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Dance Language

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The "dance language" of honey bees refers to patterned, repetitive movements performed by bees that serve to communicate to their nestmates the location of food sources or nest sites.

RECRUITMENT

If a saucer of honey is placed outdoors, many hours or days may go by before a bee finds it and feeds on it. Soon after this first visit, however, large numbers of bees will arrive. Interest in honey bees goes back to prehistory, because their colonies provided human ancestors' most concentrated source of sugar. At least as far back as Aristotle, people have inferred that the bees that first discover a food source must recruit their nestmates to share in the collection of the food, thus accounting for the rapid buildup once a discovery has been made. The same kind of buildup occurs at flowers, bees' natural source of their sugary food.

Recruitment to food is one of the most important adaptations of nearly all social insects, and there are many forms of recruitment among them. Being able to recruit nestmates to food sources allows colonies of insects to realize one of the advantages of living in groups: the ability to harvest food that would not be as readily available to an individual foraging alone. Such edible items might include prey bigger than an individual could subdue, food resources that are rich but so widely scattered that an individual would not be likely to discover their source and sources that are ephemeral and thus more effectively harvested by means of group foraging during the short time the source is available. Cooperative foraging also is important to social animals in overcoming one of the inherent disadvantages of group living: since members of groups generally will compete with other members of the group for local food resources, without some compensating foraging advantage, solitary individuals would have better access to food than those in groups.

SIGNIFICANCE OF THE DANCE LANGUAGE

The best known of the mechanisms of recruitment in social insects is the honey bee (*Apis* spp.) dance language, in terms of both its fame outside the realm of specialists and the depth in which it has been studied. The dance language is famous for a number of reasons. It is frequently cited as the premiere example of symbolic communication among nonhuman animals, and it is one of the first and best examples of such communication aside from human language. The discovery that mere insects could perform such a complex behavior led to a reassessment of the behavioral complexity possible among these animals with relatively small nervous systems, which had formerly been regarded as simple automatons governed by instinct and reflex. Finally, the dance language has provided a tool for studying the perceptual world and behavioral response of bees that has illuminated our understanding of their vision, olfaction, memory, orientation, learning, and social organization, and has provided a model for understanding these areas about insects in general.

DISCOVERY OF THE DANCE LANGUAGE

Observers of bees had repeatedly noted that sometimes a bee in a colony will perform repeated circular movements, closely followed by other bees, but it was Karl von Frisch who firmly established the connection between these movements and recruitment, and, in the course of a long career, discovered many aspects of communication by the dance language.

Von Frisch began his studies of the dance language in 1919, with the simple yet powerful approach of marking bees with paint as they fed at a flower he had enriched with a drop of sugar syrup (and in later experiments with a simple scented syrup feeder). He then watched their behavior when they returned to a glass-walled observation beehive. He served his marked bees doing circular "round dances," which were watched attentively by other bees in the hive. He then observed that bees, presumably those that had attended the dances, would investigate nearby flowers of the same type as those at which the marked bee had fed but did not investigate flowers of other types as much. Von Frisch inferred that the dance stimulated recruits to look for food, and that odor in the nectar, and on the body of the dancing bee, communicated to the recruits the scent to seek. He also described a "waggle" form of the dance in which a dancing bee rapidly waggles her abdomen laterally while moving in a particular direction on the comb, then turns back more or less to the starting point, repeats the waggle on the same course, turns back the other way, and so on, describing a squat figure-eight with the waggle in the middle. The artificially small scale of his early work, in a small, walled, Munich garden, caused von Frisch to mistakenly conclude that the two kinds of dance he saw indicated different types of food. The waggle dancers often had pollen on their legs, whereas the bees he provided with nectar did not, so he concluded that waggle dances indicated pollen and the round dances nectar.

This error persisted for 25 years, but von Frisch himself discovered the full story when, during World War II, he was forced to take his studies away from the war-torn city to rural Brunnwinkel, Austria. There, in 1944 and 1945, working under conditions that more accurately reflected the natural scale of bees' foraging, he found that when bees fed at long distances from the hive they performed the waggle dances for nectar, as well. At the same time, he also made the startling discovery that the bees were communicating the direction and distance to the food source, as well as its odor.

