Bee Dance

J Tautz and B Bujok, Universität Würzburg, Würzburg, Germany

Honeybees, living together in colonies of tens of thousands of individuals, have evolved behavioral and physiological mechanisms that allow them to maintain the colony. Compared to most other insects, two aspects are especially important: to find their way between locations of relevance (orientation between the nest site and food sites) and to recruit nest mates (communication) to support in tasks in which many helpers are needed.

The so-called dance 'language' includes both aspects. The observed phenomenon is that after one bee has by chance discovered a food site or a new nesting site, a number of bees, up to half of the colony in the case of swarming, arrive at the site. It is obvious that something must have happened between the bees inside the nest that 'know' the location of interest and those that are recruited to that site. All steps in this communication contribute to a most complex behavior, the mechanisms of which are still not fully understood.

After a successful forager returns from a food or nest site, it performs a conspicuous movement termed the 'waggle dance.' In ~1945, the Austrian zoologist Karl von Frisch discovered a correlation between certain aspects of the waggle dance and the geographical situation linked to this form of signaling. This correlation was a topic of intense debate among scientists asking the question "is this an abstract language, in the sense that bees watching a dance can read this correlation precisely and use it, or not?" The picture that we have today is a mixture of both: the dance language communication is a highly complex system of signals between the bees and cues from the surroundings, and the waggle dance is the initial and most conspicuous step in that system.

The Problem

Honeybees can fly distances up to 10 km away from the hive to which they must return. Scout bees search during such flights for flowers, water, and resin from plants or for new nesting sites. Recruitment to flowers and water speeds up the exploitation by the colony; new nesting sites must be found quickly after a swarm leaves the old home. It is much more important for a swarm to find new shelter quickly than for additional bees to collect nectar from a certain spot. Thus, it may be speculated that a high selection pressure on quick and successful home finding led to the 'invention' of the dance communication, which, after it evolved, was then also used on a small scale as a preadaptation in food recruitment.

The different types of goals have different physical properties. The task is more difficult in recruitment to a new nesting site: It is a spot in the landscape that is not sending any cues into the surrounding area, enormous numbers of bees must be recruited to it, and mistakes can be fatal for the swarming colony. The task is easier in food site recruitment: Flowers do send visual (color) and olfactory (scent) signals, there are typically many flowers distributed over a certain area, only a small number of bees are recruited, and mistakes are not fatal (it has been shown that a colony will still collect enough food even after the dance language is disturbed artificially).

Recruitment of Swarms to a New Nesting Site

Swarming bees form dense clusters of thousands of bees hanging outside on a tree. From there, scout bees screen the landscape for suitable homes. Having discovered such sites, they return to the swarm and perform, on a vertical support formed by the bodies of the other bees, the so-called waggle dance (Figure 1).

The movement pattern is stereotypic and is composed of different segments: a waggle phase in which the bee waggles its body from side to side with a repetition rate of approximately 15 waggles per second. Return runs, during which the bee walks in a loop back to where it started the first waggle phase,

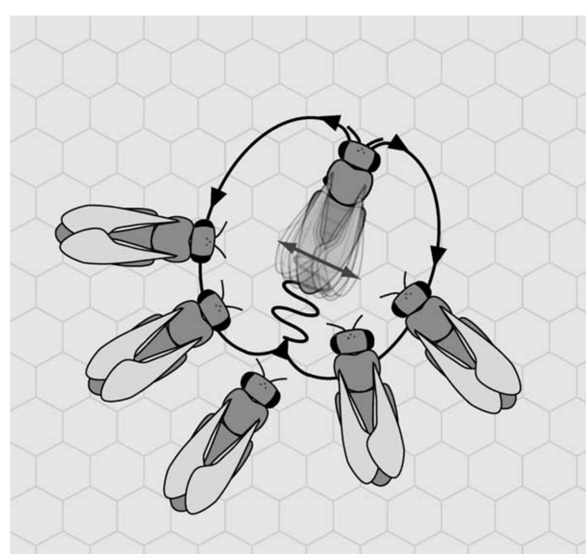

Figure 1 A successful forager returning from a food source performs a conspicuous movement pattern, the so-called waggle dance, in the darkness of the hive.

occur after termination of the waggle phase. Subsequently, the movement pattern is repeated with the next return run directed to the other side. A complete sequence is repeated many times. Figure 2 displays the correlations to the geographical situation, as discovered by von Frisch.

The time span of the waggle phase correlates positively with the distance between the nesting site and the swarm location (Figure 3); the direction of the waggle phase in relation to the direction of gravity gives the angle in the geographical triangle comprising the swarm location, the sun, and the new nesting site. In a fascinating process of consensus formation, initially many different sites are announced, but finally only dances for the best site continue.

