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THE BIOLOGY OF THE DANCE LANGUAGE

Fred C. Dyer
Department of Zoology, Michigan State University, East Lansing, Michigan 48824; e-mail: fcdyer@msu.edu

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■ **Abstract** Honey bee foragers dance to communicate the spatial location of food and other resources to their nestmates. This remarkable communication system has long served as an important model system for studying mechanisms and evolution of complex behavior. I provide a broad synthesis of recent research on dance communication, concentrating on the areas that are currently the focus of active research. Specific issues considered are as follows: (*a*) the sensory and integrative mechanisms underlying the processing of spatial information in dance communication, (*b*) the role of dance communication in regulating the recruitment of workers to resources in the environment, (*c*) the evolution of the dance language, and (*d*) the adaptive fine-tuning of the dance for efficient spatial communication.

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INTRODUCTION

More than a half century ago, Karl von Frisch put forth the astonishing hypothesis that honey bees (genus *Apis*) communicate the location of food and other resources through body movements he called dances. These dances, done by foragers on their return to the nest, had been described by many observers over several centuries and had long been assumed to play some role in communication about food. Von Frisch's realization that dances carry spatial information was surely one of the major discoveries in behavioral biology in the twentieth century. Along with discoveries by other ethologists such as Lorenz and Tinbergen, the elucidation of the dance language opened our eyes to the sophistication and complexity of animal behavior and helped establish the study of behavior as a rigorous empirical science. Furthermore, experimental studies of dance language have provided a window to the subjective world, or *Umwelt* (115), of the honey bee. This window has provided an unusually clear view not only of what it is like to be a bee, but more generally of what it is like to be an insect.

In the 1960s, von Frisch published a masterly review of research on the dance language by him and his students (116a). Since that book's publication, work on the dance language has been pursued vigorously, leading to a greatly expanded understanding of the sensory basis of dance communication, the role of the dance in the foraging strategy of the honey bee colony, and the evolution of this remarkable behavior. Reviews of this more recent research have generally focused on one or a few aspects of the dance language (19, 38, 40, 41, 58, 66, 97). I adopt a broad, synthetic approach to convey the full range of questions that are addressed by research on the dance language and to review major recent developments and current frontiers.

My review relies most heavily on studies of the several races of the western hive bee *Apis mellifera*, which is the species von Frisch studied and is still widely used as a model organism. However, I also incorporate insights from studies of other species of *Apis*, all of which live in Asia (87, 104). These species share a number of traits with *A. mellifera*, including highly eusocial colonies, the construction of a wax comb in which brood are reared and food is stored, and communication based on dances. However they also exhibit striking differences in body size, colony size, nest architecture, and properties of the dances. Study of these differences has exposed new insights into both the mechanisms and evolution of the dance (19).

THE DANCE AS A SPATIAL COMMUNICATION SYSTEM

In a typical instance of dance communication (116a), a successful forager returns home from a rich food source and is greeted by other workers who, if she is carrying nectar, induce her to regurgitate her load to them. If this welcome is enthusiastic enough, the forager begins dancing on the vertical sheet of comb. The dance consists of a series of repeated waggling runs in which the bee moves in a particular direction along the comb while waggling her body from side to side.

During the waggling run she also emits a burst of sound by buzzing her wings. After each waggling run, the dancer circles around and realigns herself to begin the next waggling run. As the bee dances, she is encircled by 1–6 other bees that face toward the dancer and follow her movements. The dance followers observe several waggling runs and then leave the nest. Many of these eventually reach the same feeding place that the dancer had found or a feeding place close by.

The orientation of the waggling run and its duration are highly correlated with the direction and distance that the forager has flown to the food (Figure 1). Specifically the angle of the waggling run relative to the upward direction on the comb

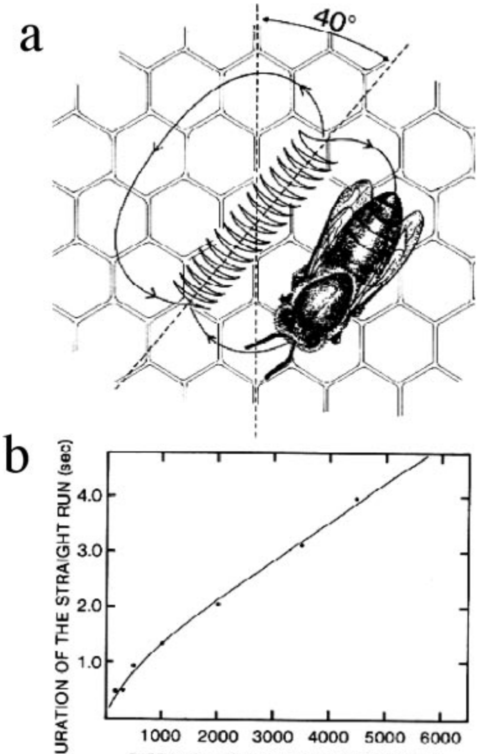

Figure 1 Waggle dance of honey bees (Modified from 92). During the flight to food or another resource, honey bees measure the direction (relative to the sun) and distance to the food. Direction is encoded in the orientation of the waggling run relative to gravity (or relative to the sun if celestial cues are visible during the dance). Distance is encoded in the duration of the waggling run. Different populations have different functions relating flight distance to waggling run duration. Other bees observing the dance use the spatial information it contains to fly to the general location of the food and odors carried by the dancer to pinpoint the actual resource.

correlates with the direction of flight relative to the sun and sun-linked patterns of polarized sky light. Dancers may also be oriented to these celestial cues directly if they can see them (e.g., when they are dancing on the surface of a reproductive swarm). The duration of the waggling run increases monotonically with flight distance, as can be observed in dances of bees trained to feeders at known flight distances. By placing arrays of feeders or baits in the environment, von Frisch found that recruits searched preferentially at baits near the one being visited by the dancer, suggesting that they had found their way there by using spatial information obtained from the dance.

Von Frisch also described another form of the dance that he called a round dance because the bee circled repeatedly in place, occasionally changing the direction of turning. This type of dance is done by bees that have flown to locations near the nest. Von Frisch suggested that round dances signal recruits to search near the nest, but they convey no information about direction. More recent research has revealed that many round dances actually contain directional information (56). Dancers produce sounds during round dances, when their bodies are aligned in the direction corresponding to that of the food. Thus, round dances may best be interpreted as waggle dances with short-distance signals. On the other hand, recruits that have followed round dances search in all directions near the nest (116a), thus they may have difficulty obtaining directional information from such dances.

Von Frisch emphasized an important role for odors in the recruitment process. Specifically, he suggested that floral odors and other environmental chemicals cling to the body of the foragers and are detected by the dance followers. Foragers also release an attractive pheromone on their return to a familiar feeding place. The spatial information in the dance allows recruits to get only to the general vicinity of the food; odors allow them to pinpoint the resource indicated by the dancer (116a). A powerful source of odors can even lead recruits to ignore the spatial information in the dance and find food in locations other than the one being signaled. This effect of odors on recruitment is strong for nearby sources of food but weakens considerably as the distance to the food increases (54), which makes sense given the inherent imprecision of odors as a cue for food location.

The interplay of spatial information and odors is at the heart of the so-called dance language controversy, which arose in the 1960s as a result of the suggestion that odors were sufficient to explain recruitment of honey bees (38, 125). The proponents of this “olfactory search hypothesis” did not deny that dances contained spatial information (123, 125). They simply challenged the evidence that recruits use this information. In most of von Frisch’s recruitment experiments, spatial and olfactory information were confounded—the location being signaled would also contain the highest concentration of odors matching those carried by the dancer. However, some of von Frisch’s results were difficult to explain by the hypothesis that recruits use odors alone. For example, when deprived of orientation cues, dancers do disoriented waggling runs, and in this situation, recruits search in all directions rather than being biased toward the feeding place that the dancers are visiting (116a).