COMMUNICATION OF DISTANCE AND DIRECTION IN THE DANCE

The waggle dance of honey bees can be thought of as a miniaturized reenactment of the flight from the hive to the food source (Fig. 1). As the flight distance to the food becomes longer, the duration of the waggle portion of the dance also becomes longer. The angle that a bee flies during the flight to the food, relative to the sun azimuth (the horizontal component of the direction toward the sun), is mirrored in the angle on the comb at which the waggle portion of the dance is performed. If the food is to be found directly toward the sun, a bee will dance straight upward. If the food is directly away from the sun, the bee will dance straight downward. If food is at 35° to the right of the sun, then the dance is performed with the waggle run at 35° to the right of vertical, and so forth. Bees make a transition from round dances for food sources near the nest to waggle dances at greater distance, with the transitional distance varying somewhat between different subspecies of *A. mellifera.*

While the bee is waggling her abdomen, she also produces bursts of buzzing sound from her wings, which are perceived by dance-following bees with the Johnston's organ at the base of the antennae. Recent work by Wolfgang Kirchner has shown that even the round dance contains directional

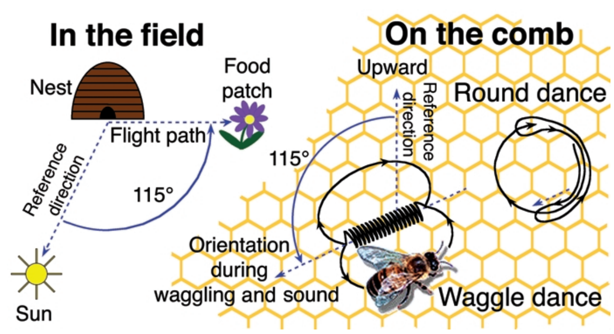

FIGURE 1 How direction to the food patch is encoded in the honey bee dance language. As a bee flies to flowers in the field (left), she learns the direction to the food patch relative to a reference direction of the sun azimuth (here the food is 115° to the left of the sun). When she dances on the vertical combs of the dark hive (right), she uses the direction upward as a reference and performs the waggling portion of the dance at the same angle, relative to this upward reference, to indicate that the food is to be found relative to the sun direction reference in the field (here, 115° to the left of upward). Dancing bees produce buzzing sounds during the waggle portion of the dance. In the round dance (far right), the dancing bee changes direction more randomly and does not waggle, but does buzz when moving in the direction that would indicate the direction to the food.

information, because these sounds are produced at the time in the round dance at which the circling bee is facing in the direction on the comb in which waggle runs would be performed for more distant food sources in the same direction. However, recruit bees seem to search the vicinity of the nest equally in all directions in response to round dances. This scatter in search area, however, is not really greater than the area searched at greater distances, though because of its proximity to the nest it includes all angles, whereas more distant searches are mostly within a restricted range of angles. Thus it is uncertain whether recruit bees can perceive the direction information in round dances.

MEASUREMENT OF DISTANCE AND DIRECTION

The ability to bees to communicate distance and direction to a food source requires that the recruiting bee and the recruits be able to measure these parameters. The study of how bees do this provides an example of how the dance language gives a readout of the perception of the bees. This in turn makes possible sophisticated analyses of the mechanisms by which bees acquire the information, analyses that are vastly more difficult to perform with insects that do not report their findings in a format entomologists have learned to decode.

Von Frisch found that wind, height differences between the feeder and hive, or adding additional weights or airfoils to bees changed the tempo of their dances. This finding indicated that something about these conditions had changed the bees' perception of distance to the food source. One aspect that was changed was the time of flight to the source, but the changes in dance tempo did not correlate well with the changes in flight time, and so this was rejected as the way the bees measured distance. Instead, it was concluded that the bees were measuring energy use, because all these conditions would affect energy use. This was consistent with observations that, on the flight to the food source, either a headwind or flying uphill would increase perceived distance, whereas either a tailwind or flying downhill would decrease it.

However, more recent work by Harald Esch and others suggests that it is not energy that is measured, but the movement of landscape objects across the visual field, or optic flow. Humans experience the apparent motion of landmarks as faster when riding in a car than when flying in an airplane. Similarly, when a bee flies close to the ground, she experiences rapid optic flow, whereas at greater altitudes the optic flow is less. In von Frisch's experiments, the changing conditions also affected the height off the ground of the bees' flight, so that energy use and optic flow were confounded. In experiments in which bees are trained to feeders at different distances from the ground, the distance that a bee perceives, as indicated by the tempo of her dances, is shorter for higher feeders, even though more energy is needed to fly to them and the length of the flight path is greater. The progress of entomologists' understanding of the mechanism by which bees measure distance provides an excellent example of how the conclusions from an experiment may reject incorrect hypotheses, but may also accept incorrect ones, if the predictions of the latter are the same as another alternative hypothesis not considered in the design of the experiment.

