Karl von Frisch: Experimental behavioral ecologist, ethologist and comparative sensory physiologist

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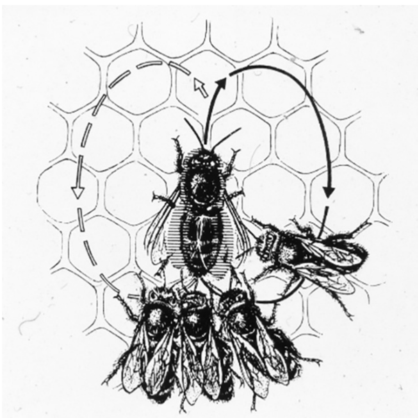
Abstract

Over the early part of the last century, Austro-German biologist Karl von Frisch made an epochal discovery in animal behavior: the waggle dance of honeybees. In 1973 he was awarded the Nobel Prize for Medicine and Physiology, together with Nikolaas Tinbergen and Konrad Lorenz. Many other significant findings are intimately connected to the experimental procedures and behavior-ecological approaches that led to this major discovery. These include studies on fish odor, sound and color perception, honeybees' color and polarized light vision, odor perception, learning during landscape exploration, guidance by the celestial compass, sound perception, and navigation. Here we follow von Frisch's academic career and the steps of his research during his 96 years of life.

Graphical Abstract

The waggle dance (von Frisch, 1967, p. 57, Fig. 46).



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Keywords

Animal behavior; Behavioral ecology; Comparative sensory physiology; Ethology; Fish: color adaptation, hearing, pineal eye; Honeybees: color vision, magnetic sense, navigation, olfaction, polarized light vision, social communication, sun compass, time sense, waggle dance

Glossary

Ephemeris function In celestial navigation an ephemeris (from Latin ephemeris 'diary') is a table that gives the trajectory of naturally occurring astronomical objects in the sky the position over time (here the sun).

Key points

- This article explores the many contributions of one of the most eminent players in animal behavior of the first half of the 20th century, Karl von Frisch, the discoverer of the waggle dance of honeybees.
- Based on detailed observations of the bee's behavior in its natural environment, and using eco-evolutionary arguments, von Frisch developed novel experimental approaches to behavioral-physiological studies in animals.
- Von Frisch's research did not fit easily into either of the two major schools of animal behavior: ethology and experimental comparative psychology (behaviorism, Pavlovian psychology). Rather, he was a pioneer who developed his own unique research strategy, that has had lasting impacts on modern approaches to the study of animal behavior.
- A crucial step in von Frisch's approach was the training of individual worker bees and then subjecting these trained bees to controlled laboratory-like test conditions.
- Around the mid-20th century, animal behavior as a subdiscipline of cognitive neuroscience underwent a shift of focus called the cognitive turn, which took neural processes into consideration. Here we also address the role of von Frisch's discoveries in the context of cognitive neuroscience.

Introduction

In the first half of the 20th century, animal behavior was comfortably ensconced within two parallel, rather independent schools: ethology and experimental comparative psychology (including behaviorism and Pavlovian psychology). Although there were significant battles between the two schools, each was rooted in a conceptually sound foundation. Ethologists preferred to investigate natural behavior in a species-specific environment and focused on those behaviors that could be reliably triggered or induced multiple times. Behaviorists worked, preferably in the laboratory, at creating repeatable test conditions using a system of training schemes. Although the research strategies and terminologies of the two schools differed greatly, they had one major thing in common: a shared the understanding that interpretive terms, particularly those that included hidden reference to brain functions, were to be avoided or even banned. Rollin (1990) neatly summarized this attitude as "how animals lost their minds". Furthermore, an additional common ground to both schools was their strict opposition to any form of "anecdotal cognitivism" or anthropomorphism as was often invoked by 19th-century zoologists including Darwin. This victory over the "unscientific attitudes of the past century" was celebrated whenever the debate about the differences between the two schools became too complicated and whenever doubts appeared emerged regarding their respective conceptual limitations.

Von Frisch was a pioneer in studies of animal behavior, who developed his unique approach under the scientific guidance of Siegmund Exner, his uncle, beginning as a schoolboy (see below). Exner was a founder of comparative physiology, brain research and perceptual psychology. One of his main areas of work was sensory physiology with studies on olfaction, color vision and on the vision of compound eyes. Based on Exner's training, von Frisch developed his unique approach to animal behavior. Von Frisch's research questions arose from studies under natural conditions and were motivated by evolutionary-ecological considerations. The methods applied were based on the learning of animals in a particular behavioral context. For example, his studies on color vision and odor discrimination in honeybees were motivated by insights into the co-evolutionary relationship between pollinating insects and flowers, and took advantage of the ability of worker bees to learn the sensory stimuli unique to each flower species. Similar arguments were applied to behavioral traits in navigation (e.g. requirements for safe return to the nest site), a sense of time as a necessity for using the sun as a compass for navigation, and social forms of communication as adaptations to social life and the economy of pollination. In this sense, von Frisch was not a typical ethologist, in that he applied training techniques and semi-laboratory test conditions in a similar way to experimental psychologists. One of his early publications dealt with psychological methods in working with bees (Von Frisch, 1922). The focus on sensory physiological questions, including his work on the waggle dance, could probably best be described as sensory ethology, since he was mainly concerned with understanding honeybee behavior as governed by their sense organs.

Von Frisch was the founder of comparative sensory physiology and behavioral research. His love of nature and boundless curiosity in nature's mysteries were his primary motivations. He described each behavior objectively, seeking the rules that govern it, how well they work, how the sensory organs modulate it via the nervous system (causal aspects). He also considered how behaviors evolve as innate behavior and modified by learning ability (phylogenetic and ontogenetic aspects). Of decisive importance here were his investigations into animal communication and orientation, especially the "dance language" of bees in connection with the orientation by the sun compass and celestial polarization pattern and the internal clock (sociobiological, etho-ecological aspects). Therefore, the life of the whole bee colony with its intimate network of social communication was a central topic of his research (the bee colony as a superorganism).

