

The tremble dance of the honey bee: message and meanings

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Summary. The nectar foragers of a honey bee colony, upon return to the hive, sometimes perform a mysterious behavior called the tremble dance. In performing this dance, a forager shakes her body back and forth, at the same time rotating her body axis by about 50° every second or so, all the while walking slowly across the comb. During the course of a dance, which on average lasts 30 min, the bee travels about the broodnest portion of the hive. It is shown experimentally that a forager will reliably perform this dance if she visits a highly profitable nectar source but upon return to the hive experiences great difficulty finding a food-storer bee to take her nectar. This suggests that the *message* of the tremble dance is “I have visited a rich nectar source worthy of greater exploitation, but already we have more nectar coming into the hive than we can handle.” It is also shown experimentally that the performance of tremble dances is followed quickly by a rise in a colony’s nectar processing capacity and (see Nieh, in press and Kirchner, submitted) by a drop in a colony’s recruitment of additional bees to nectar sources. These findings suggest that the tremble dance has multiple *meanings*. For bees working inside the hive, its meaning is apparently “I should switch to the task of processing nectar,” while for bees working outside the hive (gathering nectar), its meaning is apparently “I should refrain from recruiting additional foragers to my nectar source.” Hence it appears that the tremble dance functions as a mechanism for keeping a colony’s nectar processing rate matched with its nectar intake rate at times of greatly increased nectar influx. Evidently the tremble dance restores this match in part by stimulating a rise in the processing rate, and in part by inhibiting any further rise in the intake rate.

Introduction

Seventy years ago Karl von Frisch (1923) published his first monograph on the dances of bees. In this seminal

work he described not only the famous round and waggle dances, but also a third, less celebrated dance: the tremble dance (*Zittertanz*). His vivid description of this dance reads as follows:

At times one sees a strange behavior by bees who have returned home from a sugar water feeder or other goal. It is as if they had suddenly acquired the disease St. Vitus’s dance [chorea]. While they run about the combs in an irregular manner and with a slow tempo, their bodies, as a result of quivering movements of the legs, constantly make trembling movements forward and backward, and right and left. During this process they move about on four legs, with the forelegs, themselves trembling and shaking, held aloft approximately in the position in which a begging dog holds its forepaws. If they have brought in sugar water... often [they] will retain it until they have quieted down. The duration of this “tremble dance” is quite variable. I have seen instances where the phenomenon has died away after three to four minutes, then the bee appeared normal again and flew out of the hive. Usually, however, this dance lasts much longer and three times I have observed a bee tremble on the combs without interruption for three quarters of an hour (von Frisch 1923, p. 90; translation by T.D.S.).

The message of the tremble dance was a mystery to von Frisch, for although it – like the round and waggle dances – seemed to be a communication signal, he could neither identify its cause nor detect any effect on other bees in the hive, despite having observed more than 60 bees perform the tremble dance. This led him to the tentative conclusion that the tremble dance gives the other bees no information. Some 40 years later, in 1967 (p. 282), von Frisch repeated this stark conclusion: “I think it tells the other bees nothing.” At this time he also drew the inference from the observations of tremble dances reported by Lindauer (1948), Schneider (1949), and Schick (1953) that this dance is a result of foragers experiencing adverse circumstances – such as a marked deterioration of the food source – which might induce a kind of “nervous conflict” (von Frisch 1967, p. 283) in these bees.

In 1987, I began to suspect that von Frisch’s conclusions about the tremble dance might be mistaken and that this dance might be an important signal in the organization of a colony’s foraging. This suspicion arose from the unanticipated results of experiments involving

food-storer bees – bees that are slightly younger than foragers and that receive the fresh nectar brought back by foragers and store it in the honey combs. When I removed the food-storer bees from a colony and observed the effects on the nectar foragers, I found (as expected) that the nectar foragers searched longer to find a food-storer bee upon return to the hive, but I also found (to my surprise) that approximately 10% of the time the foragers performed a tremble dance upon return to the hive (see Table 5, in Seeley 1989). Furthermore, I observed that after about 2 h, by which time the tremble dancing had abated, the foragers no longer needed to search extensively to find a food-storer bee, which implied that the missing food storers had been replaced. These serendipitous findings led me to form a two-part hypothesis regarding the tremble dance: (1) its cause is nectar foragers experiencing long delays in finding food storers, and (2) its effect is to recruit additional bees to the task of storing nectar, or to stimulate the existing food-storer bees to work harder, or both. In short, I proposed that the tremble dance serves to remove a bottleneck in the nectar collection process by signalling the need for additional labor devoted to nectar storage (Seeley 1989).

This paper reports work done to test this hypothesis. First, I present a descriptive analysis of the tremble dance behavior [but see Nieh (in press) for a description of the acoustical component of this dance]. Next, I report an experimental analysis of the stimuli that elicit tremble dancing. Previous studies (Lindauer 1948; Seeley 1989; Seeley and Tovey, in press) have shown that a returning nectar forager will experience a long search in the hive for a food-storer bee whenever the arrival rate of a colony's nectar foragers approaches or exceeds the service rate of the colony's food storers. This occurs in nature at the start of a "honey flow," when many nectar-bearing plants come into bloom and the traffic level of a colony's nectar foragers rises dramatically. Therefore, the ecologically relevant test of my hypothesis regarding the *cause* of tremble dancing involved experimentally raising a colony's nectar influx and observing whether tremble dancing was triggered when the nectar influx was so high that returning foragers began experiencing long delays in finding food storers. In performing this test, I made sure that the quality of the foragers' food source did not deteriorate, so that I could distinguish between my hypothesis and the hypothesis suggested by previous researchers (Lindauer 1948; Schick 1953; von Frisch 1967), which is that the stimulus causing foragers to start tremble dancing is a marked deterioration in their food source. This experiment provides a critical test of my hypothesis, for if foragers do not perform tremble dances upon experiencing long search times, then this hypothesis is contradicted.