The problem now emerges: How do 20 000 bees obtain the information about the location of the new nest site when only a few bees danced on the surface of the swarm cluster? The few bees that dance interrupt their dancing now and then, visit the new site, and mark its vicinity and entrance with scent. In successive visits to the new site, more and more bees arrive there, fly around the site, and possibly scent mark it. Scouts then return to the swarm and dance. After some time, a communication process in which rising body temperature and vibration signals play a role stimulates the swarm to become airborne. What then helps the swarm to move in the correct direction are the conspicuous flight patterns of the bees that 'know' where to go, seemingly again the nest site scouts: One can watch bees flying fast and straight among the swarm bees, directing their route in the correct direction. Near the nesting site, a group of bees (again former dancers) perform slow and looping flights and scent the air around the site and the nest entrance with pheromones. Altogether we have here a complex communication process with signals in each step of the recruitment until the new nest site is occupied.

Recruitment to Food Sources

The waggle dances that we see in food source recruitment are identical to those in nest site recruitment but, in contrast to swarming, they happen in large numbers each summer day and thus can be studied easily.

Each recruitment process can be divided into five steps, which can be analyzed separately.

1. The sender must collect information it wants to pass on.
2. The sender and receiver must establish contact (direct or via media).
3. The sender must send information.
4. The receiver must receive information.
5. The receiver must use all or part of the information.

For the dance communication, these five steps are detailed as follows:

Information Collection by the Sender

The condensed information encoded in the waggle dance figure about the route to the goal is the vector that gives the direction and distance from the starting point to the goal. Before sending these details, the dancer must collect this information. The source for both sets of information is the visual sense of the bees. The direction is experienced by seeing the sun as the reference or, if the sun is hidden behind clouds, the polarization pattern in the sky. The distance is estimated by the so-called optic flow, i.e., the pictures shifting across the eyes of the bees during flight movement. This can be demonstrated by forcing

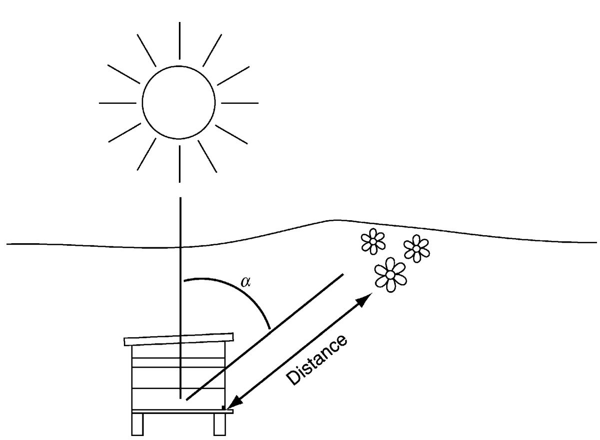

Figure 2 The dance figure contains information, maximally compressed, about the direction and distance to the food source.

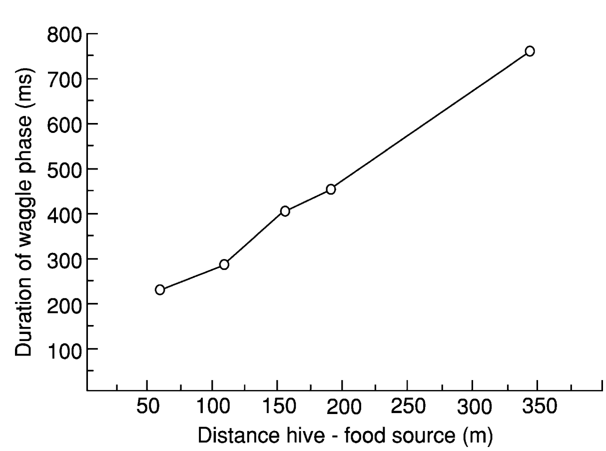

Figure 3 The distance from the hive to the goal is encoded in the duration of the 'waggle phase.'