At the time, insects were thought to belong naturally to the realm of ethology, because their behavior was so obviously dominated by innate and rather stereotypical routines. Furthermore, insects have small brains, and thus cognitive questions could be easily dismissed. Von Frisch (1962, p. 78) himself stated somewhat apodictically: "The brain of a bee is the size of a grass seed and is not made for thinking. The actions of bees are mainly governed by instinct". Von Frisch's statement is surprising. Von Frisch was a highly informed naturalist and evolutionary biologist. He certainly knew Darwin's (1859) position, as expressed, for example, in the following statements taken from *The Origin of Species by Means of Natural Selection, Or the Preservation of Favored Races in the Struggle for Life*: "... there may be extraordinary mental activity within an extremely small absolute mass of nervous matter: thus the wonderfully diversified instincts, mental powers, and affections of ants are notorious, yet their cerebral ganglia are not so large as the quarter of a small pin's head. Under this point of view, the brain of an ant is one of the most marvelous atoms of matter in the world, perhaps more so than the brain of a man."

Ethologists generally argued that insects and arthropods followed an evolutionary branch remote from that of vertebrates. Thus, the behavioral strategies vertebrates and arthropods for coping with the demands of the environment involved different adaptations, exemplified by their divergent sense organs and the highly tuned adaptations of their adjustable instinctive responses. Von Frisch's statement the brains of bees (above) is particularly startling because he himself had developed methods for training bees to perfection, documenting with each experiment how flexible and cognitively demanding the bees´ behavior is. In applying these methods, he discovered the honeybee's most impressive behavior, the waggle dance, which – as we shall see – cannot be regarded as a purely instinctive at all. There is also a second reason we should be surprised by von Frisch's statement. The brain of the honeybee had been wonderfully described as early as the mid-19th century (Kenyon, 1896), and the volume of the whole brain or parts of it (the mushroom body) had been related to the social life and complexity of behavior in solitary and social Apoidea (von Alten 1910, see Rybak and Menzel, 2024 with an annotated and translated text of von Alten 1910).

We shall here trace the development of von Frisch's research strategy, outlining how he made discoveries that are exemplary in 20th-century animal behavior, how he developed his unique path, and how he paved the way for the most important shift in animal behavior, the 'cognitive turn' around the midpoint of the 20th century.

Life of Karl von Frisch

Karl von Frisch was born in Vienna in 1886. During his 96-year life, the great biologist, gifted researcher and teacher was a pioneer of comparative sensory physiology and animal behavior. He is particularly associated with the epoch-making discovery of the waggle dance in honeybees. In 1973 he was awarded the Nobel Prize for Medicine and Physiology, together with Nicolaas Tinbergen and Konrad Lorenz (Fig. 1). Important honors had preceded this. In 1921, the Austrian Academy of Sciences had awarded him the renowned "Lieben Prize for Physiology," and in 1963 he was the first to be awarded the highly endowed "Balzan Prize for Biology". Among the numerous honorary doctorates he was given, the one from Harvard University meant the most to him. He received it at the same ceremony as the then West German Federal Chancellor Willi Brandt, and the then Secretary-General of the United Nations Sithu U Thant.

Fig. 1 Karl von Frisch at the time when he first observed the waggle dance (1921, left)) and (right) when he received the Nobel Prize together with Konrad Lorenz and Niko Tinbergen (1973).

Childhood and youth

From an early age, Karl von Frisch loved animals. During his school days at the turn of the century, he kept up to 170 different live species of animal at his parents' home in Vienna.

He conscientiously recorded what he observed, his mother Marie supporting him with loving patience. He also received inspiration from learned relatives. His paternal grandfather, a well-known medical doctor, had acquired the title 'Ritter' (Sir) von Frisch in recognition of his major contributions to the Austrian military medical system. His maternal grandfather, Franz Exner, was a professor of philosophy in at the Charles University in Prague. His uncle, Siegmund Exner (see above), was an important mentor to von Frisch as a schoolboy. Von Frisch showed Exner his growing collection of animals, mostly collected at the family's holiday home in Brunnwinkl on the banks of Lake Wolfgang (Austria). Uncle Exner impressed the young Karl that research is based on three major principles: careful and unbiased observations, clear formulation of hypotheses, and focused experiments. At age 16 von Frisch published an article about the feeding behavior of young eels in the journal *Blätter für Aquarien- und Terrarienkunde*.

Over the years, von Frisch's private collection of preserved animals housed at his family home in Vienna evolved into a small museum, open to the public, that now includes over 5000 species. Von Frisch's life-long passion for collecting animals no doubt contributed to his impressive knowledge of the diversity of living creatures and to his skills as a teacher.

Studies and doctorate

At high school he found the study of ancient languages, history and mathematics boring. After graduating high school, and at the request of his father, who taught surgery at the University of Vienna and felt that zoology was not lucrative enough, von Frisch studied medicine at the University of Vienna. After five semesters, he passed his preliminary exams with distinction. In 1908 he began studying zoology in Munich under Richard Hertwig, the most famous zoologist of the time. After four more semesters, he returned home to Vienna at the request of his parents and worked on "color changes in fishes" for his dissertation. He received his doctorate in 1910. He almost failed the oral exam, as he had omitted to answer certain questions about insignificant morphological details that did not interest him. Rather, his interest was in animals, how they behave in nature and how they most probably came into being over the course of evolution.

Postdoctoral research

Curiosity and a sense of the contradictions in the current thinking on the perceptual capacities of animals were the two motivations that drove his research as a young postdoc in Munich, Germany. One of these contradictions was the notion that all invertebrates are colorblind. Knowing from his own experience about the relationship between honeybees and flowers, he just could not believe it.

To solve the riddle, von Frisch fed some bees with sugar water in a small bowl placed on a blue paper among gray papers of different levels of brightness (Fig. 2). He wanted to find out whether the bees recognize the signal for food by the brightness of the target or by its color. In a test without sugar water, he replaced the blue and the gray papers with new ones and rearranged the locations of the papers. The bees landed exclusively on the blue and not on any of the gray papers. This seemingly simple experiment instigated a major shift in animal research by introducing a training procedure that relied on individual learning and a proper control of the experimental conditions. The opposing opinion of the time relied on testing innate phototactic responses to light of different wavelengths (Von Hess, 1913). The battle between the young researcher von Frisch and the established senior researcher von Hess was resolved by a live demonstration of von Frisch's experiments at the 1914 annual meeting of the Zoological Society in Freiburg.