Finally, I report a test of my hypothesis that tremble dances have the *effect* of increasing the labor devoted to the task of storing nectar. This test involved inducing tremble dancing by suddenly boosting a colony's nectar influx and observing whether the sharp rise in search time that resulted was followed quickly by a drop in the search time experienced by returning nectar foragers.

This is a critical test of my hypothesis, for if no drop in the elevated search time is observed, then my hypothesis is contradicted.

Methods

Study site. All of the studies reported here were conducted between 24 June and 26 July 1991 at the Cranberry Lake Biological Station (44°09' N, 74°48' W), in the Adirondack State Park, Saint Lawrence County, in northern New York State. This study site is surrounded by nearly unbroken forests and lakes, hence there are few natural food sources for bees and it is easy to train bees to forage from experimental food sources (sugar water feeders). One indication of the scarcity of natural forage is the observation that when the feeders are shut off, the traffic level of foragers from a study colony is extremely low, typically only 1 or 2 bees/min into a hive. This scarcity of food makes it possible to tightly control the forage collected by a colony – by controlling the number of bees foraging from the sugar water feeders – even though the colony's foragers can fly freely from their hive.

Observation hive and bees. In order to observe the behavior of forager bees inside their hive, I worked with a colony living in a two-frame observation hive (internal dimensions 46.0 × 50.0 × 4.5 cm). This hive was a scaled-down version of the hive depicted in Visscher and Seeley (1982). I fitted the hive's entrance with a wedge which forced all bees to enter and leave from one side of the comb and restricted passage between the two sides of the combs by blocking with beeswax all side-to-side passageways within 30 cm of the entrance. These measures directed all returning foragers to a well-defined nectar delivery and waggle dance area near the entrance on one side of the hive (see Fig. 3, Seeley 1989; Fig. 1, Seeley and Towne 1992). The hive was insulated by removable double glazing and, when not under observation, by styrofoam panels. Bees entered the hive through a rectangular tunnel 250 mm long, 50 mm wide, and 25 mm high constructed of transparent plexiglas. To protect the hive from the weather, it was housed in a portable hut (see Visscher and Seeley 1982). The hive was stocked with a colony of approximately 4000 worker bees and an Italian queen (*Apis mellifera ligustica*) on 21 June 1991.

Layout of experiments. One basic array of the hive and feeders was used in all of the experiments reported here. The observation hive and two feeders were placed in an approximately linear arrangement, with the hive in the center and the feeders 350 m to the north and 350 m to the south, in approximately 100 m² clearings in the woods.

Feeders and control of colony's foraging level. The feeding dishes were designed to provide a sucrose solution with a constant concentration *ad libitum* for up to 30 bees. They were modeled after the closed, pneumatic feeding dishes described by von Frisch (1967, Fig. 18). Each one consisted of a 60 × 35 mm Kimax recrystallization dish inverted over a circular plexiglas plate 5 mm thick, 70 mm in diameter and with 24 grooves (1 × 1 × 10 mm) cut in a radial arrangement on the upper surface. The feeding dishes were positioned on small, ant-proof tables. Each feeder was marked with scent by maintaining a pool of anise extract in a vented reservoir beneath the plexiglas plate of the feeding dish (see von Frisch 1967, Fig. 21) and by mixing 60 μL of anise extract into each liter of sucrose solution. In some experiments, when it was necessary to have 60 or more bees foraging from the north or south feeder site without congestion at the feeder, two feeding dishes were provided at the same site.

For all experiments, it was essential to control the number of foragers visiting each feeder, and thereby regulate the colony's rate of foraging. This was accomplished as follows. First, 15 bees were trained to each feeder using standard techniques (von Frisch 1967) and were labelled with individually identifiable paint marks. Next, an assistant was stationed at each feeder to capture any additional

bees recruited to his or her feeder. Each recruit was captured non-lethally by placing a plastic bag over her while she was feeding and then sealing the bag once the bee had crawled up into it. The assistants also conducted roll calls of the bees visiting their feeders at 30-min intervals. If the number of foragers visiting a feeder dropped below 15, then the assistant labeled (rather than captured) one or more of the recruits to maintain a forager group of 15 bees. In some experiments, it was necessary to increase quickly the number of foragers (to 100 or more bees) at one of the feeders. This was accomplished by ceasing further capture of recruits and releasing previously captured recruits. Each of these recruits was painted for individual identification, thereby incorporating her into the forager group at the feeder.

Recording the behavior of foragers in the hive. Data were gathered on several aspects of the behavior of foragers when they were inside the hive. One was the "search time" (called the "time to start of unloading" in Seeley 1986, 1989, and Seeley et al. 1991). This is the amount of time that a nectar forager, upon return to the hive, spends searching for a food-storer bee who will accept her nectar load. I measured search time as the time interval between when the bee entered the hive and when she began to transfer nectar to a food-storer bee. Under certain circumstances, such as when nectar foragers had great difficulty finding a food-storer bee, they performed lengthy tremble dances before unloading their nectar. In these cases, I measured search time as the time interval between when the bee entered the hive and when she began to tremble dance, i.e. ceased searching for a food-storer bee.