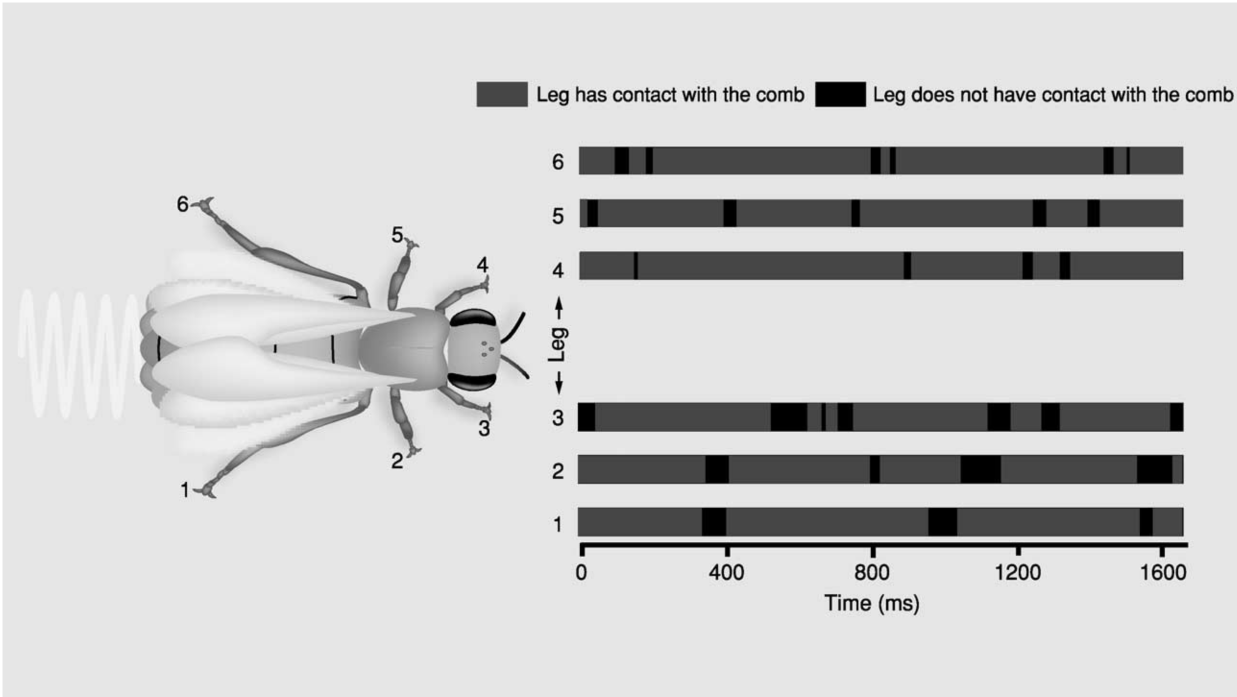

Figure 4 The central part of a waggle dance is the 'waggle phase.' It used to be called the 'waggle run' but we now know that 'waggle stand' is more appropriate as the bee clings with its feet to the rims of the cells to attain mechanical stability.

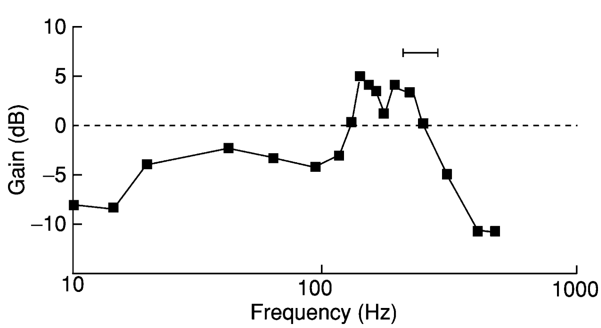

Figure 5 The mechanical properties of the comb are tuned to the frequencies produced by the dancing bee (at approximately 270 Hz). It amplifies the mechanical signals that are produced by waggle dancers and makes them conspicuous over the background noise of the colony.

bees to fly on their route to the food through narrow tunnels and thus close to visual patterns that then generate pictures moving at a rapid rate across the eyes. Such bees indicate in their waggle phase the subjective impression of a flight more than 30 times as long as the flight that they actually completed.

Sender and Receiver Establishing Contact

The dance language for food sources is performed in the darkness of the hive and is of interest to only a comparably small number of bees. Therefore, it makes a great deal of sense that there is a limited area of approximately 10 × 10 cm on the vertical surface of a comb, the 'dance floor,' on which the dancers and those motivated to meet dancers get together. The dance floor can be artificially relocated in the hive and the dance-communicating bees find it quickly to perform their communication, which indicates that it is recognized by scent.

How is a dancer detected in the darkness? Dancers emit a suite of signals and cues linked to the dance performance. These include mechanical, chemical, and thermal events. A dancing bee has a high body temperature, it smells like the food source it comes from, and it produces mechanical signals, each of which can be used to locate a dancer. The mechanical signals are the waggle movement itself and a burst of muscle contractions by the flight muscles located in the wing- and leg-carrying body segment, the thorax. During the dance, the wings are only loosely coupled to the flight muscles so that only small wing vibrations happen, which produce a faint wind detectable by bees standing nearby. The muscle oscillations are additionally transmitted as vibrations into the comb. To efficiently transmit this signal into the substratum, during the waggle-phase the dancing bee clings to the comb with its feet for as long as possible (see Figure 4).

