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Decoding the Language of the Bee

Karl von Frisch

Some 60 years ago, many biologists thought that bees and other insects were totally color-blind animals. I was unable to believe it. For the bright colors of flowers can be understood only as an adaptation to color-sensitive visitors. This was the beginning of experiments on the color sense of the bee (*1*). On a table outdoors I placed a colored paper between papers of different shades of gray and on it I laid a small glass dish filled with sugar syrup. Bees from a nearby hive could be trained to recognize this color and demonstrated their ability to distinguish it from shades of gray. To prevent too great a gathering of bees, I instituted breaks between feedings. After these breaks, only sporadic scout bees came to the empty bowl and flew back home; the feeding table remained deserted. If a scout bee, however, found the bowl filled and returned home successfully, within a few minutes the entire forager group was back. Had she reported her findings to the hive? This question subsequently became the starting point for further investigations.

In order that the behavior of foragers could be seen after their return to the hive, a small colony was placed in an observation hive with glass windows, and a feeding bowl was placed next to it. The individual foragers were marked with colored dots, that is, numbered according to a certain system. Now an astonishing picture could be seen in the observation hive: Even before the returning bees turned over the contents of their honey sack to other bees, they ran over the comb in close circles, alternately to the right and the left. This round dance caused the numbered bees moving behind them to undertake a new excursion to the feeding place.

But foragers from one hive do not always fly to the same feeding source. Foraging groups form: One may collect from dandelions, another from clover, and a third from forget-me-nots. Even in flowering plants the food supply often becomes scarce, and a "feeding break" ensues. Were the bees in the experiment able to alert those very same foragers who were at the bowl with them? Did they know each other individually?

To settle the question, I installed two feeding places at which two groups from the same observation hive collected separately. During a feeding break, both groups stayed on the honeycomb and mingled with each other. Then one of the bowls was refilled. The bees coming from the filled bowl alerted by their dances not only their own group but also bees of the second group, which responded by flying to their customary feeding place where they investigated the empty bowl.

However, the natural stopping places of bees are not glass bowls but flowers. Therefore, the experiment was modified; one of two groups of bees collected food from linden blossoms, the other one from robinias. Now the picture changed. After the feeding break, the

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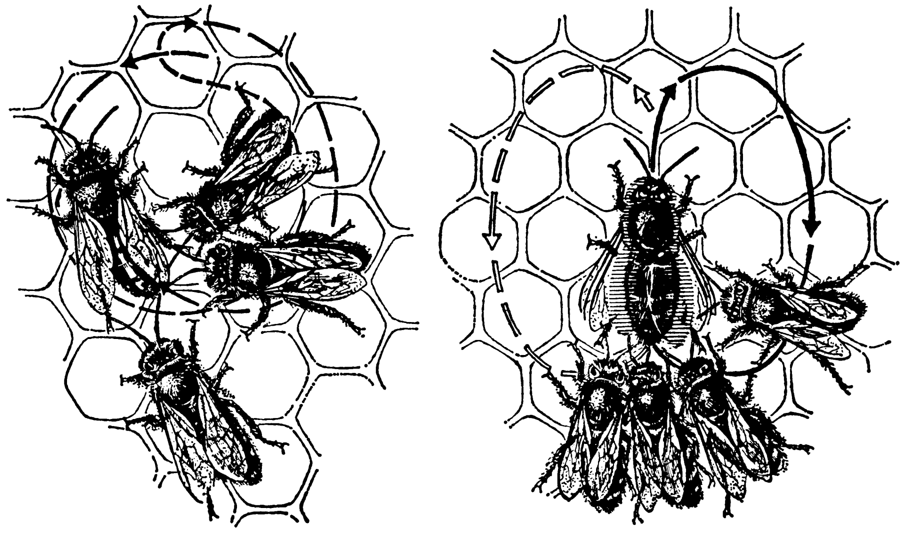
The author is professor emeritus of zoology at the University of Munich. This article is an English translation of the lecture he delivered in Stockholm, Sweden, on 12 December 1973 when he received the Nobel Prize for Physiology or Medicine, a prize he shared with Nikolaas Tinbergen and Konrad Z. Lorenz. The article is published here with the permission of the Nobel Foundation and will also be included in the complete volume of *Les Prix Nobel en 1973* as well as in the series Nobel Lectures (in English) published by the Elsevier Publishing Company, Amsterdam and New York. The lecture by Professor Tinbergen appeared in the 5 July issue, page 20, and that by Professor Lorenz appeared in the 19 July issue, page 229.