A second closely monitored aspect of the foragers' behavior was their dancing, that is, whether they performed a tremble dance, a waggle dance, or no dance at all upon return to the hive. To measure the proportion of foragers falling into each of these three categories, I followed bees one at a time from the moment of arrival at the hive to the start of waggle dancing, tremble dancing, or departure from the hive, whichever came first. Bees were selected for observation by following the next bee entering the hive that came from whichever feeder (north or south) that was appropriate for the experiment. I distinguished the bees from the two feeders by having the assistant at the south feeder apply a distinct paint mark to the abdomen of each bee visiting her feeder.

Bees that performed tremble dances were often the subject of additional observations. In 10 instances in which a bee performed a tremble dance, I followed the bee for the entire duration (60+ min) of her dance, recording observations of her behavior on audiotape. In 10 other performances of the tremble dance, I recorded the path of the dancer's travel within the hive by tracing her movements on a glass sheet taped to the side of the observation hive. Because a tremble-dancing bee is constantly twisting and turning while walking rather slowly, these traces do not record all of the tiny turns performed by bees while dancing. Finally, in 15 more performances of the tremble dance, I videorecorded the dance for later analysis with a Panasonic NV-8950 video editor. In one part of this analysis, I "froze" the video playback at 1-s intervals, as indicated by a time signal electronically recorded on the videotape. For each frozen image I recorded on graph paper laid over the video screen two parameters: (1) the position ("fix") of the dancer's thorax on the plane of the comb and (2) the angle of the dancer's body axis, in degrees clockwise of vertical. Using the measurements of body position, I calculated for each fix the velocity of the dancer's travel between this fix and the previous one. Also, using the measurements of body-axis angle, I calculated for each fix the inter-fix angle ("turning angle"), by which the body-axis angle of one fix deviated from the preceding one. Turns to the right and left were denoted as clockwise (CW) and counterclockwise (CCW), respectively. In a second part of the analysis, I froze the video playback at 5-s intervals, and for each of these images I recorded the position, relative to the dancing bee, of the front of the head of each bee that was oriented to the tremble dancer. I identified a bee as oriented to a tremble dancer if she was directly adjacent to the dancer and had turned to face the dancer in the previous 1–2 s.

To plot the spatial distribution of tremble and waggle dances in a hive, I made scans at 2-min intervals of dancing in the observation hive, recording the position and type of each observed dance on a glass sheet taped against the glass wall of the observation hive. This was done on 3 days, for 60 min each day. At the end of each day, I traced on the glass the boundaries of the comb areas containing brood, honey, and pollen.

In several experiments, it was essential to measure the rate at which nectar foragers arrived at the nest ("forager arrival rate"). To accomplish this, I made five counts every 15 min of the number of (labelled) bees returning from the feeders and entering the hive in 60 s. Since virtually all of the colony's nectar was gathered from the two experimental feeders, these counts based on foragers visiting the two feeders provide an accurate measure of the total forager arrival rate of the colony.

Statistical analyses. Measurements are given throughout this paper as the mean \pm 1 SD. Statistical tests were either *t*-tests (Student's or the test for equality of two percentages using arcsine transformation; Sokal and Rohlf 1981) or, for the circular distributions, Rayleigh's test (Batschelet 1981).

Results

Description of the tremble dance

Behavior pattern. Figure 1 depicts the behavior of a bee performing a tremble dance. This complex activity can be analyzed in terms of its three components of motion: (1) *vibrational* – the strong side-to-side, and sometimes front-to-back, shaking of the body, (2) *rotational* – the constant changing of direction of the body axis, and (3) *translational* – the slow walking forward across the comb. The vibrational movement, not analyzed quantitatively, appears to have approximately the same frequency as that of the waggle dance, which is 10–15 Hz, but a markedly different form. Whereas in the waggle dance the bee's abdomen swings back and forth as the bee pivots around a point approximately at the front of her head, in the tremble dance the bee's whole body shakes to and fro; there is no pivot point. This side-to-side shaking is punctuated – every second or so – by

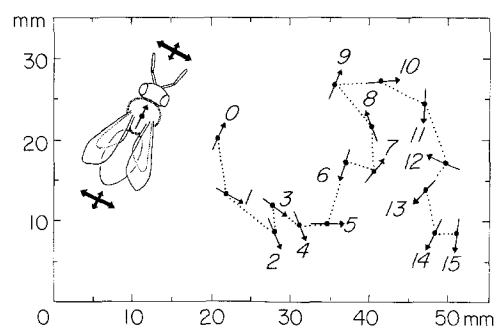


Fig. 1. Diagram of a bee's behavior while performing a tremble dance. The figure on the *left* illustrates the strong, side-to-side, vibrational movement of the body, while that on the *right* shows the rotational and translational movements of the body. The *numbered arrows* on the right denote, at 1-s intervals, the bee's position on the comb and the angle of her body with respect to vertical. During this 15-s segment of a dance, the bee walked continuously, with a mean rotational velocity of 58°/s and a mean translational velocity of 5.7 mm/s

