hive cannot tolerate more than one queen at a time. In a hive that lacks a queen several queen-bearing cells develop simultaneously in a comb, but one matures earlier than the others. Once this queen has emerged, has hardened and has become steady on her legs, she proceeds to visit other queen cells, tear them open and sting to death their potential but not yet mature queens. Often, however, the worker bees do not allow her to dispose of all her potential rivals in this way; they bar her from some of the cells. She then begins to toot and continues to do so day and night, perhaps for a week or more. Her tooting rises in intensity and sometimes can be heard more than 10 feet from the hive.

Meanwhile the maturing queen bees still in cells try to get out in their turn. The worker bees hold them back, however; as fast as one of them opens the cap of her cell the workers push it back in place and glue it shut. Thereupon the imprisoned queens also start to pipe, but in a different pattern and at a lower tone than the free queen. The workers let out some of these quackers, but only one at a time. The reigning queen and the newly released rival then battle until one is killed. Sometimes the series of fights between the survivor and the new rivals goes on until only one queen is left. This survivor, still a virgin, then flies away from the hive to mate successively with several drones (on the wing) and returns to begin laying eggs.

All this has been studied in hives set up for detailed observation. The tooting and the quacking have also been recorded and (9. analyzed spectrographically). The pattern of the first turns out to be a long toot (lasting one second) followed by several shorter toots. Its fundamental frequency is 500 cycles per second, and this is overlaid with overtones that are varied considerably in emphasis, just as they are in human speech [see "Attention and the Perception of Speech," by Donald E. Broadbent; SCIENTIFIC AMERICAN, April, 1962]. The quack differs from the toot in two ways: it has a lower fundamental frequency and it begins with short sounds instead of a drawn-out one.

Do the tooting and the quacking say different things to the bees? We investigated this question with a set of controlled experiments. First we recorded the tooting of a free, reigning queen in its hive. Analysis with the sound spectrograph showed that this tooting put the major emphasis on the third harmonic. We therefore mimicked this harmonic with an oscillator and played it in the same tooting pattern (a long toot followed by several short ones) in a second hive that contained a free queen and a caged one. To each sounding of the artificial toots the caged queen almost invariably responded by quacking (*10. see illustrations*). We then tried varying the frequency of the tone, while keeping the long-toot- short-toot pattern constant. Within a wide frequency range (600 to 2,000 cycles per second) the change in frequency seemed to make little difference: the queen still responded with quacks as long as the typical pattern of toots was the same. On the other hand, when we played the quacking pattern, the caged queen did not respond at all.

There is not much doubt that the tooting and the quacking represent certain messages. What do the messages say, and what functions do they serve? A reasonable working hypothesis is that (1) the tooting announces the presence of a free queen in the hive, (2) the quacking reports the presence of challengers ready and yearning to be freed from their cells and

(3) all this information guides the worker bees. One queen tooting and others quacking means that there is just one free queen, and a quacker (but not more than one) may be released to challenge her. This procedure will result in the rapid killing off of all but one of the contenders, but that may be to the good; it will enable the hive to settle down quickly to a peaceful regime. Occasionally, however, particularly in the spring, a virgin queen or an older egg-laying queen may leave the hive permanently, taking along half of the adult bees, in the phenomenon called swarming. In the swarming season, therefore, it is essential to have a queen in reserve when the free queen departs; a quacking queen may represent survival for the hive and is not to be released until the swarm has left.

We must come back now to the important questions: How does the bee produce sounds, and how does it perceive them? As to the production of sound, four hypotheses have been put forward, and the answer is still not clear.

The most interesting suggestion is that the bee makes its sounds by ejecting air through its spiracles: the breathing openings in the side of its body. On purely theoretical grounds it is quite plausible that the insect could produce the observed sounds by a whistling or a bagpipe effect. But recent experiments in our laboratory and also by other investigators generally negate this theory. For one thing, if helium is substituted for nitrogen in the air in which the bee produces its sounds, this does not change the frequency of the sound; if the spiracle theory is correct, it should, because the density of a gas affects the frequency of the sound produced by vibrating a column of the gas. For another thing, it has been found that the sounds of a piping queen do not always coincide with accordion-like movements of its abdomen, so that its abdominal spiracles cannot be producing the sound. Finally, James Simpson of the Rothamsted Experimental Station in England has shown by delicate spiracle-blocking experiments that the bee's thoracic spiracles play no part in sound production.

The other possibilities are that the bee produces sound by vibrating its wings or the sclerites (hard plates) at the base of its wings or the entire surface of the upper part of its body. Simpson and I and others have been investigating these possibilities. At the moment the wing-vibration theory seems to be the most promising.