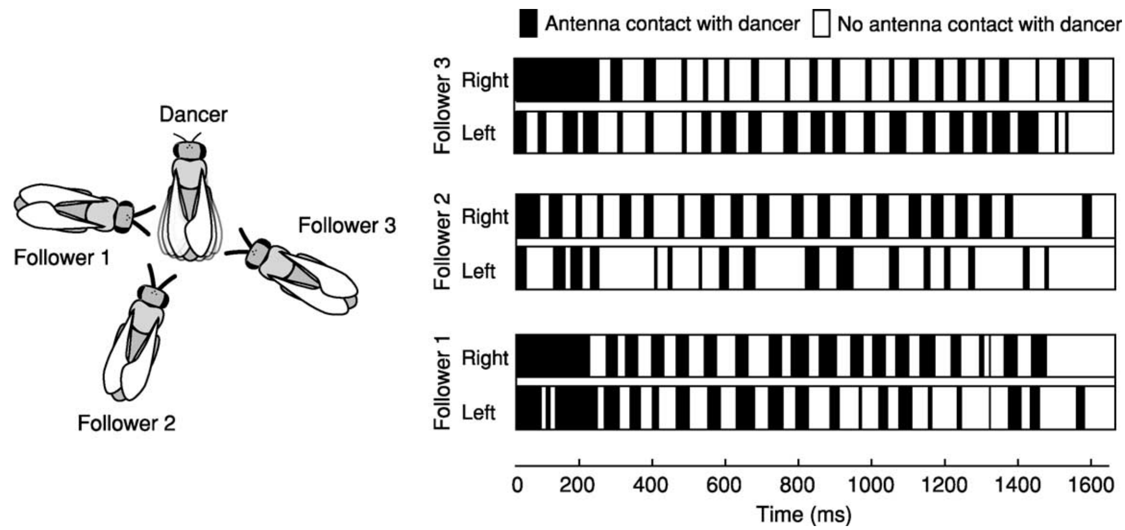

Figure 6 The dance follower bees receive from the bee dancer temporal contact patterns to both antennae from which the direction of the waggle phase can be read in the darkness of the hive.

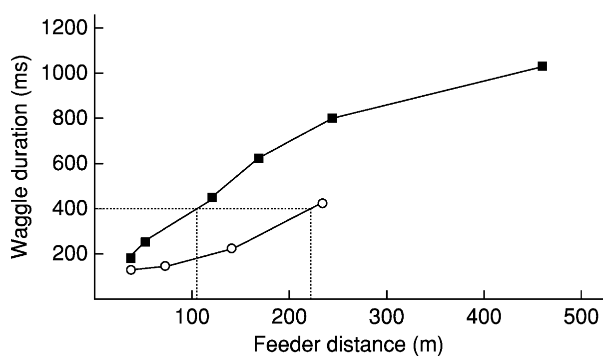

Figure 7 The information on flight distance, encoded in the waggle phase of the dance, is not absolute but depends on the landscape. A waggle duration of 400 ms can for one flight route mean 110 m and for another flight route mean 230 m.

The vibrations introduced into the comb travel as displacements in the form of a shifting of the net made from the upper rims of the cells of the comb.

It is remarkable that the mechanical properties of the comb are well adapted to the properties of the signals. The 'telephone net' of the bees, built by the bees themselves, best transmits frequencies at approximately 270 cycles/s, which is the frequency contained in the oscillation pulses produced by the dancer (see Figure 5).

Sending and Receiving the Signals

Once the dance followers have located and approached a dancer and in that way made contact, the dance followers move around with the dancer in a ballet-like manner. Each step of the dance follower is as stereotyped, but less conspicuous, as the movements by the dancer. During this ballet performance, the sender and receiver keep intense body contact. In particular, the antennae of the dance followers are touched in a certain temporal pattern by the wagging body of the dancer (Figure 6). It is during this contact that the information is transmitted and the antennae play an essential role. However, there is still a large gap in our knowledge about the details of this process.

Using the Information

Correlations do not prove causal relationships. Therefore, it was debated intensely whether and how much of the information that a human observer can read from a waggle dance is actually used by the follower bees. The arguments ranged from "it is an abstract language" to "they use nothing but are stimulated by the dance to simply search for the source of the scent that a dancer bee carries."