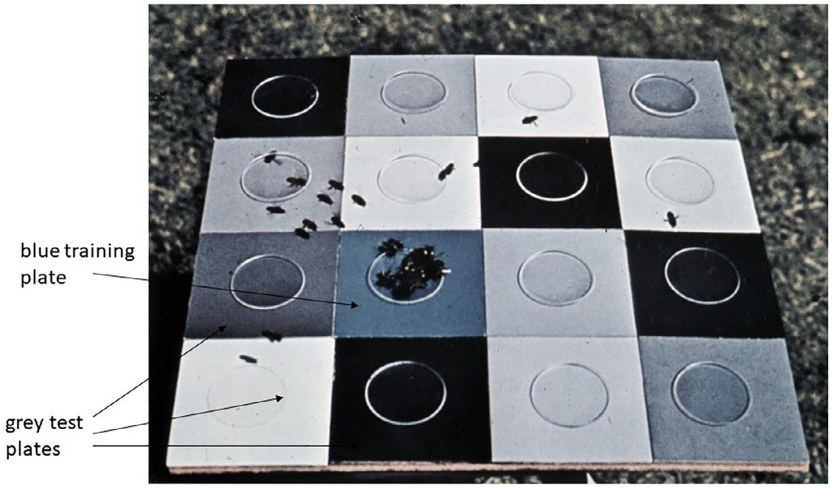

Fig. 2 Proof of color vision in honeybees by (Von Frisch, 1914). A chequerboard pattern of gray cardboards (ranging from white to black) was laid out on a table, and a blue cardboard presented at different locations carried a sucrose feeder for training bees. The picture shows a test situation in which no sucrose was offered. The bees chose only the blue cardboard. In additional experiments he found that bees also discriminate yellow from gray cardboards and do not discriminate red from black.

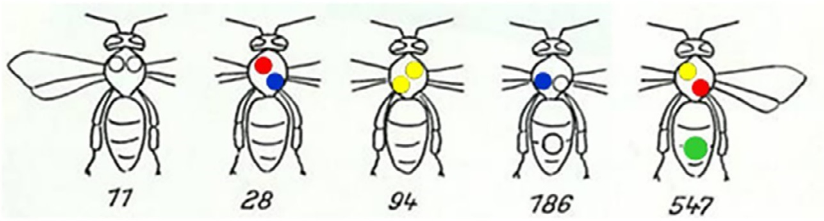

Fig. 3 Von Frisch's scheme for marking individual bees with color dots at four different locations on the thorax (front, left or right) and one dot on the abdomen to generate up to 599 numbers. A white dot at the front indicated 1, at the back 6. A white dot at the front left indicated 10 and front right 1; both together 11. In the same way blue stood for 30 (left) or 3 (right) in the front and for 80 back in the back (left) and for, 8 (right and back); yellow for 40 (left, front), for 4 (right, front), for 90 (back, left),and for 9 (back, right); green for 50 (front, right) and for 5 (back, right); Abdomen: white: 100, red: 200, blue: 300, yellow: 400, green: 500.

Thirteen years after the demonstration, Kühn (1927) discovered that bees can perceive the spectral range of UV light (300–400 nm). About 30 years later Daumer (1956) proved that bees have a trichromatic color vision system with three spectral receptor types, UV, Blue and Green. Eight years later these receptors were localized within the bee's eye using electrophysiological recordings (Autrum and von Zwehl, 1964). Thus the colors of flowers appear very differently to bees than they do to humans (Daumer, 1958). Yet bees have a sufficiently rich perception of color to discern and learn the differences between the floral floral resources that they encounter. These new discoveries were enthusiastically received by von Frisch. Even today honeybees are probably the most studied animal species (besides humans) with respect to their ecological, physiological, neural coding and psychophysical mechanisms in color vision.

Von Frisch's bee work in Munich was interrupted by the First World War. He returned to Vienna, where he helped his brother running a Viennese Red Cross hospital for the war-wounded. He performed operations and gave courses in bacteriology for nurses. In 1917 he married Margarete Mohr, the daughter of a Viennese publisher and bookseller. In 1919, the couple moved back to Munich, where he became an associate professor, gave lectures in comparative physiology, supervised his first doctoral students, and returned to the study of bees. Von Frisch now wanted to ascertain whether and how well bees perceive scents as a signal for food. He chose similar training procedures and documented the bees' choice behavior by filming them. In these experiments, multiple boxes were arranged vertically, one box containing a scent together with sugar water and the others remaining empty. In tests without a sugar reward, the bees only flew to the box with the trained scent. Bees were found to distinguish different scents about as well as humans do. Further experiments showed that bees also use visual shapes. In all these experiments, von Frisch worked with marked bees, allowing him to relate their choice behavior to their individual experience, a unique and innovative experimental approach.

In 1919 he started to mark trained bees individually (Fig. 3), and later he observed them through the glass window of an observation hive performing dances. Below, we turn to the exciting discoveries based on these two achievements, including the waggle dance. But first Karl von Frisch's path was to lead him away from bees and away from Munich. After 2 years of research and teaching as an associate professor at the Munich Zoological Institute, he was appointed full professor at the University of Rostock on the Baltic coast of Germany.

University career

After his move to Rostock, von Frisch addressed a new topic, whether fish can hear sounds. Because the vestibular organ lacks the hearing mechanics of other vertebrates, the deafness of fishes seemed obvious. The director of the Rostock Ear Clinic, Professor Otto Körner, was so convinced of their deafness that he had an opera singer sing to a dwarf catfish. Apparently, this performance made no impression upon the fish in question. In characteristic fashion, Von Frisch also got himself his own dwarf catfish, who he called "Xaverl". Von Frisch put Xaverl into an aquarium, where Xaverl liked to hang out in a tube thoughtfully provided by von Frisch. Von Frisch trained the fish by first whistling and then feeding it. The training was successful. Von Frisch invited Professor Körner to sit in front of the aquarium while he went to a corner of the room and whistled softly. Xaverl came out of his tube and looked for food. Professor Körner sank down and said, "Truly, he can hear." The publication of this experiment with the modest title "A dwarf catfish that comes when you whistle for it" triggered a wide range of research in the following period, initiating fundamental work on the physiology of hearing through to the discovery of ultrasonic echolocation in bats by one of von Frisch's doctoral students and later colleague Sven Dijkgraaf.

After 2 years in Rostock, von Frisch took over the larger Zoological Institute in Breslau, and after two more years he returned to Munich in 1925, this time as the successor to his revered teacher Richard Hertwig. In 1926 he founded a new zoology institute with the help of the Rockefeller Foundation and created one of the most modern zoology labs in Germany. The Institute quickly became a magnet for researchers from all over the world.