In spite of this evidence that odors alone are not sufficient to account for recruitment, the challenge to the dance language hypothesis was taken seriously and led to a number of clever experimental approaches that have attempted to separate the influences of spatial and olfactory information on recruitment (33, 38, 54, 67, 68, 76). The consistent lesson from these studies is that odors carried by dancers are not sufficient to explain patterns of recruitment. Instead, essentially all experimental results can be accounted for by Frisch's original hypothesis that dancers convey both spatial and olfactory information but can weight one more than the other depending on the strength or reliability of the information. The odor search hypothesis has not been abandoned by its adherents (83, 124, 125), but most researchers consider the dance language controversy to have been resolved beyond any reasonable doubt.

SPATIAL-INFORMATION PROCESSING IN DANCE COMMUNICATION

This section explores the sensory and integrative mechanisms that mediate the flow of spatial information through the dance communication system. Figure 2 shows the key information-processing steps. The forager must first measure the distance of the food and its direction relative to the sun (compensated for solar movement) to store in memory the vector pointing at the food. Bees can learn the direct route to the food even if they have flown a circuitous searching path to get there, a process called path integration. This vector that is the output of the path integration process is used for navigation on subsequent trips to the food, and it is also what the bee encodes in her waggle dance. To encode the path integration vector in the dance, the bee must measure her body orientation relative to environmental features available in the nest, which will often be different from those available during the preceding flight, and also translate her flight distance into the duration of waggling.

The spatial information must now pass to other bees observing the dance. Their task is to measure the orientation and duration of the waggling run, using

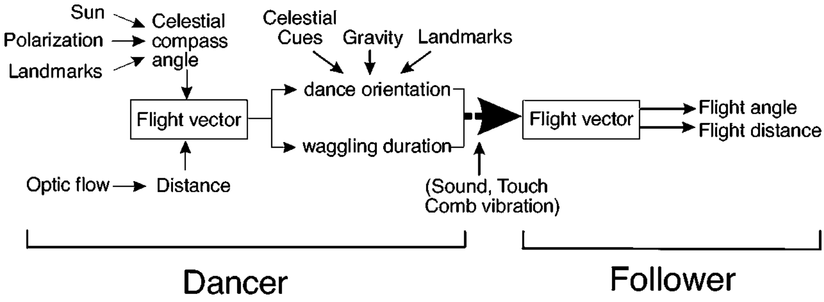

Figure 2 Processing of spatial information in dance communication. See text for explanation.

whatever sensory cues are available in the context of the dance, and to translate these measures into a vector corresponding to the direction and distance of the food. Using this vector to reach the food requires the bees to refer to sensory information available outside the nest, including the sun (which may have changed position since the dancer made her trip).

With this overview complete, I now turn to a consideration of the individual information-processing steps in this system.

Measurement of Distance

Von Frisch suggested that bees determine their flight distance by measuring the expenditure of energy during the flight and that this measure weights energy expenditure on the outward flight more heavily than that on the homeward flight. In support of these conclusions are several observations (32, 116a). (*a*) Bees loaded with lead weights signal greater flight distances than unloaded bees. (*b*) Bees signal greater flight distances in windy than calm conditions, and they signal greater distances if they have experienced a head wind on the outward flight than if they have experienced a tail wind. (*c*) Bees signal a greater distance if they have flown uphill to reach the food than if they have flown downhill. (*d*) Bees that have walked a short distance (3 m) to the food perform dances signaling a distance much greater than they have actually traveled, presumably because walking 3 m consumes more energy than flying 3 m.

Von Frisch (116a) also considered an alternative hypothesis, that bees measure distance by monitoring “optic flow”—the movement-induced streaming of visual texture across the visual field. Consistent with this hypothesis, bees that had flown to a feeder over a calm body of water (which provides weak optic flow) signaled a shorter distance than bees that had flown over land or over a wind-disturbed lake surface (either of which would provide a stronger optic-flow signal). However, although he recognized that optic flow could play some role, he regarded the energy hypothesis as more important.

Since 1990, Esch and other researchers have revisited this question in an extensive series of studies (29, 31, 32, 37, 81, 82, 105, 107, 108). In a striking turnabout, these studies have largely undermined the energy hypothesis and suggest that optic flow is the primary, if not only, source of odometric information for honey bees. This conclusion is supported by a number of lines of evidence. First, bees trained to fly upward to a feeder 50 m above the ground signal a long distance if the feeder is on a building (which offers optic-flow cues during the ascent), but they signal a short distance if the feeder is suspended from a helium balloon in open country (which offers limited optic-flow cues) (29, 32). Raising the balloon higher actually shortens the distance signal, which is consistent with the optic-flow hypothesis but not the energy hypothesis. Second, bees can be trained to fly to food through a mesh-covered tunnel that has an artificial textured pattern on the walls and floor, so that optic flow can be controlled experimentally. Bees can learn the distance at which to expect food in such a tunnel (106–108). Manipulations of airflow in the tunnel (which should affect energy expenditure) had no effect on the ability to fly the distance they had learned, but manipulations of the optic-flow stimulus had a strong effect. Finally, observations of the dances done by bees that have flown through tunnels show that bees greatly overestimate the flight distance reported in their waggle dances if the tunnel walls are textured but produce a short-distance signal if the tunnel walls are untextured (105). Also, dances by tunnel bees cause recruits to search in open country at a much greater distance than the foragers have actually flown to reach the food (33).

Esch and Burns have also pointed out that many of von Frisch's early experimental results, which he interpreted in support of the energy hypothesis, are consistent with the optic-flow hypothesis (32). For example, wind and slope would affect energy expenditure, but they also affect the height that bees fly above the ground. Bees fly closer to the ground in windy than in calm conditions and when heading up a slope rather than down a slope. Because nearby texture moves by more quickly than distant texture, the bee's height above the ground should strongly influence the optic-flow stimulus and hence the perception of distance.

The energy hypothesis has also been excluded as the odometer for desert ants (*Cataglyphis fortis*), which need to learn the distance to feeding places. On the other hand, ants can measure their travel distance when deprived of optic-flow cues (81), so they must obtain distance information from other sources, such as proprioreceptive feedback as they walk.

Measurement of Direction: The Celestial Compass

The sun has distinct advantages as a directional reference, including reliability, conspicuousness, and, because of its great distance, lack of susceptibility to motion parallax. Using the sun presents two major difficulties, however. First, it is sometimes obscured by clouds. Second, it moves.

Observations of dances when the sun is behind clouds led von Frisch to realize that bees could also obtain compass information from the polarization patterns of light coming from blue sky (116a, 120, 121). These patterns, produced when the sun's light is scattered in the atmosphere, provide a directional reference that is essentially equivalent to that provided by the sun.

Because bees can orient their dances to patches of blue sky or to polarized light coming from artificial sources, the dance provides extraordinary opportunities to explore the mechanisms of polarization vision. One can manipulate the spectral content of an artificial patch of sky, its degree of polarization, its size, and its position relative to the bee, and observe the angle of dancing to infer how the animal perceives these celestial features. These experiments are done with bees dancing on a horizontal comb, so that gravity cannot be used for orientation. Coupled with investigations of the optical and neurophysiological mechanisms by which polarized light is detected, such behavioral studies have led a complete picture of how this source of celestial information is used for orientation (84, 85, 120, 121), a story that is beyond the scope of this review.

If the sky is completely obscured by clouds, then neither the sun nor polarized light is visible to bees (4); however, overcast does not interfere with the ability of bees to find familiar sources of food and perform oriented dances. The explanation lies with landmarks. Bees can learn the path to food by reference to landmarks (18, 24, 116a). Furthermore, they can learn positions of the sun relative to landmarks, so that when they need to perform a dance on a cloudy day, they can retrieve from memory the correct dance angle corresponding to the current foraging route (17, 23).

It should be apparent that a memory of the sun (or of a dance angle based on the sun) would be useful only if it could be updated as the sun moves. Von Frisch's studies of how bees use the sun for navigation were one of the first demonstrations of a time-compensated sun compass in any animal. These experiments involved training bees to find food in a particular compass direction and then assessing the accuracy of orientation relative to the sun after various time intervals during which the sun moved (116a).