a. Round dance b. Tail-wagging dance

Fig. 1. Running curve of the bee (a) during round dance and (b) during tail-wagging dance. Bees that follow the dancer take in information.

bees returning from the linden blossoms caused only the linden bees to fly out again; the robinia collectors paid no attention to their dances. However, when bees returned successfully from robinia blossoms, the linden bees showed no interest in their dances, while members of the robinia group immediately ran to a dancer in their vicinity, following along behind her and then flying out. Some clever bees also learned to use both sources of food, depending on the occasion. They would then send out the linden gatherers after returning from the linden source, and the robinia gatherers after visiting the robinias. Thus, the bees did not know each other individually. It appeared that the fragrance of the specific blossom attached to their bodies was decisive. This was confirmed when essential oils or synthetic scents at the feeding place produced the same effect.

When feeding was continuous, new recruits showed up at the food source next to the old foragers. They, too, were alerted by the dance. But how did they find their goal?

Peppermint oil was added to the feeding place next to the hive. In addition, bowls with sugar syrup were put on small cardboard sheets at various places in the nearby meadow; some of the sheets were scented with peppermint oil and the others with other essential oils. The result was unequivocal: A few minutes after the start of feeding, recruits from the observation hive appeared not only at the feeding place next to the foraging bees but also at the other peppermint bowls posted at some distance in the meadow. The other scented bowls, however, remained undisturbed. The smell of lavender, fennel, thyme oil, and so forth had no attraction. When the scent at the feeding place was replaced by a different one, the goal of the swarming recruits changed accordingly. They let themselves be guided by the scent on the dancers.

Scent is a very simple but effective means of communication. It attains full significance, however, only in combination with another condition. If the sugar syrup becomes scarce or is offered in weaker concentrations, after a certain point the dancing becomes slower and finally stops even though the collecting may continue. On the other hand, the sweeter the sugar syrup, the more lively and lengthy the various dances. The effect of advertising is thereby enhanced, and it is increased further by the scent gland in the forager's abdomen which is activated upon arrival at a good source of supply. Thus it signals "Come hither!" to recruits searching in the vicinity. Many female insects have scent glands to attract the male. In worker bees, which are mere workhorses devoid of any sexual interest, the scent organ is put to the service of the community.

Let us now imagine a meadow in the spring. Various types of plants blossom simultaneously, producing nectar of differing concentrations. The richer and sweeter its flow, the livelier the dance of the bees that discover and visit one type of flower. The flowers with the best nectar transmit a specific fragrance which ensures that they are most sought after. Thus, in this simple fashion, traffic is regulated according to the law of supply and demand not only to benefit the bees but also to promote pollination and seed yield of plant varieties rich in nectar. A new and hitherto unknown side of the biological significance of flower fragrance is thus revealed. Its great diversity and strict species specificity communicate a truly charming scent language.

This was how things stood in 1923 (*2*), and I believed I knew the language of the bees. On resuming the experiments 20 years later, I noticed that the most beautiful aspect had escaped me. Then, for the first time, I installed the feeding place several hundred meters away instead of next to the hive, and saw to my astonishment that the recruits immediately started foraging at that great distance while paying hardly any attention to bowls near the hive. The opposite occurred when the foragers located the sugar syrup, as before, near the hive. Could they possess a signal for distance?

Two foraging groups were formed from one observation hive. One feeding place was located 12 m from the hive, the other at a distance of 300 m. On opening the observation hive, I was astonished to see that all foragers from nearby performed round dances, while long-distance foragers did tail-wagging dances (Fig. 1). Moving the nearby feeding place step by step to greater distances resulted in the round dances changing to tail-wagging dances at a distance of about 50 m. The second feeding place was brought back step by step, past the first feeding place close to the hive. At the same critical distance of about 50 m, the tail-wagging dances became round dances (*3*, *4*). I had been aware of the tail-wagging dance for a long time, but considered it to be typical of pollen collectors. My mistake was due to the fact that, at that time, bees with pollen baskets always arrived from a greater distance than my sugar syrup collectors.