During his summer experiments at Lake Wolfgang he made a surprising observation. To identify an individual fish, von Frisch developed a technique where he severed a skin nerve with a needle prick, causing part of the tail to turn dark. Surprisingly, when he put the fish back into the lake to rejoin its fellows, the shoaling behavior of its conspecifics was over. Instead of swimming together in a school, individuals now pressed themselves to the ground, and suddenly the whole school fled into the depths of the lake. Investigation of this mysterious behavior led to the discovery of a fear-inducing substance that is emitted when the skin is injured and warns others of the danger of a predator. This opened the door to new avenues of fish research. Fear-inducing substances have now been found in hundreds of fish species with variable effectiveness. Indeed, the effectiveness of fear-inducing substances is a useful character for assessing phylogenetic relationships among species.

Research during the Second World War was extremely difficult, particularly as von Frisch was harassed by the Nazi regime for being a quarter Jewish. The Institute was destroyed in a hail of British bombs in 1944. He emigrated to the University of Graz for 4 years, before returning to Munich and restoring the Institute with the help of the Rockefeller Foundation. During these years he continued his bee experiments by Lake Wolfgang, now focusing on honeybee communication within their colony.

Von Frisch was an excellent teacher and a brilliant book writer who published several scientific, popular and high-school textbooks in this period.

Retirement and final years

Von Frisch retired 1958 aged 72 years and died 1982. His grave in Vienna is a simple burial site. During his 24 years of emeritus professor, he published multiple research articles with his co-workers and summarized his major discoveries in his famous book *Tanzsprache und Orientierung der Bienen* that was first published in German 1965 and appeared in English 1967 (*The dance language and orientation of bees*). In addition, he wrote a wonderful book on animals as architects (1974, together with his son Otto, German title "Tiere als Baumeister") and a book covering the family history entitled "Fünf Häuser am See" (Five homes at a lake). Furthermore, a published a booklet that contains many of the poems and rhymes that he wrote throughout his life. Von Frisch was a great collaborator. His studies around distance estimation encoded in the duration of the waggle run and on the magnetic sense were co-authored by H. Heran and M. Lindauer and K. Daumer respectively. He was invited to present distinguished lectures in German and international academies and universities that attracted a large audience, both academic and public. Research and teaching were his life - but not exclusively. Karl von Frisch was a caring, kind, warm-hearted family man, humorous host and reliable friend. And despite the many honors, he has remained modest. He named curiosity, imagination, striving as the sources of his discoveries for truth, diligence and happiness.

When Karl von Frisch was in his 95th year, his daughters Maria and Leni, who lovingly cared for him, once complained to one of us (Karl Daumer) during a visit: "Dad is getting unbearable, he has nothing more to do". They wondered whether I might have an idea. I asked him if he would like to write a guide to his museum, including all the beautiful stories he had always told us. And this was exactly what he did, by his own hand on his old typewriter. It became his last work, 80 years after his first publication in the aquarium journal.

The discovery of the waggle dance and related findings

A short history of its discovery

A hundred years ago, the young Karl von Frisch published an observation that he later described as "... probably the most momentous observation of my life", noting: "...I could not believe my eyes. What happened here was too delightful and captivating to be described in dry words" (Von Frisch, 1923, citation from Von Frisch, 1957, p. 61). For many decades, he and his students, in particular Martin Lindauer, e.g. (Lindauer, 1959), worked on the elucidation of this observation. The importance of this research was recognized 50 years ago when von Frisch was awarded the Nobel Prize in Physiology or Medicine (together with Konrad Lorenz and Nico Tinbergen) for his discovery of the waggle dance of bees.

Let's listen to von Frisch's own words once again. His first description of the dance refers to the round dance: "The dance consists of round circles performed with great speed, and often swivels around 180°, so that the direction changes constantly. The circles are narrow, inside there is usually a wax cell, on the adjacent six cells the bee runs around, describes one or two circles in one direction, often also only a half or three-quarter-circle arc, then suddenly turning around, and continuing to turn in the opposite direction" (Von Frisch, 1920, p. 567) (see Fig. 4 here). He describes the waggle dance that he initially attributed to pollen-bearing bees as "A bee arriving . . . runs up the comb and then begins to turn in the midst of the other bees; but it does not describe full circles, as happens in the round dance, but at first a semicircle. Then it runs in a straight line over 2–3 cells back to the starting point, now turns to the other side and runs a second semicircle, which closes the earlier one to a full circle" (Von Frisch, 1920, p. 73). Twenty-five years later von Frisch recognized that the waggle dance indicates more distant feeding sites, whereas the round dance indicates closer feeding sites. At this point, he did not mention the characteristic waggling during the straight stretch, which contains the code for the direction and distance of the flight to the feeding site. Only when he resumed his work on dance communication did he investigate the coding properties of the waggle component of the dance for indicating direction and distance by means of a series of diverse and elegant experiments (Von Frisch, 1950).

The key innovation to understanding the dance language was first made when von Frisch trained bees on scents. In doing this, he used a method that allowed him to recognize individual bees (Fig. 3). This made it possible for him to know which bee was at his feeder at which time, and importantly he could also determine what it did in the hive afterwards thanks to the glass window he used from 1917 onward. Today it is common practice to glue colored number tags onto bees or attach a QR code for recognition via a video camera. Video analysis of dance behavior is now standard, allowing precise measurement of the parameters important to the dance code (the direction of the waggle run in reference to gravity, the number of waggles per run, the duration and length of the waggle run). Moreover, since bees are electrostatically charged, the electric fields emanating from their movement can be recorded, which makes the measurements of the dance data extraordinarily precise and above all makes the frequency components quantitatively evaluable over a range of 5 Hz to 5 kHz (Paffhausen et al., 2021). Since bees detect these fields with their electrostatically charged hairs and antennae, and can learn them and distinguish them, it may well be that they also use these signals for communication in the dark hive.