More recently, the dances of returning foragers have been used to study the details of sun compensation. To indicate a fixed feeding place, dances oriented to gravity (which is also fixed) must shift to compensate for the changing angle between the sun's azimuth and the direction of the food (Figure 3). If one knows

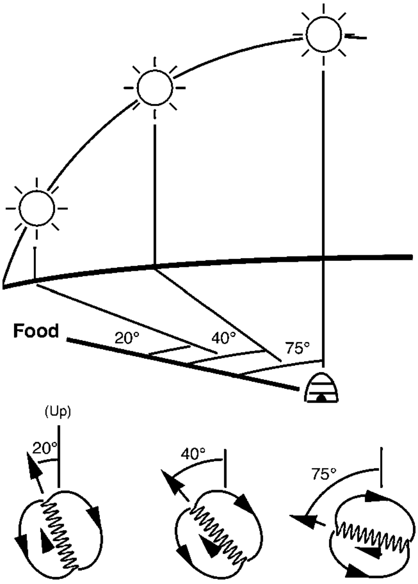

Figure 3 Dance communication as a window on the bee's ability to compensate for changes in the sun's azimuth (the sun's projection to the horizon). As the sun's azimuth shifts relative to the direction of the resource, the dance angle relative to gravity changes. By knowing the location of a resource (e.g., an artificial flower), an observer can assess the dancer's knowledge of the sun's changing position over time (21, 22).

the location of the food, the waggle dance provides a readout of where the bee has determined the sun to be (22). This technique has led to several insights into the sun compass of bees. (*a*) Observations of dances over several hours of overcast weather, when bees can see no celestial cues, have documented the accuracy with which experienced bees can compensate for the sun's movement by memory (24). (*b*) Dances revealed evidence of nocturnal sun compensation by one of the Asian honey bees, *Apis dorsata*. Workers in this species undertake foraging trips on moonlit nights and perform waggle dances to nocturnal feeding places (16). Although the moonlight is required for flight, the moon is not the reference for directional communication in these nocturnal dances. Instead, the bees signal directions relative to the extrapolated position of the sun, which they presumably find relative to landmarks visible by moonlight. (*c*) Observations of dances by bees that have experienced only a portion of the sun's course (e.g., during the 3 h preceding sunset) have provided insights into how bees learn the pattern of solar movement that is correct for the season and latitude at which they are active. We have known since the 1950s that bees learn the course of the sun during their first few days as foragers (64, 65, 116a) and that their knowledge is organized by reference to their endogenous circadian clock (65, 116a). The long-standing mystery has been how they learn it from observations of the sun's position at different times of day. Especially puzzling is the observation (64, 65) that bees can estimate the sun's position throughout the day even when they have previously seen only part of its course. Recent studies of this phenomenon (21, 22) show that bees possess an innate template describing the general pattern of solar movement. This template automatically specifies that the sun rises opposite where it sets and crosses from one side of the sky to the other at midday. By default, the template describes an approximation of the sun's course, but it is updated through experience to represent the actual pattern of solar movement more accurately.

Dance Orientation: Coding Flight Direction into Dances

Von Frisch showed that *A. mellifera* foragers could orient their dances either to gravity or to celestial cues. As far as we can tell, the orientation of dances to celestial cues involves the same mechanisms by which bees and other hymenopterans orient their foraging flights to celestial cues (120). In this sense the waggling run is a sort of pantomime of the flight (126). Orientation of the dance to gravity is mediated through proprioreceptive bristle fields between the major body segments and the segments of the legs (45, 116a).

Until the 1980s, there was no reason to suppose that bees could communicate directions relative to any features other than celestial cues or gravity. If both of these references are eliminated by forcing bees to dance on a horizontal platform without a view of the sky, the dances are disoriented (4, 116a, 120, 121). Magnetic cues provide no useful information for dance orientation (116a), even though bees can orient their bodies to magnetic fields in other contexts (11, 35, 88). On the other hand, comparative studies have revealed that landmarks visible to the dancer can play a role in dance orientation. The role of landmarks was first identified in the

Asian species *Apis florea* (15). The nests of this species are quite different from those of *A. mellifera*. A single comb is suspended from a thin branch in dense vegetation and is protected from the elements only by a blanket of interlinked workers. Dances take place on the flattened surface above the supporting branch. The first studies of dance orientation in this species (63) showed that there is no involvement of gravity but that celestial cues are used. Lindauer supposed that dancers were limited to the use of celestial cues and would be disoriented when these are blocked from view, for example, on a cloudy day. Following up on a later observation (61) that bees could remain oriented after celestial cues were blocked from view, I found that *A. florea* dancers can use landmarks seen from the nest (15). I provided bees with artificial landmarks consisting of a stripe pattern partially surrounding the dance surface. After a period during which dancers could see celestial cues as well as the landmarks, I blocked the sky from view, without making it too dark to see the landmarks. The dances continued to be oriented toward the food, and when I rotated the landmarks to a new orientation, the dance angles changed with them. The typical *A. florea* nest in vegetation would provide a rich source of landmark references. Their ability to use such landmarks for dance orientation is probably essential for dance communication when celestial cues are blocked from view.

As important as landmarks may be in *A. florea*'s communication system, there was still little reason to suspect they would play a role for *A. mellifera*. Dancers in this species almost always have either gravity or celestial cues available as a reference, and several studies had shown that dancers are disoriented when both references are eliminated. However, no one had tested whether *A. mellifera* dancers could use landmarks if they were first given the opportunity to see them in conjunction with celestial cues (as was the case in the *A. florea* experiments). When we did this experiment (9), we found that *A. mellifera* is just as good at using landmarks visible during the dance as *A. florea* is. It remains to be seen what role this ability plays in nature.

Distance Signal: Coding Flight Distance into Dances

Several features of the waggle dance contain information about the distance the dancer has flown to food. Von Frisch's standard measure was tempo, which he recorded as circuits per 15 sec (116a). Each circuit consists of a waggling run plus the return run that takes the bee back to begin the next waggling run. Tempo is easily measured by eye by recording the time period over which the dancer completes a given number of circuits. The same data can be used to compute average circuit duration, which is inversely related to the tempo. Tempo decreases with flight distance, whereas circuit duration increases. Other measures of the distance signal are hard to obtain in real time and instead must be obtained from video or audio recordings of the dance. For example, the duration of the waggling run, the duration of the sound produced during the waggling run, and the number of waggles produced during the run all increase with flight distance. Within a population all of these variables are highly correlated, and thus provide essentially redundant information about distance.

The function by which flight distance is mapped onto the distance signal varies across different populations and species of *Apis*, producing so-called dialects (3, 116a). Interpopulation differences are also observed in the flight distance at which round dances give way to clearly directional waggle dances (3, 116a). Evidence that this dialect variation has a genetic basis comes from experiments in which workers from different *A. mellifera* races were reared together in the same colony and did not converge on a common dialect (116a). The evidence for a genetic basis to distance dialects suggest that the tools of modern genetics may be applied in studying the mechanisms by which the visual signal from the odometer, which is recorded over a flight lasting perhaps several minutes, is translated into a duration of waggling lasting only a few seconds. One recent study provided evidence of a Mendelian pattern of inheritance for the flight distance corresponding to the transition from round dances to waggle dances (79). However, it is hard to interpret this in light of the evidence that a truly nondirectional round dance may not exist (56).

Information Transfer from Dancer to Follower

Given that the dance language is first and foremost a communication system, it is surprising how little is known about how the information in the dance passes to the follower bees (66). Dances provide a rich variety of potential communicative stimuli, but it is unknown which stimuli the bees use. In considering the possibilities, note that the features of the dance that help followers find and stay with dancers need not be the features that carry the signal of spatial location.

Three alternative sensory modalities have been suggested as the channel of information transfer in *A. mellifera*, none involving vision because dances of this species normally take place in complete darkness. These are (*a*) airborne sounds produced by the dancers' wings (and detected by the follower via the antennae), (*b*) vibrations of the substrate (detected via the subgenual organs), and (*c*) tactile cues (detected via the antennae and other sense organs on the head).