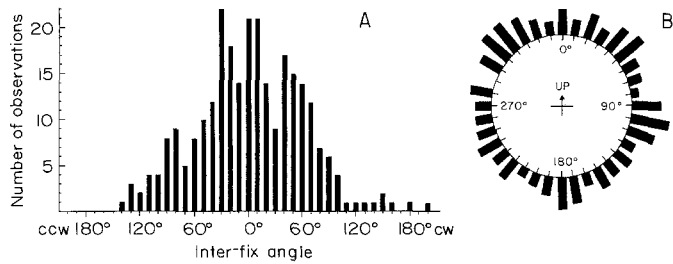


Fig. 2A, B. Body rotation patterns of one tremble dancing bee. **A** Distribution of 269 consecutive inter-fix angles, with each inter-fix angle representing the change in body angle between “frozen” video images of the dancing bee, spaced one second apart (see Fig. 1). The average inter-fix angle is $48 \pm 37^\circ$. **B** Circular distribution of the dancing bee's body angle, as measured for 270 consecutive fixes. The dancer's body is oriented at random [mean orientation vector (r) = 0.04; Rayleigh test: $z = 0.525$, $P > 0.10$]. Body angle measurements from video records of four other tremble-dancing bees yielded patterns virtually identical to those shown in **A** and **B**. *CW*, clockwise; *CCW*, counterclockwise

momentary pauses, hence the dance has a rather jerky, non-rhythmic appearance. During each pause, the bee rotates her body to face a different direction. The rotational movements are large and frequent. A series of 269 consecutive measurements of the inter-fix angle of one typical dancer, with fixes taken at 1-s intervals, revealed an average inter-fix angle of $48 \pm 37^\circ$ (disregarding the direction of the turn, CW or CCW; see Fig. 2a). These frequent turns produce a random orientation of the bee's body axis with respect to gravity (Fig. 2b). While performing the lateral shaking and rotational movements, the bee also moves across the comb. This translational component of the tremble dance has a low velocity, only 6.0 ± 2.3 mm/s ($n = 500$ inter-fix path lengths, from $n = 5$ bees), but the movement is continuous; a tremble dancer is constantly on the move. The low translational velocity, combined with the high rotational velocity, results in each dancer tracing out a highly convoluted, frequently criss-crossed travel path. Nevertheless, as is shown in Fig. 3, within a 2-min period, a tremble dancer's path can cover an area of more than 100 cm^2 .

Time course and spatial distribution. A forager typically begins her tremble dance in the vicinity of the nest entrance, where she has tried without success to find a food-storer bee in order to unload her nectar (see below). (A forager attempting to unload nectar is easily recognized: she walks forward with her mandibles spread and with a glistening droplet of nectar regurgitated onto the slightly projected base of her proboscis.) Once she has started her dance, on average she will continue to dance for a long time: 27.3 ± 24.3 min (range 2–82 min, $n = 10$). During this time, the bee will travel deep inside the hive, much deeper than she would if she had been able to follow the typical course of action of a returning nectar forager: locate a food-storer bee, unload nectar, perhaps perform a waggle dance, and finally leave the hive to resume foraging. A comparative plot of the locations of tremble and waggle dancers (Fig. 4) shows that trem-

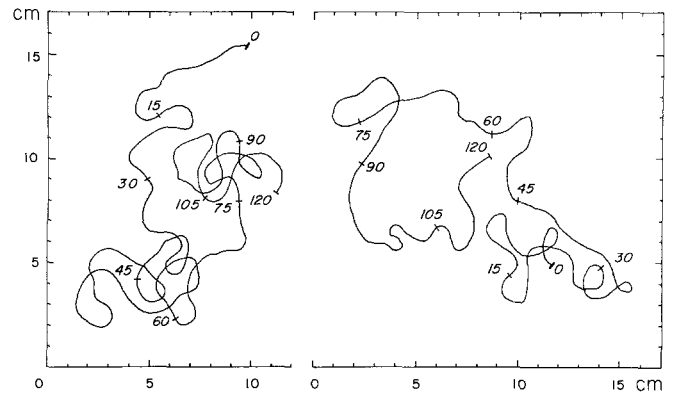


Fig. 3. Diagrams of two bees' travel paths while tremble dancing, continuously recorded over 120 s. For the sake of clarity, time markers (*cross bars*) were plotted only every 15 s. Note that for each diagram the 0 s time marker denotes the start of the recording, not the start of the dance, and that these diagrams depict only a small portion of the total path traveled by each bee during her tremble dance. During the 2-min period, each bee covered an area of more than 100 cm^2 . Comparable diagrams for 8 other tremble dancing bees show travel paths similar to the two shown here

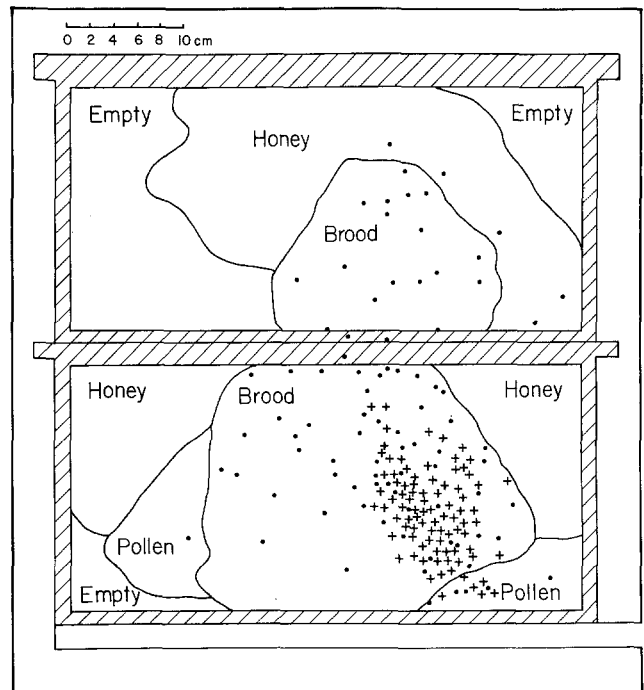


Fig. 4. Spatial distributions in a two-frame observation hive of 88 tremble dances (•) and 88 waggle dances (+), obtained by plotting the positions of dancers observed in scan samples made at 2-min intervals over 60 min. Tremble dances are distributed throughout the broodnest whereas waggle dances are clustered near the hive entrance. Analogous data gathered on two other days yielded spatial distributions virtually identical to those shown here

ble dances are distributed throughout the broodnest portion of the hive, in contrast to waggle dances which are concentrated near the hive entrance. As they travel slowly about the hive, shaking their bodies, the tremble dancers rarely stop to groom or to unload nectar. Indeed, even though a dancer's abdomen may be swollen