Until recently this idea was rejected on two grounds: that a bee's wings are too small to produce sounds of the frequencies and intensities heard, and that experimenters who have clipped the wings have not found that this changed the intensity of the bee's piping. The second idea is simply wrong; careful experiments show that clipping the wings does affect the bee's sound-making. It raises the frequency and reduces the intensity of the sound, and the change is proportional to the amount of wing removed [*11. see illustration*]. It appears, therefore, that wing vibration is responsible at least for amplification, and probably for production, of the bee's sounds. It is hoped that experiments now under way will

answer the question more
definitely.

Other recent studies have shed some light on how bees "hear" sound. In the experiments in which artificial tooting was played to a caged queen it was found that the queen responded only when the sound was transmitted via a vibrator attached to the hive; when it was transmitted through the air, even with the vibrator suspended close to the bee, she did not respond at all [*12. see illustration*]. Similarly, worker bees show no reaction to piping when it is airborne. On the other hand, a disturbed hive can be quickly quieted by drawing a wet finger along the observation window, which causes a squeaking sound that arises from vibration of the glass. All these observations indicate that the bees receive sound through their legs from the vibrating structure on which they stand. Quite possibly they have receiving organs for sound on their legs below the knee.

There is also evidence that they receive sound through their antennae. Eleanor H. Slifer of the University of Iowa has found that each bee antenna has thousands of "plate organs" that are remarkably like the larger tympanic (eardrum-like) organs of other insects. She has established that these plate organs are not permeable to chemicals that might be used for communication. Although this finding does not eliminate the possibility that these organs are chemoreceptors, there is now good reason to entertain the notion that they do respond to mechanical stimuli. Charles Walcott of Harvard University has made some experimental findings that support this view: he discovered that vibrations transmitted to a bee's antennae caused electrical impulses to be generated in the antennal nerves.

Conceivably the honeybee receives sound both through its legs and through its antennae. Thus it may receive a sound communication from another bee directly by touching the other bee's body with its antennae – as evidently occurs during the foraging bee's dance in the hive. The double receiving system would have a great advantage for bees in a noisy hive: in spite of the din of piping, which they apparently receive through their legs from the hive's vibrations, they would still be able to perceive the faint dance sounds by touching the dancer with their antennae.

Listening to the sounds of bees, recording them, analyzing them and designing experiments to explore their meaning, one cannot help feeling that much of this is akin to the problem of communicating with beings on another planet. With bees we have the advantage of being able to study them here and now.

The Author

ADRIAN M. WENNER is assistant professor of biology at the University of California at Santa Barbara. A native of Minnesota, Wenner received a B.S. in mathematics from Gustavus Adolphus College in 1951. He also acquired an M.S. in biology from Chico State College in California in 1955 and a Ph.D. in zoology from the University of Michigan in 1961. He joined the Santa Barbara faculty in 1960.

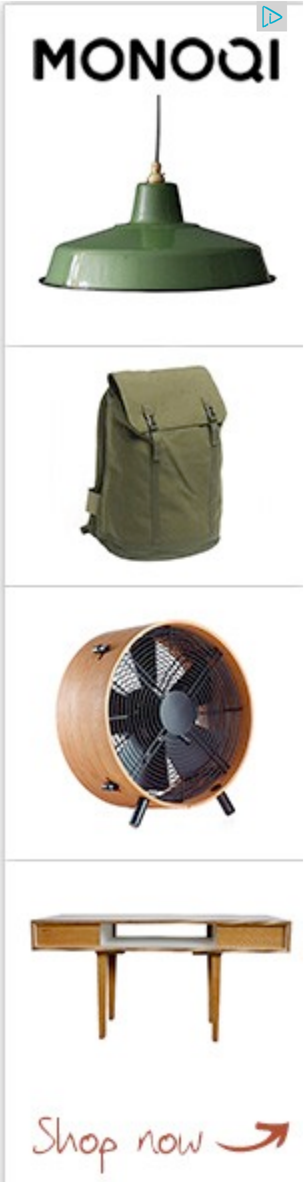
Bibliography

COMMUNICATION AMONG SOCIAL BEES. Martin Lindauer. Harvard University Press, 1961.

COMMUNICATION WITH QUEEN HONEY BEES BY SUBSTRATE SOUND. Adrian M. Wenner in *Science*, Vol. 138, No.
3538, pages 446-447; October, 1962.

SOUND PRODUCTION DURING THE WAGGLE DANCE OF THE HONEY BEE. A. M. Wenner in *Animal Behaviour*, Vol. 10, No. 1/2, pages 79-95; 1962.

UBER DIE SCHALLERZEUGUNG BEIM WERBETANZ DER HONIGBIENE. Harald Esch in *Zeitschrift fur Vergleichende Physiologie*, Vol. 45, No. 1, pages 1-11; October, 1961.



© 2015 Beesource.com | All Rights Reserved | Chicago, Illinois | Advertise with us | Site Updates | Disclaimer | About Beesource