Evidence that airborne sounds play a role come from several observations, each of which is subject to some uncertainty. First, bees show spontaneous or conditioned behavioral responses to sounds in the frequency range typical of dance sounds, which suggests that they can hear these sounds (53, 112, 114). The relevance of these findings has been challenged on the grounds that the observed thresholds may be too high to allow bees to detect dance sounds (66).

Second, recruitment rates are lower in several situations in which sounds are missing from the dance: (*a*) when dancers are spontaneously silent (as occasionally happens), (*b*) when the dancer's wings have been removed just prior to the dance, and (*c*) when the dancer carries a mutant allele that causes diminutive wings (50, 57, 58). However, it is possible that the motivation of dancers was reduced in each of these situations, affecting other relevant features of the dance. Or, perhaps sound serves to attract followers but carries no spatial information, so a silent dancer may have fewer followers, and hence reduced effectiveness in recruitment.

Third, the production of airborne sound is necessary for a mechanical model bee to recruit bees to feeding places in the environment (68). Here again the possibility exists that the sound merely helps followers to stay oriented to the dancer but is not the channel through which spatial information flows. Furthermore, the recruitment efficiency of the model bee is low, suggesting that something beyond the presence of sounds and the correct pattern of body movement is needed for effective communication.

The hypothesis that substrate vibrations carry the dance signal is supported by various lines of evidence, all rather circumstantial. First, it has been argued that inefficiency of the mechanical model in recruiting bees is a consequence of the fact that the model is not in contact with the comb where the follower bees are standing, and hence cannot transmit vibrations to them (109). Second, bees appear to seek out open rather than wax-sealed brood cells when performing their dances, and recruitment efficiency is higher when dances take place on open cells than when they are on sealed comb (109). Sealed comb is presumed not to transmit vibrations as well as open comb. The problem with this evidence is that the experiment did not control for the possibility that fewer recruits attend dances on sealed comb, or, alternatively, that recruits have difficulty following dances on sealed comb. Such differences in recruit behavior might develop if, for example, prospective recruits avoided sealed comb because they are unlikely (normally) to find dancers there, or if they found it harder to maintain their footing while following dances on sealed comb. Third, it is possible to measure slight vibrations of the comb in the vicinity of a waggling bee (74), although these vibrations are so weak they might be swamped by background noise during a normal dance.

Set against these lines of evidence supportive of a role for substrate vibrations is evidence that, whatever role they may play in some restricted circumstances, they are clearly not necessary for dance communication to occur. For example, in reproductive swarms of *A. mellifera* and on the exposed nests of the Asian honey bees *A. florea* and *A. dorsata*, dances take place on top of a curtain of interlinked worker bees (19, 63, 110, 111). Because dancer and dance follower typically stand on different curtain bees, there is no path for the transmission of a vibratory signal. In such situations, a modality other than substrate vibration must be involved.

A possible role for tactile cues is supported by the observation that there is substantial physical contact between dancers and dance followers during the waggling run. The challenge is to understand whether the tactile information is precise enough to account for the efficiency of recruitment (80).

Other observations of the Asian honey bees make the picture even more complex. Based on sound and video recordings of dancers, Towne (110) reported an absence of dance sounds in two species that nest in the open (*A. florea* and *A. dorsata*), but intense dance sounds in the Asian hive bee *A. cerana*, which, like *A. mellifera*, normally nests in enclosed cavities. Towne also observed striking differences in the postures of dancers in open- versus cavity-nesting bees. Both

A. mellifera and *A. cerana* waggle their bodies side to side with their wings folded flat over the abdomen. *A. florea* and *A. dorsata,* by contrast, both add a dorsoventral oscillation to the waggling motion, so that the abdomen appears to flail wildly during the waggling run, and both species also hold their wings flared out to their sides. Towne suggested these postural features in the open-nesting species serve to make the dancer visually conspicuous to followers. Thus vision, as opposed to sound, may be an important modality for communication in open-nesting species.

Subsequent studies using improved recording equipment confirmed that *A. florea* is indeed silent during its dances but that *A. dorsata* produces sounds similar to those of *A. mellifera* and *A. cerana,* although less intense (12, 51). A role for sound in *A. dorsata*'s dances is further supported by the observation that dances are noisier when bees are dancing at night, when dances would be harder for followers to see (12). On the other hand, a close relative of *A. dorsata* from the Himalayas, *Apis laboriosa,* which appears never to fly at night, always dances silently (52).

Although these various observations complicate the pattern described by Towne, they are largely consistent with his basic idea that sounds play a role in dances that take place in low-light conditions and that dances that take place in the open may provide information through postural (visual) cues. It remains to be seen whether a cavity-nesting, sound-producing species such as *A. mellifera* can make use of visual cues when the dance takes place outdoors, for example on a swarm, and whether visual cues actually carry spatial information or if they merely serve to attract followers to the dancer.

Setting aside the question of which sensory channel carries the signal, a further issue concerns how bees translate the duration and orientation of the waggling run into a flight vector. This problem is perhaps straightforward in the case of the distance signal, where the duration of the signal (however it may be perceived) may directly translate into the magnitude of the flight vector. The problem is potentially more difficult in the case of the direction signal. At any given moment during the dance, followers are arrayed in various orientations relative to the dancer. Working out the compass direction being signaled in the dance would require the follower to measure her own orientation relative to both gravity and the dancer and then, in effect, transform her gravity angle into that of the dancer. The challenge of calculating this transformation would be further compounded by the difficulty of measuring relative body orientations using touch or sound. Theoretically, the bee could do this by exploiting spatial patterns in the sound field around the dancing bee (66), but this hardly simplifies the problem.

A pair of observations suggest the problem may be simpler than it would appear. First, the choreography of dance following has the effect of frequently bringing dance followers behind the dancer and into alignment with her. If the follower could detect when she is behind a waggling dancer, then by measuring her own current body alignment at this point she is also measuring the dancer's waggling angle. Second, by using individually marked bees, Judd (49) found that recruitment rates are higher for follower bees that have had the opportunity to occupy the position behind the dancer than for followers that have observed dances from other angles.

Thus, even if bees can measure relative body angles and calculate the necessary transformations, they may not be good at it.

Does the Waggle Dance Communicate Height?

The power of flight enables foragers to find food at various heights above the ground, and this realization led von Frisch to wonder whether there were any "words" in the honey bee dance language for height (116a). He trained bees to find food by flying up or down tall cliffs or human-made structures. He found no evidence that the dances of these bees carried information about height nor that the recruits had obtained such information.

More recently, studies of an Asian cavity-nesting species, *Apis koschevnikovi*, have suggested that, given a choice between feeders at two different heights in a forest canopy, recruits will arrive preferentially at the one being indicated by dances (86). However, the authors point out that this need not imply that height is being signaled in the dances. Instead, the recruits may head in the direction and distance indicated in the dances and then range vertically to locate the odors of their nestmates at the food.

DANCE COMMUNICATION AND DECISION MAKING BY COLONIES

Dancing behavior is not an all-or-none stereotyped affair. Sometimes returning foragers do not dance at all but simply unload whatever they have collected and then return to the food source to collect more. If they do perform a dance, it may consist of just a few dance circuits or of a hundred circuits. This variation in the tendency to dance strongly affects where the colony's recruits are sent. It has been known since the 1950s that the regulation of recruitment is not haphazard but results in the allocation of recruits to resources that are of greatest benefit to the colony. For example, bees are more likely to perform dances to nectar sources that are higher in concentration or closer, either of which would enhance the energetic profit to the colony. If the colony is heat-stressed, dances to sources of water become more common and more intense than dances to nectar (116a).

Although a role for dances in the regulation of recruitment was recognized long ago, only in the past 20 years have the mechanisms underlying this regulation become clear. These mechanisms can be summarized by extending the information-processing perspective developed in the previous section. However, whereas the previous section focused on spatial information, here the focus is on the processing of information about the value of alternative resources (see Figure 4). Furthermore, the flow of information is mediated not only by the forager's experience in the environment but also by activities of nestmates with whom she interacts. In fact, the social nature of the decision-making process leads us to consider the colony as the decision-making entity, faced with the problem of allocating a finite number of recruits.