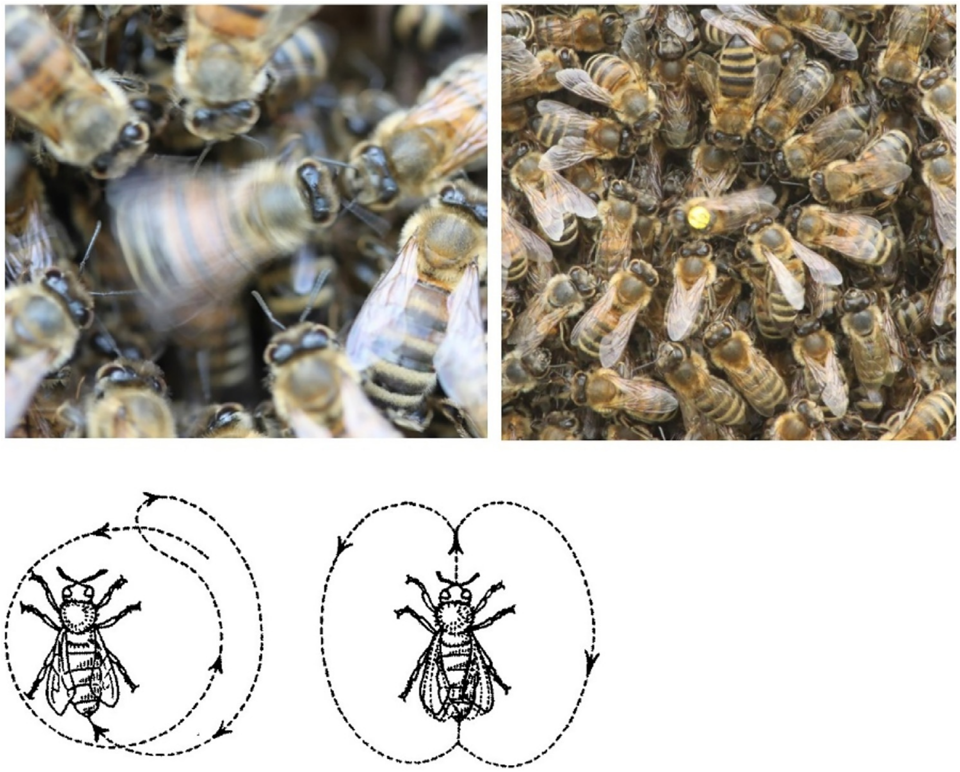

Fig. 4 Waggle dance and round dance. The two upper pictures show a waggle dancing bee surrounded by dance followers. Note that the dance followers are located all around the dancing bee. The lower diagrams show the running pattern of a bee performing a round dance (left) and a waggle-dancing bee (right). From Von Frisch K (1950) *Bees: Their Vision, Chemical Senses and Language*. Cornell University Press.

The behavioral elements of the waggle dance

Karl von Frisch's Nobel-Prize-worthy discovery consisted in deciphering the code for the distance and direction of the flight to the feeding site indicated by the dancer. He found the distance to be encoded by the number of waggles per run, the duration of the run, its length, and the duration of the runs back to the starting point. Each of these related parameters increases with distance. It also became clear that for distances less than 80 m the round dance is used. It is now known that in the waggle dance each waggle codes 65–75 m in flight to the feeding site. The secret of directional coding was more difficult to unravel. For a given feeding place, the direction of the waggle run relative to vertical changed gradually over the course of the day. From this von Frisch inferred that the position of sun might play a role in orientating the dance. And indeed, von Frisch eventually deciphered that bees use a solar compass to orientate their dances, and the directional information contained therein. Waggle runs directed upward signify that the flight direction is towards the position of the sun (azimuth) at the time of the dance. The bee does not necessarily have to see the sun; the pattern of polarized blue-sky light is sufficient, since this pattern correlates with the sun's current position. The bee also has an internal clock and learns the ephemeris function, the local time dependence of the sun's movements. All these observations were further confirmed by multiple experiments carried out over subsequent decades by von Frisch, his students, and independent researchers ever since. In the light of all his discoveries, von Frisch was able to read the flight vector to the feeding site from the waggle run and thus discern its meaning as the human experimenter. But do the dance followers extract the same information? This was the controversial question that generated a lot of debate at the time.

Von Frisch faced a problem in that he could not record the flight of the dance followers, the foraging bees that were recruited by the dancer to its feeding site. To resolve this difficulty, he provided the sucrose feeder for the dancing bees with an odor. In the test situation, multiple additional sites were established with the same odor but without the reward. These test stations were arranged either in in a radial fashion at different angles as seen from the hive but at the same distance (Fig. 5A) or in a stepwise fashion at shorter or longer distances in the same direction (Fig. 5B). Many further experiments were run with similar designs. The use of an odor as a bait was necessary because only in this way could the dance followers searching for the feeder indicated by the dancer be counted, since they settled at the test stations only if the odor they detected on the dancer was the same as the odor provided at the feeder. This observation amounted to an important finding in itself, namely that the dance followers learn the odor of the feeding site from the dancer. However, it also made it impossible fully to rule out that the odor might be the only guiding cue. Controls of all kinds tried to exclude this possibility (e.g. a strong wind blowing from the side or from behind), but the objections put forward by opponents (Wenner et al., 1969) could not be totally refuted.

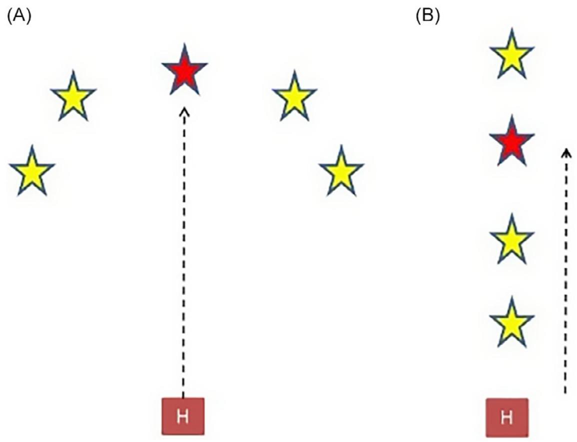

Fig. 5 To verify the direction coding and distance coding, von Frisch and his co-workers carried out many experiments of this kind. The dancers were trained at a scent-marked place (here marked by the red star). In the test, feeding was terminated. At each of the locations marked with a star, there was an observer who noted each arriving bee. These places were also marked with the scent of the feeding station. A group of bees was trained to a scent-marked feeding site a few hundred meters from the hive. Test sites marked with the same scent were placed either at the same distance but at different angles to the hive (A) or in the same direction but at different distances (B). By far the greatest number of bees was noted at the dancer's feeding site, with slightly more at the closer ones than at the more distant ones. The conclusion was that the dance followers decode the information on both direction and distance, and thus the semantic information.