Martin Lindauer described the way in which bees measure the angle of body with respect to gravity, using groups of sensory hairs in the joints between head and thorax and thorax and abdomen. When Lindauer severed the nerves to these hairs, bees were no longer able to do oriented dances on a vertical comb. When flying in the field, bees use their compound eyes to measure their angle of flight relative to the sun, searching out the patterns of polarized light in the blue sky itself, even if the sun is not visible. The polarized light is produced by a phenomenon called Rayleigh scattering; the angles of polarization occur in a pattern that is consistent relative to the position of the sun, and this pattern moves across the sky as the earth moves relative to the sun. Rüdiger Wehner and S. Rössel discovered that the bees use a "celestial compass" to interpret the polarization patterns, namely, of a layout of ommatidia in the dorsal portion of the bees' compound eyes. Each ommatidium is selectively sensitive to a particular angle of polarization of light, and each ommatidium also gathers light exclusively from a particular region of the visual field of the bee. The layout of the ommatidia is such that when a bee is facing directly away from the sun, each ommatidium is looking at the region of the sky that contains the angle of polarized light to which it is most sensitive. Thus, as the bee rotates in flight, the summed response from these specialized ommatidia will reach a peak when the bee is aligned with the sun azimuth and fall away as she turns off it. Although the way in which a bee uses this system to hold a fixed course at a particular angle relative to the sun is not known yet, this compass provides a beautiful example of how a solution to a tremendously complex analysis can be built into the design of the sensory system, so that only relatively simple neural processing is needed to execute the behavior.

USE OF THE DANCE LANGUAGE

Honey bees are known to use the dance language to recruit nestmates in several contexts. In the context of foraging, bees dance to indicate the location of sources of nectar, pollen, water, and propolis (a resinous material collected from plants and used to seal cracks and waterproof the nest cavity). As far as is known, the dances for these different materials are the same, but this area has not been systematically investigated.

When a swarm of bees leaves its natal colony to build a new nest elsewhere, scout bees report the location of cavities they have found by means of the dance, and other bees inspect the advertised sites and may dance in turn. Over the course of hours or days the swarm views alternative sites discovered by different scouts and arrives at a unanimous decision on a single site. The swarm then takes off and flies to the new nest site. Only a small minority of the bees in the swarm has ever visited the chosen cavity. Therefore, although the information transferred by the dance could be important in guiding other bees to the site, there are probably other mechanisms, perhaps visual or olfactory, involved as well. The question of how swarms find their way, and the question of just how the dance language is used in the course of the swarm coming to a collective decision on a single nestsite, are still being investigated.

The sharing of information about food sources makes it possible for a honey bee colony to serve as an information center, pooling the reconnaissance of its many foragers, surveying a vast area around the nest, and focusing the bulk of its foraging force on the best sources discovered. In the 1980s a study by Kirk Visscher and Tom Seeley decoded the dances of a colony living in a deciduous forest in New York State to show the dynamics of colony food patch use that result from these interactions. Research by Seeley has shown that integration of foraging information via the dance language is quite flexible, and Seeley has worked out many of the mechanisms by which a honey bee colony responds rapidly to changes in the relative quality of food sources and colony need for food.

THE DANCE LANGUAGE CONTROVERSY

In the late 1960s Adrian Wenner, Patrick Wells, and Dennis Johnson challenged von Frisch's interpretation of the bee dances. While they did not question that the dances contain correlations of distance and direction, they pointed out that many experiments claimed by von Frisch to show that bees actually used this vector information in their searches could also be interpreted as indicating an exclusive reliance on odor. These ambiguous results were recorded when the recruiters' feeder was placed in the center of an array of scented bait stations and recruits were observed to come more frequently to stations near the center. This behavior, von Frisch's critics argued, would be predicted regardless of whether bees were using distance and direction (and odor) information or just odor information. Johnson and Wenner performed experiments at relatively short distances and with strong odors, and the results followed the expectations of recruits relying strongly on odor produced by bees feeding at the bait stations, but not the expectations of the location information in the dance.