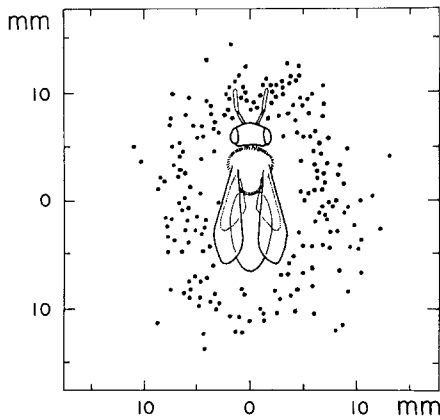


Fig. 5. Spatial distribution of the bees orienting to a tremble dancer, obtained by plotting from scan samples at 5-s intervals the position of the head of each bee that was adjacent to the dancer and that had turned to face the dancer in the previous 1–2 s. All data were taken from the videorecording of one tremble dancer. Total number of points plotted: $n=200$

with nectar, generally she does not attempt to unload the nectar until the end of her tremble dance. The tremble dancers also do not press themselves against adjacent bees, but instead move about by walking in the spaces between the surrounding bees. Only once did I see a tremble dancer conspicuously push against a nearby bee; this dancer butted with her head against the thorax of a bee standing directly in front of her. Occasionally a tremble dancer will stop dancing for several seconds to perform a dorso-ventral abdominal vibration (“shaking

dance”, Milum 1955; “jerking dance”, von Frisch 1967) on another bee. Most tremble dancers conclude their dance by stopping to regurgitate their nectar load to another bee. Following this, as a rule, they groom themselves, beg a bit of food, and fly out of the hive to resume foraging.

Behavior of bees adjacent to a tremble dancer. A tremble dancing bee clearly attracts the attention of bees immediately adjacent to her. These nearby bees frequently will turn to face the dancer and will touch her with their antennae. They may maintain contact with the dancer for a few seconds (rarely more than 5 s), walking along behind her for several centimeters (rarely more than 5 cm). As is shown in Fig. 5, the bees that are oriented to a tremble dancer do not preferentially face a particular region of the dancer’s body. Separation of a dancer and a dance follower usually happens by the follower bee backing away from the dancer and crawling off. Bees that have oriented to a tremble dancer do not show a noticeable increase in their level of activity, at least not during the minute or so following contact with the dancer.

The cause of the tremble dance

Influence of in-hive search time. When nectar foragers are presented with a highly profitable food source, and their colony’s nectar influx is kept low – so that upon

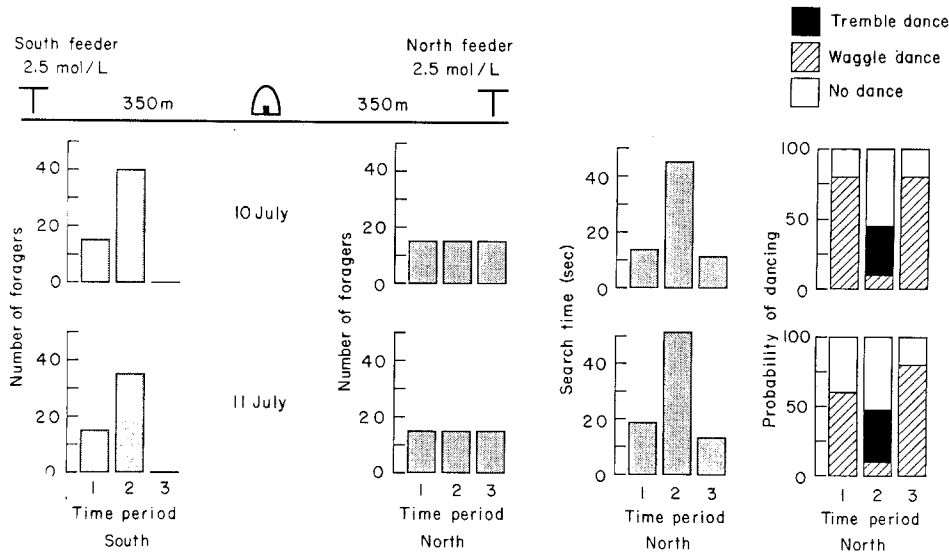


Fig. 6. Experimental array and results of the test of the hypothesis that a lengthy search in the hive to find a food-storer bee is a critical stimulus causing a forager to perform tremble dances. The colony’s nectar influx was varied by adjusting the number of foragers (0–40) visiting the *south feeder*, and data were taken on the search times and dance behaviors of the foragers (always 15) visiting the *north feeder*. Whenever the nectar influx from the south feeder was kept low (*time periods 1 and 3*), the north-feeder bees experienced short search times and they performed waggle dances (*shaded bars*). In contrast, when the nectar influx from the south feeder was raised to a high level (*time period 2*), so that the north-feeder bees had to perform lengthy searches in the hive to find