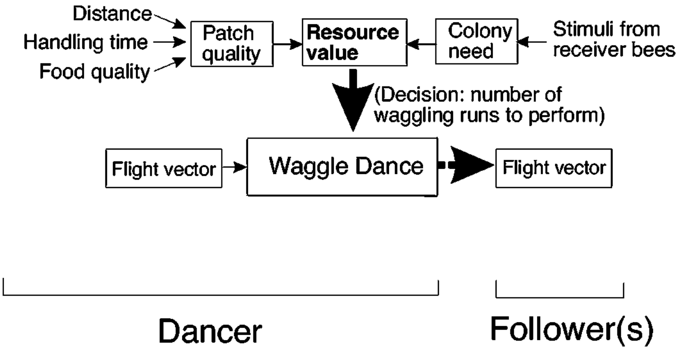

Figure 4 Modulation of dance communication according to the value of the resource (a combination of intrinsic resource quality and the colony's need for the resource). The mechanisms for assessing resource quality and colony differ for different resources (e.g., nectar, pollen, water, nest sites). See text for details.

These decision-making processes have been studied in four domains: nectar-foraging, water-collection, pollen-foraging, and the selection of a new nest site by a reproductive or dispersing swarm. I give only a brief summary of the insights from this research because much of it was beautifully reviewed in Seeley's 1995 book (97).

A critical factor determining the level of recruitment for a particular resource is the number of dance circuits performed by bees that have discovered it. In the case of nectar sources, the decision of how many circuits a dancer should perform (if any) is based on the value of her resource relative to others currently available (93, 94, 96, 97, 101). This decision is partly influenced by information available only to the forager, including the distance to the flower patch, the handling time in the patch, and the sweetness of the nectar. Such cues indicate the intrinsic profitability of a patch but not its value relative to other patches. Because foragers do not directly compare patches, they cannot assess relative value directly. Instead they do so via a well-calibrated network of social feedback mechanisms that provide foragers information about the needs of the colony (92, 97–99, 101). The proximate indicator of colony need (i.e., whether food of that quality merits additional recruitment) is the latency with which the forager is greeted by other bees and relieved of her cropload of nectar. Shorter latencies increase the probability of a forager's doing a large number of waggle dances to a patch she has found; longer latencies result in fewer waggling runs or none at all. The latency to be unloaded is affected by two critical factors. First, if a large amount of nectar is coming in from the environment, unloader bees tend to be occupied, in effect forcing foragers to queue up to be unloaded. Second, if the colony is already full of honey, unloader bees take a long time to find an empty cell to deposit the nectar they have taken from foragers, thus they will be unavailable to receive incoming foragers.

The number of waggling runs done by a forager can be viewed as an indicator of the overall value of the resource (reflecting both its intrinsic profitability and colony need). This may not be the only signal of resource value provided by the dances. Many observers have noted that bees dancing to good patches seem more vigorous or lively than those dancing to poor patches (116a), but it has been hard to quantify this subjective impression. In the case of round dances, Waddington and colleagues (117, 118) documented various acoustic and locomotor correlates of food source quality, including a more rapid rate of circling, but such patterns were not obvious in waggle dances (103). More recently, however, Seeley and colleagues (102) reported faster return runs in waggle dances to more profitable food sources. Whether follower bees respond to these correlates of profitability is unknown, although it is possible that the liveliness of the dance serves to attract more followers and hence more recruits.

The immediate effect of long unloading times is to reduce the amount of dancing and recruitment to a given patch of flowers, hence limiting the rate of nectar intake from that resource. Clearly, however, it would be in the colony's interest to continue to harvest nectar from a highly profitable resource, if the capacity to handle the incoming nectar could be increased. Honey bee colonies have at least two feedback mechanisms that do this on different time scales. First, foragers that have experienced long unloading times can provide a signal to the colony of the need to increase the capacity to handle the incoming nectar. This signal is the so-called tremble dance, in which the forager meanders across the comb jerking her body and buzzing her wings in a characteristic way (55, 95). Workers that encounter a tremble dancer have a tendency to assume the role of unloader bee, hence decreasing the queueing time for incoming foragers. The second feedback mechanism, which works on a longer timescale, is the building of new comb, resulting in an increase in the capacity to store nectar (97). Although it is well established that the secretion of wax and the construction of new comb are initiated in times of high nectar flux (78, 97), it remains unclear what proximate cue triggers these processes (97).

The mechanisms regulating recruitment to resources other than nectar exhibit some differences from those I have summarized above, but they share some basic properties. First, the decision-making process is decentralized, with no direct comparison of alternative patches by any bee in the colony. Second, the decision of whether to dance is influenced by information obtained directly about the intrinsic quality of the resource and information obtained indirectly about the state of the colony or of the relative value of the resource. For details about the regulation of recruitment to these other resources, see the references listed [water (43, 92), pollen (5, 6, 14, 34), new nesting sites (20, 92, 97)].

EVOLUTIONARY ORIGIN OF THE DANCE LANGUAGE

Attempts to understand the evolutionary history of the dance language have relied on comparison of the communication systems of different living species of social bees. In many species of social Hymenoptera, including the social bees most closely related to honey bees, returning foragers interact with nestmates and arouse them to search for food. In some species these interactions are reminiscent of honey bee dances (28, 30, 63, 71, 75), and a consideration of these simpler dances will be useful for making inferences about the origin of the honey bee dance language. However, we begin with comparisons within the genus *Apis* itself in order to provide a detailed picture of the diversity of phenotypic characters that an evolutionary hypothesis must address.

Origins: Insights from the Genus *Apis*

Martin Lindauer's pioneering studies of the three *Apis* species that live in Sri Lanka (then Ceylon) led him to propose that the extant species of *Apis* exhibit a progression in the complexity of dance communication that corresponds to the phylogenetic development of the dance during *Apis* evolution (63). The three species that Lindauer studied were the open-nesting "dwarf bee" *A. florea*, the "rock bee" *A. dorsata*, and the cavity-nesting Asian hive bee *A. cerana*. At that time these three species and *A. mellifera* were the only species recognized in the genus *Apis*; now other Asian species are recognized, but each of the new species is biologically similar to one of the species Lindauer studied, and so his comparisons captured the relevant diversity in behaviors related to dance communication.

Lindauer suggested that the ancestral bee from which the dance language evolved was much like *A. florea*, building a single comb in the open and orienting its dances to celestial cues but lacking an ability to use gravity as a substitute for the sun. In the initial stages, this dance may have consisted merely of excited, disorganized movements that served merely to arouse nestmates to search for food. However, as these movements came to be oriented relative to celestial cues, and as nestmates acquired the ability to bias their searching flights according to the orientation of the dances they observed, the communication system would have been heavily favored by natural selection. A later evolutionary stage is represented by rock bees such as *A. dorsata*, which Lindauer thought depended on a view of celestial cues while dancing on their exposed nests but nevertheless seemed to translate their solar flight angle into a dance angle relative to gravity. The most advanced stage is represented by cavity-nesting hive bees such as *A. cerana* and *A. mellifera*, which can use celestial cues if they are available but can also use gravity. In fact, the evolution of the ability to use gravity was supposed to have set the stage for the ancestor of hive bees to move into cavities.

Lindauer's hypothesis has an element of circularity, in that it depends on a hypothesis about phylogenetic relationships based on the characters (nest architecture and characteristics of the dance) whose evolution he was trying to explain. Indeed, his suggestion that the ancestral *Apis* species nested in the open overlooks the fact that the construction of nests in the open is not observed in other social bees, hence appears to have been derived within the genus *Apis* (59). Without independent support for Lindauer's phylogenetic hypothesis, one could not exclude the hypothesis that cavity nesting was the ancestral condition among honey bees with

	dwarf bees	rock bees	Eastern hive bees	Western hive bee
Landmarks used	Y	?	?	Y
Slope compensation	Y	N	N	N
Typical dance plane	0°-80°	90°	90°	90°
Gravity used	N	Y	Y	Y
Sky cues used	Y	Y	Y	Y
Nest exposure	open	open	cavity	cavity

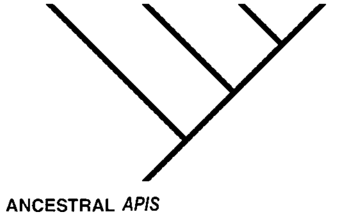

Figure 5 Phylogenetic diversification of the waggle dance, as inferred from comparisons of directional communication and nesting behavior within the genus *Apis*. Phylogeny is based on molecular and morphological characters (1, 27). The information on dance characters reflects both the original observations by Lindauer (63) and newer work (15, 16, 19, 59–61). The cladogram shows only four taxa, but actually there are at least two species of dwarf bees, two species of rock bees, and four eastern hive bees in addition to the western hive bee *A. mellifera* (104).

respect to nest architecture and that the dance language evolved in an enclosed cavity rather than in the open.