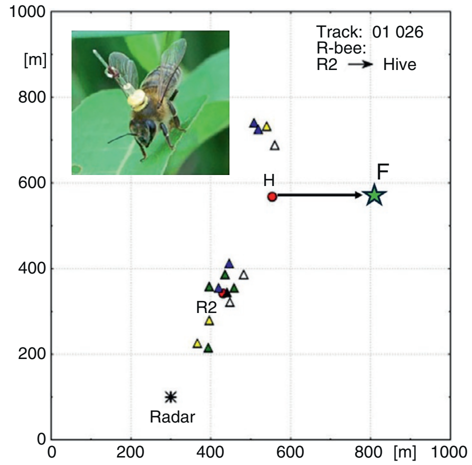

Fig. 6 Flight trajectory of a dance follower tracked by harmonic radar. The bee had followed a dancer for F, the dancer's feeding site, and was then moved to the release site R2. R2 is located 300 m south of hive H. The bee first flies 200 m to the east (red trace) and then back to the release site (blue trace). There it decides to fly back to the hive H (green track). The frame indicates the distances. The experiment was performed on a large, mowed meadow. The insertion shows a bee equipped with a radar transponder. After Riley JR, Greggers U, Smith AD, Reynolds DR, Menzel R (2005) The flight paths of honeybees recruited by the waggle dance. *Nature* 435: 205–207.

The influence of the scent can be ruled out with certainty if one tracks the flight of the recruited bee over its full flight and if the recruited bee starts not at the entrance to the hive but is moved to another location. Full-flight tracking is possible with a harmonic radar system (Riley et al., 2005). Such an experiment is shown in Fig. 6, which illustrates the flight trajectories of dance followers seeking the feeding site marked by F in the fig. (200 m east of the hive). In Fig. 6 A, the bee is moved to site R2 about 300 m south of the hive and released there with a transponder. It flies exactly 200 m to the east (red part of the flight track), searches around for a short time, flies back first to the release site R2 (blue track), then flies directly back to the hive. Of course, there are no bees and there is no food at the point 200 m to the east (the virtual location corresponding to the endpoint of the vector encoded in the dance). Visual landmarks did not play a role either, as the whole experiment was conducted in a mowed meadow lacking a profile of the horizon. Moreover, to rule out for sure the close-range effect of the scent at the feeding site, all the experiments using harmonic radar tracking were conducted without scent at the feeder. This experiment conclusively shows that the bee followed the directional and distance information encoded in a dance that she had followed, and that odor is not required for successful transfer of information about forage locations.

The waggle dance experiments provided von Frisch and his research group with tools to unravel the sensory and cognitive capacities involved in this unique example of communication and navigation. Let us now turn to the bees' measurement of distance, the sky compass, the time sense, and the spatial memory of the environment.

Distance measure: The outbound component is the most important part of the flight for measuring distance. Since dancers encode greater distances if they fly uphill, against the wind, or with a load glued to the thorax, it has been concluded that it is the energy consumed that provides the essential information. However, bees flying in a narrow tunnel with close random black/white patterns indicate much greater distances in their dances than the true length of the tunnel, leading to the conclusion that the optic flow is an essential factor in the measurement of distance (Srinivasan et al., 2000; Esch et al., 2001). It is now known that this component loses its guiding effect if the bees can see the explored environment around the tunnel (Menzel and Galizia, 2024). This latter finding suggests a more complex form of navigation than just encoding and decoding the outbound vector component (see below).

Direction measure by a sky compass: Young bees explore the environment around the hive before they start foraging or following dances. Exploration also results in the bees learning about the solar ephemeris function, the time course of the movement of the sun during the day in relation to the local landmarks. If bees trained to a particular time of the day are then shifted overnight with their colony from the east coast of the USA to California or from a location south of the equator to one north of the equator, these bees indicate the wrong direction in their dances and fly in the wrong direction when following the dancers, proving that they have learned the timing and the local ephemeris function during their exploration flights at their original location. It has also been proven that bees extrapolate the whole-day ephemeris function even if they have only been exposed to the afternoon part. If dancers are stimulated to perform dances at night, they do this correctly according to a sun azimuth they have never experienced (von Frisch, 1967).

Polarized-light detection: An additional capability was discovered when von Frisch moved the comb of an observation hive into a horizontal position. By doing so, he managed to expose the bees either to the full sky including the sun or only to the blue sky without the sun. In both conditions, the dances were correct in their indications of direction. In a famous experiment known as the *Ofen Rohr* (Furnace Pipe) Experiment, the dancing bees could only see a small part of the blue sky, yet they danced correctly. When von Frisch then put a polarization filter in front of the pipe and rotated it, the dancing bees rotated their directions correspondingly. We now know that bees detect the linearly polarized light in UV with a specialized region of their compound eyes, the dorsal rim area. The rule for extrapolating the great circle of the sun's path (thus the sun's azimuth at the time of the day) from the polarization pattern is rather simple. The pattern of the direction of polarization is mirror-symmetrical in relation to the sun's great circle. The pattern of the polarization sensors in the rim area is also mirror-symmetrical in the two eyes. Thus, if the bee rotates its whole body, the sun's great circle will be detected by the optimal signal of all the polarization sensors when the axis of the bee's body length is aligned with the great circle of the sun's path. Additional parameters (e.g. the chromatic gradient of the sky) help to resolve any ambiguity in the polarization pattern of the sky (e.g. the distinction between the sun and the anti-sun).

Magnetic sense: Analysis of a large number of dances in terms of the directions they indicate has shown a small but systematic change over the course of the day (the so-called daily "misdirection"). This effect depends on the direction of the combs relative to the earth's magnetic field and disappears when the magnetic field is eliminated (Lindauer and Martin, 1972). Furthermore, when swarming bees build their new nest in a circular box, the direction of the combs is found to be the same as in their former nest, indicating a memory of the combs' direction in relation to the earth's magnetic field in their former nest.