food-storer bees, they performed mainly tremble dances (*filled bars*). (*Open bars*, no dance). This indicates that a critical stimulus for tremble dancing is a long in-hive search time, caused by a high nectar influx. Time periods: 10 July, 1=11:00–12:00, 2=13:30–14:15, 3=14:30–15:00 hours; 11 July, 1=8:30–9:30, 2=10:45–12:00, 3=12:15–12:45 hours. During each time period, 20 bees from the north feeder were monitored upon return to the hive, and their search times and dance behaviors were recorded. On both days of the test, 10 and 11 July, both the average search time and the probability of tremble dancing were significantly ($P < 0.001$ for both) different between time periods 1 and 3 versus 2

return to the hive these bees search only briefly to find a food-storer bee – they exhibit a high probability of waggle dancing. This is to be expected from previous experiments (Seeley 1989), since under these circumstances the colony can handle a higher nectar influx, the foragers are visiting an under-exploited nectar source, and by performing waggle dances they can increase the number of foragers exploiting their rich nectar source. In Fig. 6, two experiments are shown in which, for time period 1, only 30 bees in total were bringing nectar into a colony, the average search time of the north-feeder bees was only 13–19 s, and these bees showed a high probability (0.80) of performing waggle dances.

When the colony's nectar influx was raised dramatically, by letting the number of bees gathering nectar from the south feeder rise from 15 to 35–40, the bees foraging at the north feeder switched from waggle dancing to tremble dancing (Fig. 6, time period 2). To fully appreciate this result, it is important to note that the only change between time periods 1 and 2 experienced by the north-feeder bees was a change inside the hive, namely an increase in the difficulty of finding a food-storer bee, indicated by the marked rise in the average search time, from 13–19 s to 45–51 s. Even though the north feeder was unchanged and so still provided highly profitable foraging, the north-feeder bees obviously were no longer trying to recruit additional foragers to their feeder.

Finally, when the colony's nectar influx was dramatically lowered, by shutting off completely the south feeder, thereby greatly lowering the average search time for the north-feeder bees to 10–13 s, these bees ceased tremble dancing and resumed waggle dancing. Hence only when the search time was long did the north-feeder bees perform any tremble dances.

Lengthy searches in the hive were thus reliably followed by nectar foragers performing tremble dances. Figure 7 shows the general relationship between duration of search time and probability of tremble (or waggle) dancing for bees visiting one highly profitable (2.5 mol/L) nectar source. Whereas the majority of foragers experiencing a search time of 20 s or less performed a waggle dance, the majority of foragers experiencing a search time of 50 s or more performed a tremble dance. Interestingly, there was a rather broad range of intermediate search times (20–50 s) in which the foragers tended not to perform either dance, indicating that it is unlikely that a forager will be motivated to perform both dances simultaneously.

The influence of food-source profitability. It has been shown that a long search time will reliably elicit tremble dancing, but we must also ask whether it is sufficient to stimulate this behavior. The answer is no. This becomes clear if one recreates the experimental conditions shown in Fig. 6, time period 2, but instead of providing 2.50 mol/L sucrose solution at both feeders, one provides this concentrated sugar solution at one feeder and a more dilute solution (1.25 mol/L) at the other feeder. The results, shown in Fig. 8, are clear-cut. Although bees

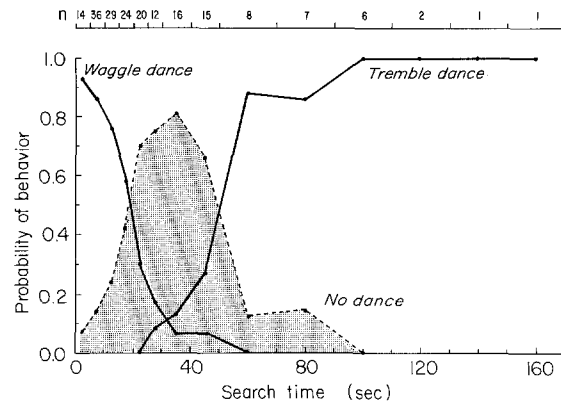


Fig. 7. Dance behavior as a function of in-hive search time for foragers visiting a rich food source. Data were gathered from 15 bees visiting a 2.5 mol/L sucrose solution located 350 m north of the hive. As is shown in Fig. 6, search times were varied for these bees by altering the number of bees bringing in nectar from a second feeder, south of the hive. Hence the only change underlying the switch from waggle dancing to tremble dancing was the change in search time. Total number of data points: $n = 191$

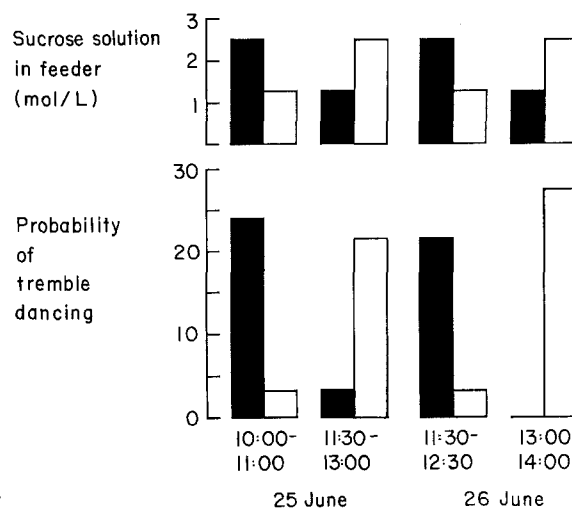


Fig. 8. Probability of performing tremble dances in relation to food-source profitability. Bees from one hive were trained to forage from two feeders (see Fig. 6), loaded with either a 1.25 or a 2.50 mol/L sucrose solution (filled bars, north feeder; open bars, south feeder). The number of foragers visiting the two feeders was kept sufficiently high (50–65 bees total) so that these foragers always experienced long search times to find food-storer bees (37–42 s on average). For each feeder and each time period, 30 bees were followed upon their return to the hive and monitored for tremble dancing. The probability of tremble dancing was always far higher for the feeder loaded with the richer sugar solution ($P < 0.01$ for all 4 time periods). This result implies that in order to have a high probability of tremble dancing upon return to the hive, a forager not only must experience a long search time, but also must return from a highly profitable nectar source

from both feeders experienced the same long (average: 37–42 s) search time, only the bees from the highly profitable feeder showed a high probability of performing tremble dances upon return to the hive.