Thus it became evident, and subsequent experiments confirmed (*5*), that the round dance is a signal that symbolically invites the hive members to search the immediate vicinity of the hive. The tail-wagging dance sends them to greater distances, not infrequently several kilometers. The signal "closer than 50 m" or "farther than 50 m" alone would not be of much help. In fact, however, the pace of the tail-wagging dance changes in a regular manner with increasing distance: its rhythm decreases. According to the present state of our knowledge, information on flight distance is given by the length of time required to go through the straight part of the figure-eight dance in each repeat. This straight stretch is sharply marked by tail-wagging dance movements and simultaneously toned (in the true meaning of the word) by a buzzing sound (*6, 7*). Longer distances are expressed symbolically by longer tail-wagging times. For distances of 200 to 4500 m, they increase from about 0.5 second to about 4 seconds (*6, 8*) (Fig. 2).

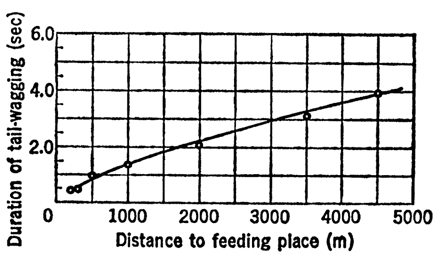


Fig. 2. Duration of the tail-wagging run for feeding places at various distances; based on film data.

The tail-wagging dance not only indicats distance but also gives the direction to the goal. In the observation hive, the bees that come from the same feeding place make their tail-wagging runs in the same direction, whereas these runs are oriented differently for bees coming from other directions. However, the direction of the tail-wagging runs of bees coming from one feeding place does not remain constant. As the day advances the direction changes by the same angle as that traversed by the sun in the meantime, but in the opposite rotation. Thus, the recruiting dancer shows the other bees the direction to the goal in relation to the position of the sun (*5, 6*). Those hours at the observation hive when the bees revealed this secret to me remain unforgettable. The fascinating thing is that the angle between the position of the sun and the dancer's path to the goal is expressed by the dancer in the darkness of the hive, on the vertical surface of the comb, as an angular deflection from the vertical. The bee thus transposes the angle to a different area of sense perception. Figure 3 shows the key to the transposition. If the goal lies in the direction of the sun, the tail-wagging dance points upward. If the goal is located 40° to the left of the sun's position, the dancer shifts the straight run 40° to the left of the veritcal, and so forth (*5, 6*). On the comb, members of the hive move after the dancer and maintain close contact with her, especially during the tail-wagging runs, and take in the information offered. Can they follow it and with what accuracy?

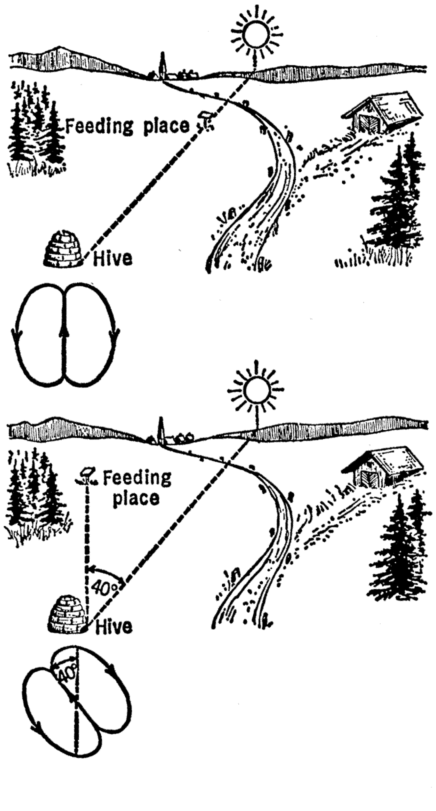
The indication of direction was tested by us using the following method (*9*). At a certain distance from the hive, a feeding place was installed at which numbered bees were fed on an unscented platform with a sugar solution so dilute that they did not dance in the hive and therefore did not alert forager recruits. Only at the start of the experiment did they receive concentrated sugar solutions slightly scented with (for example) lavender oil. At 50 m closer to the hive, plates baited with the same scent but without food were placed in a fan-shaped arrangement. The number of forager recruits arriving at the plates was an indication of the intensity with which they searched in various directions. Figure 4 shows, as an example, the result of an experiment in which the feeding place was located 600 m from the hive.