In recent years, studies of morphological and molecular characters have provided such an independent phylogenetic hypothesis (1, 27). These studies have vindicated Lindauer's (63) intuition that dwarf bees indeed diverged early on from a lineage that leads to the rock bees and then to the hive bees (Figure 5). This would seem to support Lindauer's contention that the dance language evolved on an exposed nest and that the return to enclosed cavities by the ancestor of hive bees occurred after the evolution of the ability to orient dances to gravity. However, parsimony is still equivocal on this point (1): (*a*) Open nesting may have arisen in the ancestral *Apis* prior to the evolution of the dance language, followed by a reversion to cavity nesting in the ancestor to the hive bees (Lindauer's hypothesis); or (*b*) open nesting may have arisen independently in the dwarf bees and rock bees after the origin of the dance language.

Behavioral comparisons done in the past 15 years have further complicated the picture that emerged from Lindauer's work. For example, although there remains no evidence that dwarf bees use gravity in their dances, rock bees can use gravity in the complete absence of celestial cues, just as in the hive bees (16, 19, 60).

Thus, among the extant *Apis* there exists a dichotomy, rather than an evolutionary progression, in the use of gravity.

Additional evidence of a phylogenetic dichotomy in the organization of dances emerged from a detailed comparison of the behavior of dancers on slopes. Lindauer's (63) studies of the dwarf bee *A. florea* gave the impression that dances in these species are confined to a near-horizontal region atop the nest. Indeed, he reported that bees became confused when forced to dance on the vertical flanks of the nest. Later, however, I discovered that *A. florea* dancers frequently move down the steep slopes flanking the rounded dance area and can dance with a consistent orientation even if forced to dance on the vertical sides of the nest (15). Although *A. florea* dancers exhibit a consistent pattern in their orientation in these experiments, their orientation differed strikingly from that seen when *A. mellifera* dancers orient to celestial cues on steep slopes. If an *A. mellifera* dancer is exposed to the sun or a bright artificial light source, it will orient its waggling runs to the apparent azimuth of this source relative to the plane on which the dance takes place. In *A. florea,* by contrast, dancers use the actual horizon as the reference for determining azimuth, even if they are dancing on a rather steep slope. The difference arises because *A. florea* dancers counterrotate their heads to compensate for slope, so that their visual field remains in a stable relationship relative to the actual horizon. In *A. mellifera,* by contrast, the head rotates with the body as the dancer walks onto steeper slopes, so the plane on which the dancer is standing defines the apparent horizon to which celestial cues are referenced (15). Figure 6 shows an example of this difference.

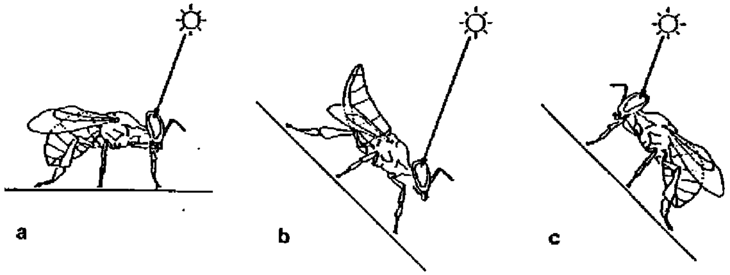

Figure 6 Interspecific differences in the pattern of orientation to celestial cues by dancers that see the sun from a slope. (*a*) When dancing on a horizontal surface, both *A. mellifera* and the dwarf bee *A. florea* align their waggling runs so that they have the same view of the sun they observed during the flight (straight ahead in this example). (*b*) On a slope, *A. florea*, rotates its head to compensate for the slope, keeping its visual coordinates in a constant position relative to the horizon. (*c*) On a slope, the heads of hive bees are rotated along with their bodies so that the plane on which the bees are dancing defines the subjective horizon and the sun's apparent azimuth. In this example, to see the sun straight ahead the bee has to align her waggling runs uphill (19).

These observations suggest that there are two types of waggle dance with respect to the communication of direction: the type seen in the dwarf bee lineage (as exemplified by *A. florea*) and the type seen in the lineage that includes rock bees and hive bees (as exemplified by *A. mellifera*). This pattern complicates the problem of making inferences about the evolution of the dance language from comparisons within the genus *Apis* because it provides no way of assessing under parsimony which type is ancestral and which is derived. One way of obtaining additional clues would be to find evidence of hidden similarities between these two lineages. Traits that are present in all taxa, even if not routinely expressed, can be interpreted as plesiomorphic for the genus. An example is the ability to use landmarks as references for dance orientation. As mentioned earlier, this ability was first described for *A. florea* (15) and was presumed to be absent in other species; hence at first it appeared to be one of a suite of characters unique to the dwarf bee lineage. However, later studies uncovered evidence of this ability in *A. mellifera* (9). Thus, this trait may be a universal property of honey bee dances, supporting the conclusion that it was part of ancestral dance language (19). Conceivably, the same sort of evidence could be adduced for other components of the dance language.

Origins: Insights from Other Social Bees

Comparisons of the extant *Apis* species have uncovered a number of ambiguities concerning the polarity of key evolutionary transitions. The standard way that phylogenetic methods resolve such ambiguities within a group is to study character states in outgroups that exhibit homologous traits. One complication in doing this with the dance language has been the difficulty determining the phylogenetic relationships among honey bees (tribe Apini) and their closest relatives. These relatives include the stingless bees (Meliponini), which like the honey bees are highly eusocial; the bumble bees (Bombini), which are primitively eusocial; and the orchid bees (Euglossini), which are solitary (69). Interest in the phylogenetic relationships among these four taxa has been driven primarily by the question of whether eusociality arose once in a common ancestor of honey bees and stingless bees, or independently in these taxa (8, 10). For the purpose of understanding the evolution of the dance language, however, the value of a phylogenetic hypothesis is to indicate which taxon is the sister to the honey bees, and hence is the best choice for outgroup comparisons. In spite of some lines of evidence placing bumble bees or orchid bees as the sister taxon to honey bees (8), a total evidence phylogenetic analysis favors the stingless bees (10).

Even if we work from the assumption that stingless bees are the relevant group for outgroup comparisons, we still face the problem of identifying behavioral traits that we might use to polarize evolutionary changes in the dance language of honey bees. The difficulty is that the communicative interactions in stingless bees show few obvious similarities to the features of the honey bee dance language that allow for accurate spatial communication.

Most species of stingless bees studied to date exhibit a behavior reminiscent of the dances of honey bees (30, 46, 48, 63, 70). Returning foragers run among their nestmates buzzing their wings and dispensing samples of the food that they have brought back. These dances arouse other bees, which move out of the nest and fly in search of food. In some species, these dances play a role in spatial communication, leading to the recruitment of nestmates to locations near where the foragers have been feeding rather than at control feeders offering food in other locations. In some cases, this spatial communication is mediated entirely by odor marks deposited by the knowledgeable foragers on their way back to the food (63). On the other hand, a role for odor trails has been excluded in some species of *Melipona* by training bees to locations across water and showing that recruits still preferentially arrive at the station visited by the dancers (28, 48, 72, 75). Experiments of this kind have suggested that the bees' dances might communicate not only direction and distance but also height.