The effect of the tremble dance

We have seen that nectar foragers returning from a rich food source will perform tremble dances if they experience a long search time in the hive, symptomatic of an excessive influx of nectar relative to the colony's capacity for processing the nectar. This fact suggests that an important effect of tremble dances might be an increase in the colony's capacity for processing nectar. In principle, this could arise by the tremble dances either recruiting additional bees to function as food storers, or stimulating the existing food storers to work harder (i.e., take larger loads or process them faster), or both. The most straightforward way of testing this hypothesis was to boost strongly a colony's nectar intake, thereby raising the search time experienced by the nectar foragers, and

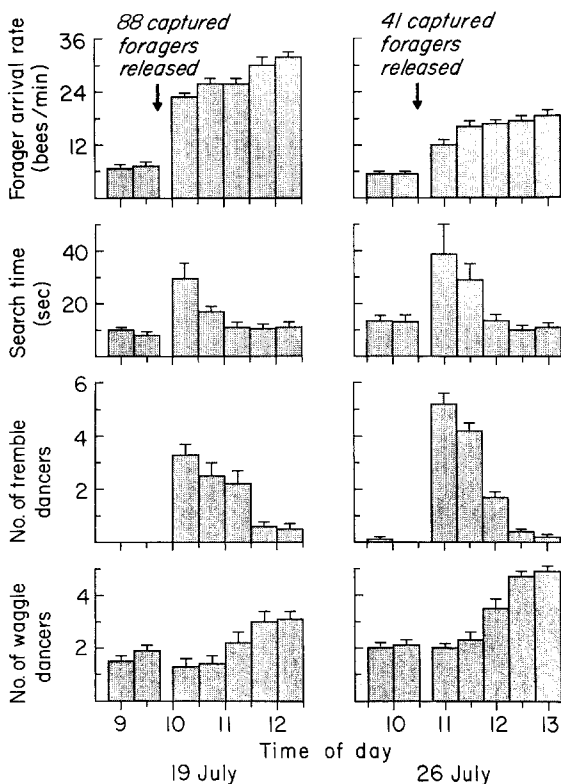


Fig. 9. Two trials of the "stress test" of the hypothesis that the effect of tremble dances is an increase in a colony's nectar processing capacity. Data were gathered from bees visiting two feeders, each providing a 2.50 mol/L sucrose solution, as depicted in Fig. 6. Initially, only 15 bees were allowed to forage from each feeder and all additional foragers were captured at the feeders. When the captured foragers were released, the colony was stressed with a suddenly higher nectar influx, which resulted in the foragers experiencing greatly increased search times and performing vigorous tremble dances. Over the next few hours, while the tremble dances were being performed, the colony raised its nectar processing capacity, thereby lowering the average search time to its initial, low level. The number of measurements made for each variable during each 30-min period was as follows: forager arrival rate, 10; search time, 12–14; number of tremble dancers, 10; number of waggle dancers, 10. All search time measurements were based on the original 30 bees, whereas the other variables' measurements were based on all the bees visiting the two feeders. $\bar{x} \pm SE$

to observe whether the tremble dancing that resulted was followed consistently by a decay in the average search time, indicative of an increase in the colony's capacity for processing nectar.

Two trials of this "stress test" were performed (Fig. 9). At the start of each test, only 15 bees were allowed to forage from each of the two feeders (all additional bees arriving at each feeder were captured non-lethally), resulting in a low rate of forager arrival at the hive. Direct observations revealed that upon return to the hive these foragers found food-storer bees quickly and performed only waggle dances. After an hour of observations under these control conditions, the foragers that had been captured at each feeder (41–88 bees) were released there. The vast majority of these bees flew immediately to the feeder to resume loading, and within another minute or two were headed back to the hive, thereby producing an almost instantaneous doubling or quadrupling of the forager arrival rate at the hive, and a corresponding multiplication of the colony's nectar influx. Observations begun 15 min after the release of the foragers indicated that the resulting rise in nectar influx was sufficient to create long in-hive search times (average: 30–40 s) and to trigger tremble dancing. Most importantly, however, I observed over the next 2 h that despite a forager arrival rate that remained elevated and continued to rise even higher, the average search time experienced by the foragers dropped to the same level as the initial 10–12 s, implying that the colony's nectar processing capacity had been raised to match the new, higher level of nectar influx. The level of tremble dancing was high when the search time was being lowered (i.e. when the nectar processing capacity was being raised) and then fell to essentially zero once the search time stabilized at its normal, low level. Hence in both trials there was a strong correlation between the occurrence of tremble dances and the rise in the colony's capacity for processing nectar.