Since such fan experiments proved that indication of direction was successful, we made a step-by-step test of distance-indicating procedures. Here, all scented plates were located in the same direction as the feeding place, from the hive area to a distance well beyond the feeding place. Figure 5 gives an example of an experiment in which the feeding place was located 2 kilometers from the hive. Incoming flights of forager recruits to the feeding site itself were of course not evaluated because here an additional attractant was created by the food and the visiting bees (*6*).

To sum up, this and preceding experiments taught us that the information on the direction and distance of the goal was adhered to with astonishing accuracy—and not only in gathering nectar and pollen. The same dances are observed on a swarm. Here the scout bees indicate to the waiting bees the location of the domicile they have discovered. Of greatest interest here is that the intensity of the promotional message depends on the quality of the domicile discovered, that the various groups of scouting bees compete with each other, and that therefore the decision is finally made in favor of the best domicile (*10*).

While not doubting that direction and distance of the goal can be discerned from the tail-wagging dances, a group of American biologists led by A. M. Wenner does not agree that the forager recruits make use of this information. According to them, these bees find the goal by using their olfactory sense only (*11*). This view is incompatible with many of our results (*6, 12*). It is refuted by the following experiment, to cite only one.

Numbered bees from an observation



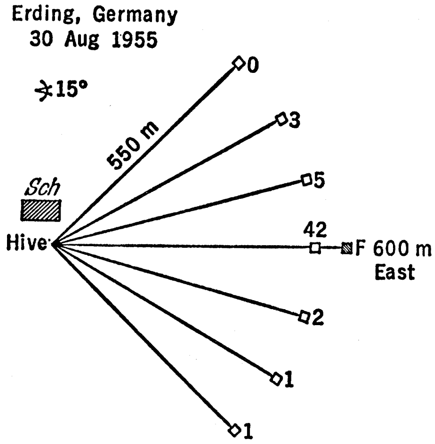


Fig. 3 (left). Indication of direction by tail-wagging dance. In the top picture, the goal is in the direction of the sun; in the bottom picture, the goal is 40° to the left of the sun's position. Dance figures, enlarged, are on the left below pictures. Fig. 4 (right). Fan experiment. The feeding place (*F*) is 600 m from the observation hive. Scented plates without food are arranged in fan shape 550 m from the hive. The numbers indicate the number of forager recruits arriving during the first 50 minutes of the experiment; *Sch*, shed.