Encoding and decoding the dance message: Let's reflect on what an amazing feat the bees' symbolic dance communication is. The distance indicated by the dance has no direct relation to the way the flight distance is measured by a flying bee. The directional information is also symbolic because the angle relative to the current azimuth of the sun during the outward flight is transferred to the angle relative to gravity on the vertical honeycomb in the darkness of the hive. This transfer does not require short-term perception of the sun's azimuth and, as mentioned above, bees give the correct direction even at night when they are stimulated to dance. On overcast days, bees derive the sun's azimuth from the landmarks they have learnt. Taken together, the dance followers read the meaning from synthetic symbols, the movements of the dancer. How this is embedded in their navigation during foraging and nest finding will be discussed below.

Is the waggle dance a language?

Von Frisch frequently emphasized that he used the term "language" as a metaphor, but he also insisted: "It would be equally wrong and a denial of the facts if one were to place the bees' method of communication on a par with the warning calls of many other animals or the similarly simple 'communications of social associations'" (von Frisch, 1953). Indeed, if flight instructions were being communicated simply by means of fixed relations between the angle of the waggle run relative to gravity and the outbound direction relative to the present azimuth of the sun and between the distance and the number of waggles, it would not be classified as an intelligent communication system. Rather, it would be interpreted as a communication system that is limited to synthetic information and does not involve a decoding of meaning. The question, therefore, is how the encoding and decoding processes are connected, and thus how meaning arises.

The encoding and decoding of direction does not require the sun to be visible, for the polarization pattern of the blue sky and the landmarks are sufficient. Dances occur at night with correct codes for a feeding site that has been trained during the day. The bees dance only after they have explored the environment. The meaning is embedded in the context. Dancers on a swarm encode the location and quality of a potential nest site, whereas foragers for nectar, pollen, water or resin encode the location of the respective material to be collected at the site they indicate. Thus, waggle dance communication is a symbolic form of communication based on gestures, motor patterns, and accompanying stimuli, which constitute the syntax of the dance, and the encoding depends on the context, which supports the extraction of the meaning. How should one deal with the question of which level of cognition the communication takes place on? Von Frisch said in a public talk: "But what about thinking? Can one speak of a symbol even where there is no thought behind it? . . . But insects are differently organized. They show no sign of deliberation, no hint of any emotion. And if one wants to argue that we cannot identify what goes on in the ganglion cells behind the chitin-armored brow of a fly, all their actions and omissions are proven to be innate in every detail, given to them as a pre-formed instinctual act that, from their point of view, would not be worth thinking about. . . . [T]he symbolic dances in a colony of bees . . . are not only triggers for an action but communicate complex facts and, almost like the words and sentences of our language, give very specific instructions for the action that is to be undertaken. They serve not only as keys to a lock, but rather – if I may stay with the image – they offer the partner a rich view through the open gateway" (Von Frisch, 1959). Indeed, communication with symbols has a certain similarity with human language. In his first publications, von Frisch put the word "language" in quotation marks. Even the simplest human language has an abundance of symbols, which can be put together in free combination to produce different meanings in each case, thus forming words. These can in turn transmit new meaning according to the rules of grammar. The amount of learning in this context is extraordinary, and only a few basic structures are genetically anchored, as in bird song. The case of symbolic dance communication is quite different. There are very few symbols, and the ways of combining them are very limited. However, different contexts (for example, nest site and flower locations) have different meanings for the same coding system. Could this be understood as a very simple form of "grammar"?

Landscape memory and dance information

As mentioned above, bees start their foraging activities only after they have explored the area around their hive. Exploratory learning is a form of learning that receives its reinforcing component from the intrinsic exploratory drive rather than from extrinsic signals such as a reward. Multiple experiences, first in the area just around the hive and then in a wider area (of about 500 m radius), together with the capacity to generalize between different views of the same landscape feature, lead to a rich landscape memory embedded in the bees' sun compass and sense of time. "Generalization occurs in learning and is essential for deriving knowledge from experiences and for skills of all kinds. It is the basis of predicting future situations from past experience and for drawing analogies" (Gregory and Zangwill, 1987, p. 284). Thus, generalization is a key component of the cognitive dimensions of memory used in problem-solving. In the case of landscape memory, pictures learned at one particular site will be transferred to another site depending on the similarities between these learned pictures. Partly overlapping memory contents of spatially closely related sites will lead to some measure of "neighborhood" connecting these sites. Such a landscape memory can best be conceptualized as a mental or cognitive map (Menzel, 2023). Is this map-like memory also used in dance communication? If such is the case, the dance followers would be using the vector information not only as a flight instruction, namely, to fly from the hive to the feeding site indicated by the dancer, but also to determine a location in their landscape memory. Fig. 7 shows a dance follower starting its search flight not at the hive but rather at a different site at a distance from the hive within its explored area (at R5). It first flies a short distance in accordance with the flight instructions (straight green track in the direction of vF, the virtual feeding site of the dancer); then it starts its search flight (light blue track), which leads it to the area close to the release site and most importantly back to the hive via the feeding site F indicated by the dancer (yellow track). Many such experiments have shown: 1. that the more the area over which the bee flies deviates from what would correspond to a direct flight from the hive to the foraging site indicated by the dancer, the shorter the initial vector flight, indicating that dance followers expect landscape features when decoding the dance message; 2. that the search flights are directed to the location indicated by the dance; 3. that search flights directed towards the true location are initiated at various points during the vector flight or the return flight to the release site. Such behavior is only possible if the dance follower has a map-like landscape memory, because it requires knowledge of the dancer's feeding location and the landscape features on the way towards it (Wang et al., 2023). Thus, dance followers refer not only to the vector information in their search flights, but also to information about the true location of the dance vector endpoint derived from their spatial memory. This finding has been interpreted as showing that dance followers translate the communicated vector into location-specific information. Since dancers are frequently switching between dancing and dance following, we can assume that both the dancers and their recruits refer to a map-like memory. Taken together, the dance message is fully integrated into a map-like memory.

The cognitive dimensions of von Frisch's discoveries

The "danger" of anthropomorphism

Von Frisch himself struggled with the problem of avoiding anthropomorphism while still capturing the fascination of his discoveries (see above on the use of the term "language" in the context of the waggle dance). In a public talk on the waggle dance in Von Frisch (1959), he described his way of thinking lucidly: "Insects have a much more invisible brain, also in relation to their body size, not created for thinking or making inventions. [Yet] They, too, perform amazing mental feats, intricate and meaningful actions. But they do not consider what they should reasonably do in a given situation. How they are to behave is essentially already fixed in their cradle. Innate actions, 'instincts', guide them on their path through life. Tried and preserved through hundreds of thousands of years, inherited through countless generations, instincts only fail when they are suddenly confronted with unfamiliar tasks. They don't need a lot of brain matter because they limit themselves to a few tasks. They are tailored to the normal case, for which of course the circuits of the nervous process are then perfect ". Elsewhere he reflects: "Are bees great thinkers after all?