Discussion

When the honey bee's tremble dance was discovered (von Frisch 1923), it was suggested that it tells nothing to the other bees in the hive. However, the main support for this hypothesis was negative evidence: no consistent set of circumstances experienced by bees prior to performing the tremble dance could be identified. Or in the original words of von Frisch (1923, p. 91), "Ich konnte keinerlei feste Beziehung herausfinden zwischen dem Auftreten des Zittertanzes und dem, was die Biene vorher erlebt hat." Likewise, in 1948, Lindauer reported observing 237 instances of a bee performing the tremble dance, but was unable to specify what factors trigger this behavior. Identifying these antecedent factors is crucial to deciphering the message of the tremble dance, for as Smith (1977) has so cogently argued, the key to understanding the message of any communicatory behavior is knowing what the sender consistently experiences before performing the behavior. In this paper I

identify one set of experiences that has a high probability of being followed by a tremble dance: a bee visits a highly profitable nectar source and upon return to the hive experiences great difficulty finding a food-storer bee to receive her nectar. These findings lead me to propose that the message of the tremble dance is "I have visited a rich nectar source worthy of greater exploitation, but already we have more nectar coming into the hive than we can handle."

Having identified the message of a communicatory behavior, one naturally wants also to identify the meaning of the behavior to the individuals that respond to it. Following again the thinking of Smith (1977), we note that the key to understanding the meaning of a communicatory behavior is knowing what the responders consistently do after encountering the behavior. Furthermore, we note that since any one communicatory behavior can be experienced by different types of individuals, with different responses, a single communicatory behavior can have multiple meanings. It appears that the tremble dance has at least two meanings. One is suggested by the results of the stress tests (Fig. 9). These show that the performance of tremble dances in a colony is followed quickly by a rise in the colony's nectar processing capacity, indicating that more nectar storing labor becomes available when tremble dances are performed. This suggests that certain bees working inside the hive respond to tremble dances by switching to the task of processing nectar. If so, then for these bees the meaning of the tremble dance is "I should switch to the task of processing nectar." A second meaning of the tremble dance is suggested by the recent experimental findings of Nieh (in press) and Kirchner (submitted), that the performance of tremble dances in a colony is also followed quickly by a drop in waggle dancing by bees gathering nectar. These findings are corroborated by the data on waggle dancing depicted in Fig. 9. When the captured foragers were released and tremble dancing was triggered, the number of waggle dancers remained stable despite a doubling or quadrupling of the number of foragers; hence the per capita probability of waggle dancing declined. Only once the tremble dancing had subsided was there any rise in the number of waggle dancers. Evidently, for bees working outside the hive gathering nectar, the meaning of the tremble dance is "I should refrain from recruiting additional foragers to my nectar source."

The proposed message and meanings of the tremble dance make good sense from the perspective of functional design. Honey bee colonies experience large, day-to-day changes in their rate of nectar intake (Visser and Seeley 1982), an inevitable consequence of phenological and meteorological changes that influence nectar availability. For example, during a "nectar dearth", a colony's nectar influx may be only several grams per day, and then a few days later, during a "honey flow" its nectar influx may skyrocket to several kilograms per day. Faced with a highly variable food supply, a honey bee colony needs a mechanism for adjusting its nectar processing rate to match its nectar intake rate, otherwise there will be a bottleneck in the foraging process whenever

er there is a dramatic rise in the nectar availability. In now seems clear that the tremble dance serves as this mechanism. Whenever a colony's nectar influx rises to a level exceeding its nectar processing capacity, nectar foragers produce tremble dances, and tremble dances evidently both increase the processing rate and limit further increase in the intake rate.

The net result of these two effects is an eventual match between processing rate and intake rate. Once this match is achieved, the stimulus causing tremble dances (long in-hive search times) is eliminated, hence this rate-matching device is under negative feedback control. Evidently this negative feedback is tuned so that the colony does not overshoot the proper balance between processing rate and intake rate. In both trials of the stress experiment (Fig. 9), the colony adjusted itself internally so that the search time smoothly declined to the value (approximately 10 s) observed before the stress was applied.

As far as other social insects are concerned, division of labor between food gathering and food processing/storing has been documented in paper wasps (Jeanne 1991), yellowjacket wasps (Jeanne 1991), stingless bees (Michener 1974), leaf-cutter ants (Wilson 1980), honey pot ants (Rissing 1984), fire ants (Sorensen et al. 1985), fungus-growing termites (Badertscher et al. 1983), and is likely to occur in still other groups. Probably all of these social insects experience strong temporal variation in the availability of food, hence they, like the honey bee, face the problem of keeping a colony's food processing capacity matched to its food intake rate. It therefore seems likely that signals serving the same function as has been proposed for the tremble dance will prove common among social insects, though as yet none have been identified.

Although the cause of the tremble dance now seems clear, many questions remain regarding its effects, particularly on the colony's rate of nectar processing. The correlational evidence presented in this paper (Fig. 9) strongly suggests that the tremble dance triggers a rise in the colony's nectar processing rate, but this cannot be considered proven. Some other cue or signal, itself tightly correlated with the tremble dance, might be the critical stimulus, though this seems doubtful given that the tremble dance is such a striking signal. If we make the reasonable assumption that the tremble dance is the critical stimulus for the rise in the nectar processing rate, then we face the puzzle of exactly what happens in response to the tremble dance that raises the nectar processing rate. Are the existing food-storer bees stimulated to work harder, or are additional bees recruited to the task of storing nectar, or are both effects produced? If there is recruitment of additional food-storers, then there arises a further question: who are the new food-storer bees? The fact that the tremble dances are performed throughout the broodnest region of the hive suggests that the new food-storer bees may be individuals previously engaged in the task of rearing brood ("nurse bees"). Future work will have to solve these tantalizing puzzles about the effects of the tremble dance.

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