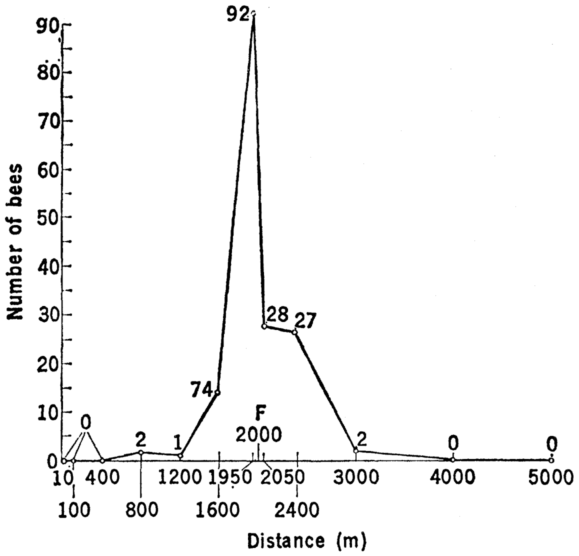


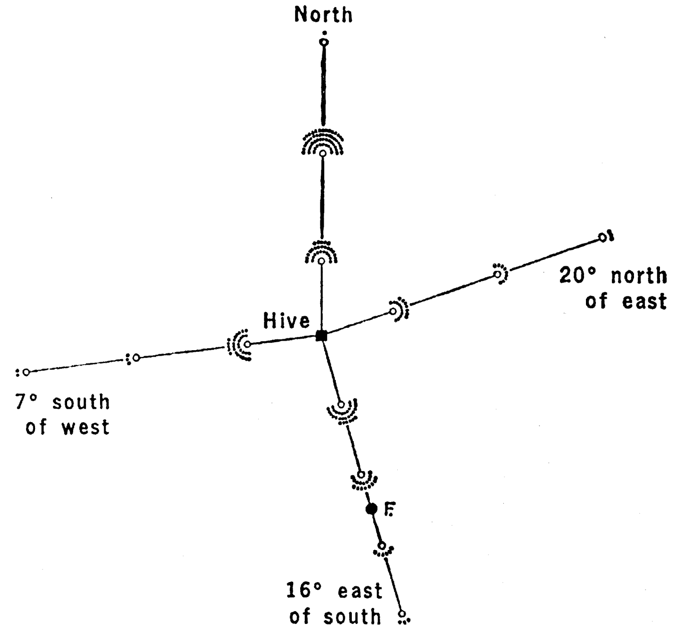
Fig. 5. Step-by-step experiment. The feeding place (*F*) is 2000 m from the observation hive. The numbers indicate the number of forager recruits that settled on the scented plates (without food) during the 3-hour observation period.

hive collected at a feeding place 230 m from the hive. The hive was turned on its side so that the comb surface was horizontal; the sky was screened. Under these conditions, the dancers could orient themselves neither by gravity nor by the sky, and danced confusedly in all directions. Plates with the same scent as that at the feeding place were located at various distances in the direction of the feeding place and in three other directions. They were visited in all directions and in great numbers by forager recruits (Fig. 6), with no preferences being given to the direction of the feeding place. The observation hive was now turned back 90° to its normal position so that the dancers could indicate the direction of the goal on the vertical comb surface. Within a few minutes, the stream of newly alerted bees flew out in the direction of the feeding place; the scented plates in this direction were increasingly frequented, and in a short time no forager recruits at all appeared at the scented plates in the three other directions (Fig. 7). No change had occurred at the sources of scent in the open field or in the other external conditions. The change in the behavior of the forager recruits could be attributed only to the directional dances.

It is conceivable that some people will not believe such a thing. Personally, I also harbored doubts in the beginning and desired to find out whether the intelligent bees of my observation hive had not perhaps manifested a special behavior. I opened an ordinary hive, lifted up one of the combs and watched the expected dances. Curious as to what would happen, I turned the comb in such a way that the dancing area became horizontal. Gravity as a means of orientation was thus eliminated. However, without any signs of perplexity, the bees continued to dance and by the direction of their tail-wagging runs pointed directly to the feeding place, just as we show the way by raising an arm. When the comb was turned like a record on a turntable, they continued to adjust themselves to their new direction, like the needle of a compass (*13*).

This behavior can be studied at leisure at a horizontal observation hive. It is basically very easy if we recall that the direction of the tail-wagging run relates to the sun's position. During the tail-wagging run on the comb, the bee has only to set itself at the same angle to the sun as it maintained during its flight to the feeding place (Fig. 8). Afterward, when the recruits set their line of flight at the same angle to the sun, they are flying in the direction of the goal.

This type of directional indication is nothing unusual. Incoming foragers not infrequently begin to dance facing the sun on the horizontal alighting board of the hive if they are met here