It turned out that the truth is a combination of both assertions. The dance transmits information and aids in the field are given to pinpoint the goals. If forager bees are forced to fly through narrow tunnels that produce a high rate of optic flow, one can create 'lying' bees. These bees dance for a different location than that which they actually found, by performing a waggle phase for more than 30 times as long a distance as they had really flown. Observing the recruits, it becomes clear that they do not fly to the forager's real site, but they can be caught in an area around the spot indicated by the dance. Thus, the dances recruit followers in roughly the correct area.

Because the distance communicated depends on the optic flow that a landscape offers to the bees, it is clear that bees do not communicate distance as an absolute quantity (Figure 7). However, as long as

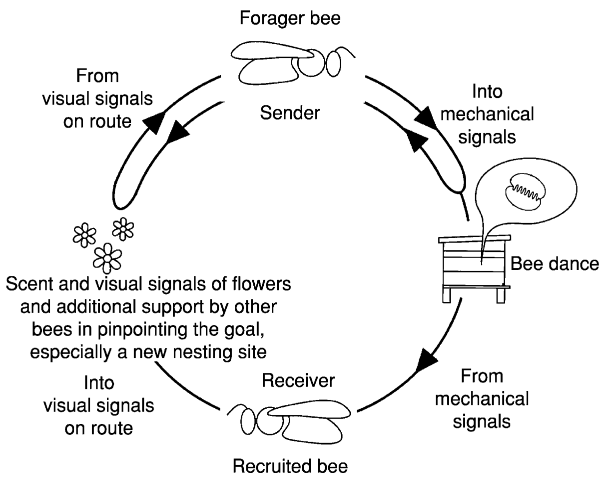

Figure 8 The 'dance language' is a highly complex phenomenon in which multiple translations of information within one bee and between sender and receiver bees take place. The dance language is one form of information transfer embedded in a continuous flow of information between the members of a honeybee colony.

follower bees fly out in the same direction as the dancer, the 'mistakes' that both bees make are the same and cancel each other out.

However, nonmanipulated dancers also send recruits not to a spot, but into a larger area. This area has an almost constant size independent of the distance from the hive. The reason for this is that the directions of consecutive waggle phases are not perfectly identical but show a certain degree of deviation. This deviation is smaller the further away the food source is. This leads to a scatter of the follower bees across a certain range and it makes more sense than having all bees that followed a dance go to one flower.

The identification of flowers in the area that bees have been sent to is thus easy to accomplish when recruited bees follow the scent of flowers. When bees are offered unscented food, events identical to the swarming recruitment result: Experienced bees synchronize their flight so they arrive in groups at the feeder, and once there they fly around in slow looping movements and release scent from a special gland to mark the area. Inexperienced bees then land together with experienced bees at the food source.

Thus, it becomes clear that bees keep contacts and exchange signals not only during the waggle dance. The waggle dance is one component, and the most conspicuous component, in a highly complex communication process in honeybees (see Figure 8).

See also: Animal Communication: Deception and Honest Signaling; Animal Communication Networks; Animal Communication: Overview; Development of Communication in Animals; Insect Communication; Traditions in Animals.

Bibliography

Dyer F (2002). 'The biology of the dance language.' *Annual Review of Entomology 47,* 917–949.

Esch H, Zhang S, Srinivasan M V & Tautz J (2001). 'Honeybee dances communicate distances measured by optic flow.' *Nature 411,* 581–583.

Lindauer M (1975). *Verständigung im Bienenstaat.* Stuttgart/New York: Gustav Fischer Verlag.

Seeley T D (1995). *The wisdom of the hive.* Cambridge, MA: Harvard University Press.

Srinivasan M V, Zhang S W, Altwein M & Tautz J (2000). 'Honeybee navigation: Nature and calibration of the "odometer."' *Science 287,* 281–283.

Tautz J & Sandeman D C (2003). 'Recruitment of honeybees to non-scented food sources.' *Journal of Comparative Physiology 189,* 293–300.

von Frisch K (1967 and 1993). *The dance language and orientation of bees.* London: Harvard University Press.

Wenner A M & Wells P H (1990). *Anatomy of a controversy: The question of a 'language' among bees.* New York: Columbia University Press.

Behaviorism: Varieties

P Poirier, Université du Québec à Montréal, Montréal, Québec, Canada

The term 'behaviorism' refers to a family of doctrines that emphasize the importance of behavior over mind, or cognitive processing, in psychology, notably as its proper subject matter or its ultimate evidential basis.

Psychological Behaviorism

Early in the 20th century, James Watson wove together three 19th-century ideas – Darwin's evolutionary theory emphasizing the physical as well as psychological continuity between animals and humans, Wundt's experimental method in psychology, and James's functionalist psychology – into both a method and theoretical overview for animal and human psychology. In 1913, he published what came to be known as