Not all of von Frisch's experimental results were readily reinterpreted in terms of the odor-only hypothesis. For example, when a hive is turned on its side, bees are unable to use gravity as a reference for their dances and so do disoriented dances, and von Frisch showed that recruits were less well oriented under these conditions, although odor cues would not have been affected. Several lines of subsequent work have indicated that the search distribution of recruits can indeed be influenced by distance and direction information from the dance alone. The challenge in such studies is that normally odor information and dance vector information is highly correlated, so definitive experiments required means of unlinking them.

In the 1970s James Gould unlinked the location (and odor) of the food source on which dancers had foraged from the directional information in their dances. To achieve this, he shined a bright light from the side as bees danced. In this situation, recruiters or recruits will normally perform or interpret dances using the position of the light as the "sun" angle reference, rather than the direction upward. However, if a bee's ocelli are painted over with opaque paint, the bee becomes less sensitive to light, and so this shift in reference does not occur. By having recruiters with painted ocelli (and a reference of up) dancing, followed by recruits with unpainted ocelli (and reading the dances relative to a reference of the light, at some other angle), Gould was able to show that recruits could interpret a direction from the dance that was independent of the direction to the food source. The recruits then searched principally in the direction predicted by the modified dance information, rather than the true direction of the feeder, as would have been predicted by the odor-only hypothesis.

In the early 1990s Axel Michelsen, Martin Lindauer, and Wolfgang Kirchner constructed a computer-controlled robot bee that mimicked the behavior of a dancing bee. Recruits followed this robot bee and searched for food preferentially in the directions indicated by the dance angles programmed for the robot. Changes in the length of the robot bee's dances also changed the distribution of distances at which recruits were captured. The robot bee recruited rather imprecisely, with even more scatter than the rather large scatter of recruits from real bee dances. However, the demonstration that changing nothing but the computer programming was enough to cause significant shifts in the search distribution of recruits in the predicted manner was conclusive evidence that recruits were decoding distance and direction information from the dances.

CURRENT QUESTIONS

Although it is now quite clear that bees do decode the dances, odor does play a strong role in recruitment to food sources. It is appropriate to think of the dance as giving recruits a general idea of the direction and distance to the food source. Recruits then search in this area for sources matching the odors they have learned from the food carried by the dancing bee. Depending on the distribution of available food sources, the distance and direction information might be crucial in organizing a colony's food collection, or relatively unimportant. However, the relative importance of these two mechanisms in different habitats is just beginning to be investigated.

The angular scatter in the dance itself decreases with increasing distance indicated, as von Frisch reported. This change in scatter may be the result of changing duration of the waggle runs of the dance, but it also may be an adaptation to recruit bees to patches of more or less constant size at varying distances. This idea is supported by Seeley and Burmann's finding that the dances of scouts for nest sites, which are always single points rather than patches, have less scatter than those of nectar foragers. However, these results differ from those reported by Will Towne on the same issue, and this remains a question of current research.

The evolutionary origin origin of the honey bee dance remains incompletely discerned. All species of *Apis* perform recruitment dances, though there are interspecific variations in a number of the aspects discussed earlier. The stingless bees (Meliponini), the bumble bees (Bombini), and the orchid bees (Euglossini) are the closest relatives of *Apis,* but the phylogeny of these different taxa within the Apidae remains controversial. Stingless bees are highly social and have a variety of mechanisms of recruitment that may provide possible antecedents to the dance language, but a determinination of how the current form of the dance language might have arisen from these components must await both a greater understanding of recruitment mechanisms within the stingless bees and a more firmly established phylogeny within the family Apidae.

See Also the Following Articles

Apis Species • Feeding Behavior • Orientation • Recruitment Communication

Further Reading

Dyer, F. C. (2002). The biology of the dance language. *Annu Rev. Entomol.* **47,** 917–949.

Frisch, K. von. (1967). "The Dance Language and Orientation of Bees." Cambridge, MA: Harvard University Press.

Moffett, M. W. (1990). Dance of the electronic bee. *Natl. Geogr.* **177(1),** 135–140.

Seeley, T. D. (1995). "The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies." Cambridge, MA: Harvard University Press