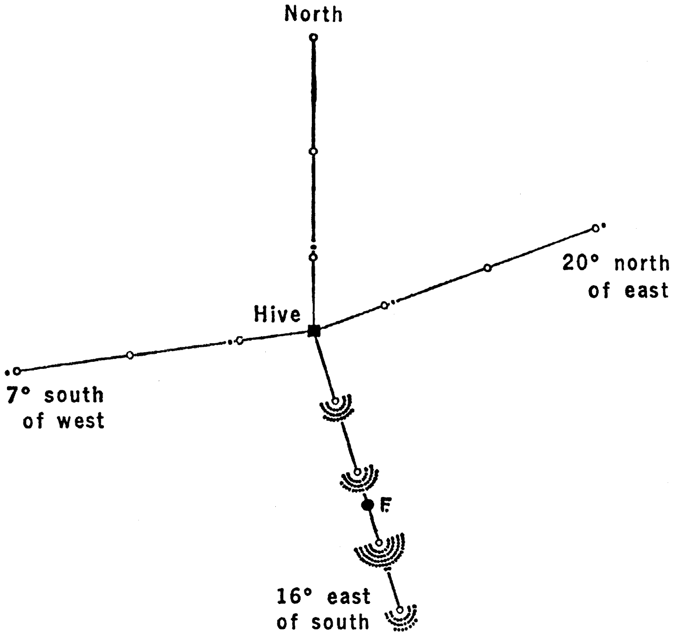


Fig. 6 (left). Effect of placing observation hive horizontally. The dances are disoriented. Scented plates with the scent of the feeding place are visited by great numbers of forager recruits (small dots) in all four directions; *F*, feeding place. Fig. 7 (right). Hive placed vertically after experiment in Fig. 6. The dances now indicate the direction of the feeding place. Within 10 minutes the stream of forager recruits turns in this direction. Flights no longer arrive in the three other directions.

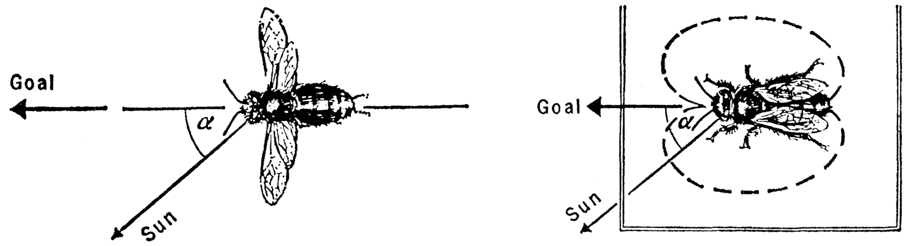


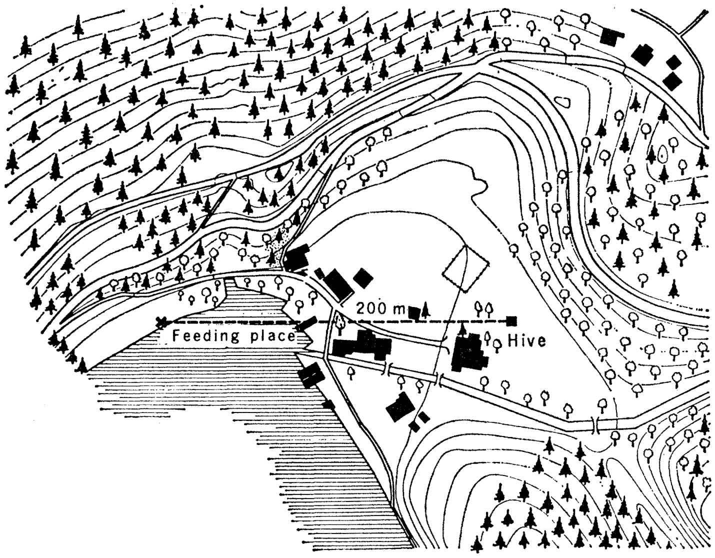
Fig. 8. The principle of direction indication during the dance on a horizontal plane. The bee (right) during the tail-wagging run positions itself in such a way that it views the sun from the same angle as earlier during its flight to the feeding place (left).

by nonworking comrades. The transmission of information through horizontal dancing is easier to understand than that when the angle is transposed to the vertical comb surface. We also seem to have here the original, phylogenetically older type of directional indication. In India there still exist several strains of the species *Apis*. My student and co-worker, Martin Lindauer, went there to use them for "comparative language studies." The small honeybee, *Apis florea*, is on a more primitive level than our honeybee and other Indian strains. The colony builds a single comb out in the open on a branch; the comb has a horizontally extended top edge that serves exclusively as a dancing floor. When these bees are forced onto the vertical comb surface of the side, they cannot render the sun's angle by dancing and their tail-wagging dances become disoriented (*14*).