It remains unclear just how this information might be communicated, but sounds made by the dancers offer an intriguing possibility. In *Melipona panamica*, the durations of sound bursts produced by the dancer were found to correlate with flight distance, and other sounds made by the forager as she was unloaded correlated with the height she flew (73). No obvious feature of the dance correlated with flight direction, leading to the speculation that direction is signaled by foragers performing exaggerated flights toward the food as they depart on their next trip to the food (28, 71).

As intriguing as these speculations are, it is important to bear in mind that the evidence for spatial communication by *Melipona* dances is weak. In one species that shows spatial biases in recruitment, *M. quadrifasiata*, detailed measurements of dance features found no evidence of spatial information in the dance (46). Furthermore, in no species have odors been excluded as the factor biasing the searching of recruits toward the location visited by the dancer. It is true that odor trails deposited by foragers have been eliminated as an explanation in some cases, but it is possible that recruits can orient to other feeding-site odors carried by the dancer. Thus, all of the same concerns raised against von Frisch's recruitment experiments during the dance language controversy arise here, especially in light of the fact that stingless bee recruitment experiments take place over relatively short distances. Even in *A. mellifera*, recruitment over short distances is strongly influenced by odor, independent of the availability of spatial information (54).

Even though the question of whether the dances of stingless bees signal spatial information remains unresolved, these dances support at least one conclusion concerning the evolution of dance communication. Dance behavior—an intensive interaction at the nest between returning foragers and their nestmates—arose prior to the origin of the genus *Apis*. Hence these dance precursors must have arisen in bees that nested in an enclosed cavity, where bees would be deprived of celestial orientation cues and would be forced to provide vibratory or tactile signals. Beyond this, however, it is impossible to determine on the basis of these comparisons whether an *Apis*-like dance, with precise directional and distance communication, could have arisen in an enclosed cavity.

The lesson of this section thus far is that comparisons of overt dance-like behavior by returning foragers provide little guidance regarding the polarity of key transitions in the evolution of the honey bee dance. An alternative approach might be to consider the polarity of behavioral elements that may play a role in dance behavior and that may be expressed in a noncommunicative context in outgroup taxa that lack dances. One example is the ability to orient to gravity, which in most insects is expressed as simple geotaxis and plays a role in escape responses. Comparisons of geotaxis in various bee taxa revealed that the *Apis* species that use gravity in their dances exhibit a phylogenetically derived form of geotaxis, whereas *A. florea*, which does not use gravity in its dances, resembles outgroup taxa in its geotactic response on slopes (47). This is consistent with Lindauer's hypothesis that *A. florea*'s inability to orient dances to gravity is a primitive condition. This interpretation is not without ambiguity (19, 44, 45, 59), but this example still stands as a nice illustration of how to make outgroup comparisons when the outgroup taxa do not exhibit the trait in question.

ADAPTIVE DESIGN OF DANCES FOR EFFICIENT SPATIAL COMMUNICATION

Viewing the dance language as the product of evolution invites us to consider ways in which it may have been optimized by selection for its function of communicating spatial information. As in the case of the historical question of how the dance originated, studies of this functional question have relied on comparative studies, here examining how the dance varies with the goal being indicated or how it varies across different populations or species of honey bees. One possible example of this, discussed earlier, is the tendency for species that dance in darkness to produce sounds during the waggling run and those that dance in the open to have exaggerated postures that may enhance visual information transfer. Here I consider three additional aspects of dance communication that have been studied as possible instances of the adaptive fine-tuning of the dance language.

Distance Dialects

Boch's (3) and Lindauer's (63) discoveries of population and species differences in the slope of the distance-dialect function led von Frisch (116a) and others (25, 39) to speculate about the possible adaptive significance of these differences. Von Frisch's hypothesis was that the slope of the dialect function evolved under two major influences. First, he suggested that steeper slopes allowed for more precise communication, in that a given amount of error in producing or reading the signal would translate into a smaller amount of error in the distances searched by recruits. Second, he suggested that the steepness of dialect functions would be limited by a constraint on how long the distance signal could be for dances indicating the limits of the colony's flight range. If the function were too steep, waggling runs for distant sites might be so long that the recruits would have difficulty staying with each waggling run, let alone sampling several of them.

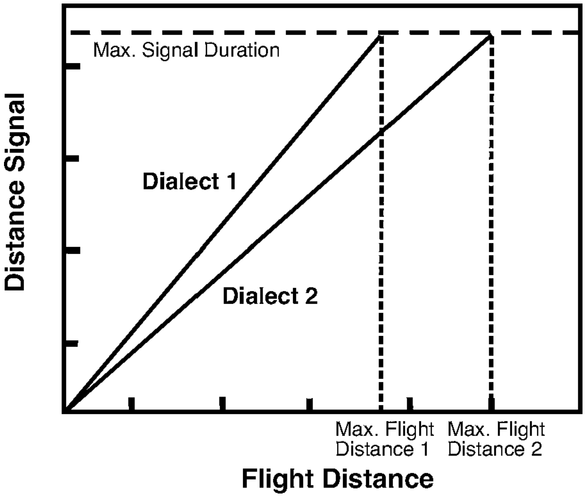

Figure 7 Summary of von Frisch's hypothesis that distance dialects are tuned to ensure maximum precision over the flight range of the bees (where flight range is determined independently by ecological factors or body size). Steeper dialect functions are assumed to be more precise (see text), but a function that is too steep would produce waggling runs that may be hard for other bees to follow. Assuming a common upper limit on distance-signal duration, then populations with a shorter flight range should evolve steeper dialect functions (19, 25, 116a).

This hypothesis makes the prediction that the steepness of the dialect curve and the maximum typical flight range of bees in the population should be inversely correlated (Figure 7). In populations where flight range is constrained (by body size and ecological factors) to a shorter typical distance, dialect curves should evolve to be steeper. Testing this prediction requires a comparison of flight range and dialect curves in the same population. It is relatively easy to measure the dialect curve—one trains the bees to a series of known distances and records the dances, although a potential difficulty is that the shape of the curve may vary among foraging routes depending on visual features of the terrain that influence the optic flow experienced by foragers (33). Another challenge is to get an accurate picture of foraging range. Earlier studies used the unreliable technique of training bees as far as they would fly to an artificial feeder (63) or compared flight ranges in disturbed habitats (77).

More recently, Dyer & Seeley (25), in a study of *A. florea*, *A. dorsata*, and *A. cerana*, used the technique of "forage mapping" (116), whereby one observes dances to infer how far bees have flown to natural feeding sites. Our evidence appears at first to undermine the adaptive-tuning hypothesis. We found that the dialect curves of these three species in Thailand were virtually identical in their slope. This contrasts with the situation in Sri Lanka, where Lindauer (63) and others (77) found dialect differences among these species. Given the similarities among the dialects in Thailand, the adaptive-tuning hypothesis predicts that the maximum flight distances in this region would be similar for bees in the same habitat. We found, by contrast, that *A. cerana* had a short flight range (approximately 2 km) compared with *A. florea* (11 km) and *A. dorsata* (12 km).

Although we rejected the adaptive-tuning hypothesis as an explanation for the dialects of different species, an interesting pattern emerged in the forage-mapping data that may support an altered version of the hypothesis. Von Frisch supposed that different populations of honey bees are subject to a common constraint on the maximum feasible duration of the distance signal. We found, by contrast, that the longest distance signals seen in dances of *A. florea* and *A. dorsata* (≈30 sec) were about 3 times the maximum signal duration observed in *A. cerana* in Thailand or in earlier studies of *A. mellifera* in North America (116) or Africa (90). Thus there is not a universal upper limit on signal duration. Instead, there may be a different constraint for the open-nesting species than for the cavity-nesting species, perhaps related to the differing roles of vision and sound in dance following. If so, then a fair test of the adaptive-tuning hypothesis would require comparisons between dialect and flight range only among open-nesting species or among cavity-nesting species. Considering only data collected in relatively undisturbed habitat, the predictions of the adaptive-tuning hypothesis, controlled for nest architecture, are supported (19, 25).

Tuned Error in the Divergence Angle

A peculiar feature of the waggle dance of *A. mellifera* noticed by von Frisch (116a) was that waggling runs are consistently aligned in the direction of the food only when the flight distance is fairly long (i.e., several hundred meters). In dances to short distances, successive waggling runs diverge from each other, alternately missing to the right and left of the true direction. Von Frisch described a steady decrease in this divergence angle as flight distance increased.