Let us now return to our own bees and the observation of dances on a horizontal hive. There can be no doubt that the sun's position is decisive for the direction of their dancing. The sun may be replaced by a lamp in a dark tent. By changing its position, the bees are made to dance in any desired direction. But there was one big puzzle. To prevent excessive heating during most of the experiments, a protective roof was installed over the observation hive. The dancers were unable to see the sun. Nevertheless their dance was usually correct. Orientation by heat rays, by penetrating radiation, as well as other explanations seemed possible and had to be discarded—until I noticed that a view of the blue sky is the same as a view of the sun. When clouds passed over the section of the sky visible to the bees, disoriented dances immediately resulted. Therefore they must have been able to read the sun's position from the blue sky. The direction of vibration of polarized blue light differs in relation to the sun's position across the entire vault of the sky. Thus, to one that is able to perceive the direction of vibration, even a spot of blue sky can disclose the sun's position by its polarization pattern. Are bees endowed with this capacity?

The following test furnished an answer. The observation hive was set horizontally in a dark tent from which the dancers had a lateral view of a small area of blue sky. They danced correctly toward the west where their feeding place was located 200 m away. When a round, rotatable polarizing foil was placed over the comb in a way as not to change the direction of the vibration of the polarized light from that part of the sky, they continued to dance correctly. If, however, I turned the foil right or left, the direction of the bees' dance changed to the right or the left by corresponding angle values.

Thus, bees are able to perceive polarized light. The sky, which to our eyes is a uniform blue, is distinctly patterned to them (*13*, *15*). They use this extensively and, in their orientation, guide themselves not only by the sun's position but also by the resulting polarization patterns of the blue sky. They also continue to recognize the sun's position after it has set or when it is obscured by a mountain. Once again the bees appear to us miraculous. But it is now clear that ants and other insects, crayfish, spiders, and even octopuses perceive polarized light and use it for orientation, and that among



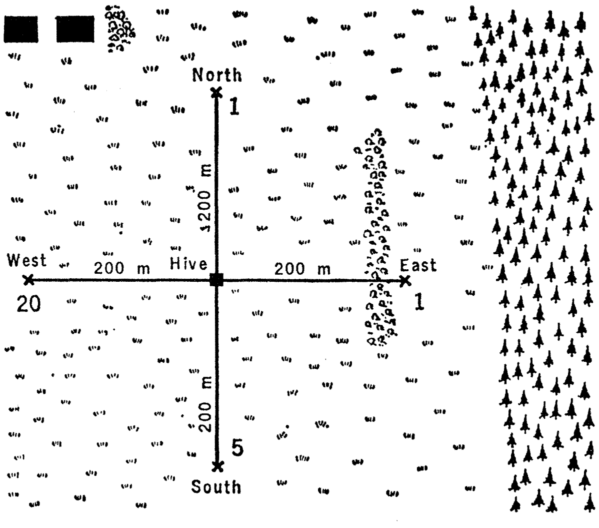


Fig. 9 (left). Observation hive in Brunnwinkl on the Wolfgangsee and line of flight of a group of numbered bees to feeding place 200 m west. Fig. 10 (right). The hive in Fig. 9 transported to a scene unfamiliar to the bees. Small feeding platforms with the familiar scent were placed 200 m from the hive in each of the four directions. The numbers indicate the numbers of arriving bees in the experimental group.

all these animals the human being is the unendowed one, together with many other vertebrates. In one respect, however, bees remain singular: Only they use polarized light not only for their own orientation but also to communicate to their colonies the direction to a distant goal (*6*).

Thus the language of the bee, which was initially brought to our attention by the physiology of sense perception, has now led us back to it. It also had already led to general questions of orientation in time and space. When bees use the sun as a compass during their own flights as well as to inform their comrades, one difficulty arises: With the advancing hour of the day, the sun's position changes, and one would imagine that it can serve as a geographic marker for a short time only.