Haldane & Spurway (42), in their pioneering paper applying information theory to the communicative signals of animals, proposed a functional explanation for the relationship between divergence angle and flight distance. They suggested that divergent dances tend to spread out recruits so that they would more rapidly discover the full extent of a floral resource distributed in a patch rather than as a point source. Furthermore, the decrease in the divergence angle with flight distance was explained by the fact that patches of a given size would subtend a smaller angle at the nest when at greater distances. Thus, the divergence angle was interpreted as a source of useful error, optimally tuned to the spatial distributions of resources in the environment.

There was little evidence bearing on this intriguing hypothesis until Towne (113) took up the problem in a wide-ranging experimental and comparative study. One prediction of the hypothesis is that the absolute error in the distribution of recruits attracted to baits in the field should be roughly constant as the searching distance increased, as a result of the decrease in the signal error at greater flight distances. Towne found that the searching error actually increased with searching distance, but did so gradually. The diameter of the search area at 700 m was roughly twice as large as that of the search area at 100 m. However, the angle subtended at the nest by the search area at 700 m (15°) was only one fifth that at 100 m (75°), in support of the hypothesis that recruits were guided by more precise information at greater flight distances.

In another experiment, Towne (111) compared dances to feeding places with dances (by bees on swarms) to nest boxes. Because nests are always point sources and never diffuse patches, the tuned-error hypothesis predicts a smaller divergence angle in dances to nests than in dances to food. Towne found no differences in the dances to these different types of resources. More recently, Weidenmueller & Seeley (122) found the difference predicted by the tuned-error hypothesis: small divergence angles for nest sites and larger divergence angles for food at the same distance. They suggest that Towne failed to find the difference because the bees he observed dancing to a nest box had first been trained to a feeder placed on the nest box, and thus may have had difficulty detecting the change in behavioral context. When they trained bees to a nest box using food rather than letting them discover it as house-hunting scouts, they too observed no difference between food dances and nest-site dances.

Towne (111, 113) also provided comparative evidence that supports the hypothesis that the spatial precision of the waggle dance is tuned to the spatial distribution of resources. He studied three tropical species of *Apis* (*A. cerana*, *A. florea*, and *A. dorsata*), which he reasoned would be confronted with flower patches that would typically be small (e.g., single flowering trees) in comparison to flower patches in temperate zones. The tropical bees would therefore be more heavily penalized by a large divergence angle at an equivalent flight distance. As predicted by the tuned-error hypothesis, all three species showed divergence angle only at short flight distances. Their divergence angles were reduced to less than 5° for flights of only 150 m. Races of *A. mellifera* from temperate regions, by contrast, show divergence angles of 20–25° at equivalent flight distances.

In short, both experimental and comparative data provide support for the hypothesis that spatial precision of the dance, and the dispersion of search activity by recruits, is adaptively tuned in a way that corresponds to the spatial distributions of resources being communicated.

Migration Dances

Recent studies of two tropical honey bees have uncovered evidence of a different style of dance communication in the indication of migratory direction. One of these species is the African hive bee *A. mellifera scutellata* (91), and the other is the Asian rock bee *A. dorsata* (26). In both species, colonies make seasonal migrations of tens or hundreds of kilometers (60) in response to regional shifts in rainfall and the availability of floral resources. Migration, and the role that dance communication plays in colony movement, is different from what is seen in the two other main types of colony movement—reproductive swarming and emergency absconding—when the colony is under threat of predation or natural disaster (20). Swarms and absconding colonies move temporarily to a resting spot near the natal nest and from there send out scouts to find new nesting sites nearby. The scouts return to perform dances indicating the locations of candidate nest sites (7, 62, 100).

Migrating colonies of both *A. dorsata* and *A. mellifera scutellata* depart directly from the natal nest on a long flight in the migratory direction. In both species (91), the dance has been modified to play a role in organizing the initial move. The migratory dances begin a few days before colony movement, and by the time the colony takes off, dozens of bees perform dances. These dances signal the compass direction in which the colony ultimately departs, and hence resemble nest-site dances on reproductive or absconding swarms. They differ in interesting ways, however. First, whereas dances on swarms contain accurate information about both the direction and the distance of the new nest site, the migratory dances are accurate only with respect to direction. Migratory dances are much more variable with respect to the distance signal than are dances to discrete resources. Furthermore, the average duration of the waggling run is extremely long, corresponding to flight distances of many tens or hundreds of kilometers. Such distances are well beyond the flight distances that bees could be expected to travel from the nest. Finally, observations in the early morning showed that migration dances begin before any bees leave the nest, suggesting that the bees do not base the signal on spatial information gathered on a trip just preceding the dance (26). These dances could be based on information gathered during flights on previous days, but this behavior still differs dramatically from that observed in dances to discrete resources. In short, the migration dances reflect the emergence of a colony-wide consensus about the direction that the colony should travel, but they do not signal actual locations sampled by the dancers. Nothing is known about how migratory directions are chosen or how the consensus is reached.

FUTURE DIRECTIONS

Karl von Frisch once described the honey bees and their dance language as a “magic well” of scientific discovery, remarking that “the more you draw from it the more there is to draw.” This well continues to yield new insights and new questions. Here I want to point to two additional questions that have received relatively little attention in this review and that in my view represent especially fruitful lines of future inquiry.

First, the ability of bees to code navigational information in waggle dances and to translate dances into a vector that can be used to guide a searching flight suggest that bees can solve an interesting computational problem. At the most general level, this is a mapping problem: how to translate spatial coordinates of a resource, measured visually over several minutes of flight, into the motor commands necessary to control the orientation of the waggling run (relative to gravity) and its duration. Follower bees must solve this same mapping problem in reverse.

It remains puzzling how all this happens. To some extent the mappings involve innate transformations of sensory data. This is true of the mapping of flight distance to waggling run duration (32, 105) or of the mapping of solar flight angle into a gravity angle (116a). Some of the mappings are learned, however. For example, bees learn to compensate correctly for the sun's movement, and thus must have some way of learning the function (or fine-tuning an approximate innate function) that describes the progression of the solar azimuth over time relative to fixed features of the terrain (21, 22). What sorts of neural events might underlie these various mapping processes is unknown. Given the importance of such processes in navigation by other animals, their study in bees (where the dance provides a window onto the processes) may produce insights of general interest to neurobiologists.

The second area of research is the use of the dance as a tool for studying the foraging ecology of bees. One can infer the flight distances traveled by bees by measuring the distance signals in randomly sampled dances to natural foraging sites and then using the dialect function to decode the distance traveled. By measuring the directions indicated in the dances, one can compile a two-dimensional map of the colony's foraging activity over a given period of time. This forage mapping procedure has already been used to study shifts in a colony's use of different foraging patches over time (90, 116) and to compare the foraging activities of different colonies in the same habitat (25, 89, 119). The full potential of this technique has yet to be realized. Of special interest are studies in natural habitats where honey bees are important indigenous pollinators—especially the African and Asian tropical forest. Given that tropical forest plants are predominantly insect pollinated, understanding the foraging ecology of pollinators is relevant to an understanding of forest community ecology. Among the most important questions to answer about pollinator behavior is flight distance, which directly affects dispersal distances of pollen. This question is easily answered through forage mapping (P. Batra & F.C. Dyer, manuscript in preparation). When combined with other information, such as the composition of the diet (determined by sampling pollen brought back by foragers), the rate of foraging from colonies, and the sizes and densities of colonies in the environment, it may be possible to obtain a detailed picture of the dynamics of pollen flow in the environment.

These two lines of future research illustrate how deep Karl von Frisch's magic well really is, allowing us to address fundamental questions about the sensory and computational mechanisms underlying behavior, as well as questions about community ecology. The use of the dance to study questions about sensory mechanisms, adaptive design, and evolution of behavior also remain active areas of research. Thus, we are far from exhausting the capacity of this amazing behavior to teach us about the workings of the natural world.

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