I had long contemplated an experiment whose execution was postponed from one year to the next by the feeling that it would not amount to much. However, in the early morning of a fall day in 1949, we sealed the entrance of our observation hive standing in Brunnwinkl on the shore of the Wolfgangsee, transported it across the lake, and placed it 5 km away in a completely different area unknown to the bees (*15*). Numbered bees from this colony had visited a feeding place 200 m to the west on previous days (Fig. 9). From the familiar lakeshore and steep wooded hills they now found themselves in flat meadows; none of the known landmarks could be seen. Four feeding bowls with the same scent as at the former feeding place were placed 200 m from the hive toward the west, east, north, and south, and the entrance was then opened. Of the 29 marked bees that had visited in the west during the previous afternoon in Brunnwinkl, 27 found the bowls within 3 hours: 5 in the south, 1 each in the east and north, but 20 in the west (Fig. 10). Each was captured on arrival and was thus unable to send others out by dancing in the hive. Only the sun could have guided those who arrived. It, however, was southeast of the hive, while on the preceding day during the last foraging flights it had been close to the western horizon. Bees possess excellent timing, an inner clock, so to speak. During earlier experiments, by feeding at certain hours only they trained themselves to arrive promptly at the table at that time—even if the table was not set. The above trial, repeated in many modifications (*6, 15, 16*), has now taught us that they are also familiar with the sun's daily movement and can, by calculating the hour of the day, use this star as a true compass. The same discovery was simultaneously and independently made by Gustav Kramer using birds (*6*).

During the past few years, an old and persistent question has opened a new field of work for bee researchers. In discussing the direction indication, I initially kept something from you. The dancers did not always point correctly to the food sources. At certain hours they were markedly off to the left or the right. However, no inaccuracies or accidental deviations were involved; the errors were consistent and, when recorded under the same conditions, time and again gave the same curves for a typical daily routine. Thus they could correct, for example, for a different spatial position of the comb. Errors arose only with transposition of the dancing angle; in horizontal dances there is no "incorrect indication of direction." Observations over many years, made jointly with my co-worker Lindauer, finally led us to a conclusion which seemed acceptable (*6*). However, it was disproved by Lindauer, who persisted in his experiments together with his student H. Martin. They recognized the magnetic field of the earth as a cause for incorrect indication of direction. If this is artificially screened out, the error disappears; and by artificially altering the course of the lines of flux, the incorrect indication of direction was changed correspondingly (*17*). The idea that the magnetic field might play a role in the puzzling orientation performance of animals was rejected for a long time. During the past years it has been confirmed by new observations, especially in birds and insects (*18*). Nothing so far points to the possibility that bees, in their purposeful flights cross-country, are making use of the earth's magnetic field. Unexpectedly, however, it proved equally significant biologically but in a different way. When a swarm of bees builds its combs in a hive furnished to them by the beekeeper, their position in space is prescribed by the small suspended wooden frames. In the natural habitat of the bee, perhaps in the hollow of a tree, there are no wooden frames present. Nevertheless, thousands of bees labor together and in the course of one night achieve an orderly structure of parallel combs; the individual animal works here and there without getting instructions from a superintendent. They orient themselves by the earth's magnetic field and uniformly have in mind the comb position which they knew from the parent colony (*20*).

However, these are problems whose solution is fully under way, and we may expect quite a few surprises. By this I do not mean that problems such as the perception of polarized light have been conclusively solved. On the contrary: A question answered usually raises new problems, and it would be presumptuous to assume that an end is ever achieved.

It was not possible to present more than just a sketchy illustration in this lecture and to point out a few important steps in the development of our knowledge. To corroborate and extend them requires more time and work than the outsider can imagine. The effort of one individual is not sufficient for this. Helpers presented themselves, and I must express my appreciation to them at this time. If one is fortunate in finding capable students of whom many become permanent co-workers and friends, this is one of the most beautiful fruits of scientific work.

References and Notes

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4. The threshold of transition from the round dance to the tail-wagging dance varies with each race of honeybees; according to R. Boch [*Z. Vergl. Physiol.* **40**, 289 (1957)], it is about 50 m for *Apis mellifica carnica*, about 30 m for *A. mellifica mellifica* and *A. mellifica intermissa*, about 20 m for *A. mellifica caucasia* and *A. mellifica ligustica*, and 7 m for *A. mellifica fasciata*. The fact that the strain we used mostly in our experiments, the Carniolan bee, has the largest round dance circumference was of benefit in our experiments.
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