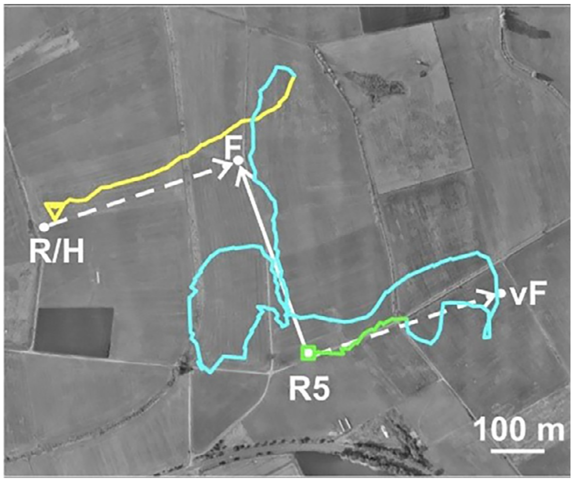

Fig. 7 Representative flight trajectory of a dance follower for the feeding site F indicated by the dancer. The bee was transported from the hive to R5 to the southeast of F and then released. The green track marks the vector component of the flight, the light blue track marks the search component, and the yellow track marks the homing component. R/H: location of the radar and the hive, F: feeder for the dancer, R5: release site of the dance follower, vF virtual feeder location, the location defined by the vector communicated by the dancer. From Wang Z, Chen X, Becker F, Greggers U, Walter S, Werner MCR, Gallistel R Menzel (2023) Honey bees infer source location from the dances of returning foragers. *Proceedings of the National Academy of Sciences* 120: e2213068120, their Fig. 1C.

Can this strange process be interpreted in any other way than that the bee colonies had gathered one day and decided: the direction upwards on our honeycomb means the direction towards the sun, etc.? A dung beetle teaches us otherwise. Dung beetles are in pretty much every respect the antithesis of bees in the insect world. Moreover, dung beetles do not form states and certainly have nothing important to say to each other in terms of food sources. But a dung beetle may also use the sun in order not to lose track. It maintains a certain angle to the light source when crawling on the ground. If it is now suddenly placed in darkness and on a vertically standing surface, it takes the angle to gravity that it had previously maintained in relation to the light. This has no biological significance for it. But it sticks to its angle of orientation, perhaps out of a kind of mental inertia; when the light fails, it adheres to another useful orientation stimulus, in this case gravity. This has been observed in several insect species. The transposition of the bees, which seemed so mysterious at first, is apparently not due to a council decision after all. Rather, it is a widespread, primary peculiarity of nervous centers, which is admittedly uniquely placed at the service of a biological task in the bee colony. So again, it is nothing to do with bees as thinkers. But does man think of all the symbols he uses? Does he think about the clenched fist with which he expresses his anger, the punch he could throw?" (Von Frisch, 1959).

Intentionality

The last few sentences of von Frisch's statement reveal an important twist, which becomes clearer if we add "conscious" to his words "decision, thinkers, think". Many, probably most, decisions in humans are made "unconsciously", and thus in a mental state characterized by what philosophers designate with "intentionality" – a mental or psychological process that is directed at a goal while at the same time producing associations with that goal and the route towards it. In simple terms, there are four minimal conditions for intentionality in animals: (1) identification of the brain as the mental center with its body (self-awareness), (2) the anticipation of future conditions (expectation), (3) the assessment of these conditions with regard to the then prevailing conditions or needs of one's own body (evaluation), (4) the selection of a behavior from two or more options (decision-making). The actors are intrinsic neuronal processes that are characterized by their contents. These simulate future conditions, relate them to oneself and one's current needs, evaluate them, and choose between them. It is then and only then that target-oriented behavior occurs, conditions we observe in waggle dance communication.

The question of whether insects and in particular honeybees engaging in social communication possess intentionality in this sense can be approached in two ways: by means of behavioral analysis and by targeting the neuronal mechanisms (the latter aspect will not be dealt with here). Let's take the first two conditions: self-awareness and expectation. All animals with a nervous system differentiate between self-generated stimuli and those from the environment, which are independent of the animal. The neuronal mechanism is based on the processing of neuronal commands not only to the motor centers (efference copy) but also to the entrances to the sensory organs. This simplest form of self-experience already contains the criterion of expectation, because the circuitry is such that only a specific perception is offset by the relevant efference copy. The social self in its simple form, as in honeybees, classifies the animal's own body in relation to others as a body that belongs to the same or to a different group. The recognition of group membership may be a simple sensory-motor act such as the differentiation of hive-mates from foreign animals at the hive entrance based on body odors, or a complex act such as occurs when the bee generates a stop signal in a swarm, inhibiting another scout bee's efforts to continue advertising for a potential nest site inferior to the one she has herself discovered (Seeley et al., 2012). The evaluation of criteria and decision-making require standards of comparison and at least two behavioral options.

The bees' mental states can be recognized by the different behaviors with which the goal is reached. Referring to the paradigm characteristic of a cognitive map, the novel shortcut, this means that the goal selection takes place in an adaptive way; for example, a bee that has followed a dance flies to the goal indicated via a path that it has never experienced before and that reflects the shortest distance to the goal even from an unexpected starting point (see Fig. 7). The uncovering of options requires that the animal is removed from its ongoing behavioral context and placed in an unexpected situation. This is evident, for example, in its selection of routes and goals: e.g. fly back directly to the hive, fly towards a formerly visited natural food source, fly only the vector and then back to the hive, fly to the location indicated by the dance. This involves some form of representation of the potential goals and the respective routes towards them without having access to the features of these goals. These conditions have been met in the experiments that proved the existence of a cognitive map.

The results of these experiments were not known to von Frisch. It would be exciting to know whether he would have accepted the logic of these arguments and whether he would have agreed that the term "intentionality" in honeybee dance communication captures what he meant in the above-cited quotation. To a certain extent, this interpretation was anticipated by the eminent behavioral biologist William Homan Thorpe, who, describing his excitement about the waggle dance after watching von Frisch's experiments, observed: "I think it may be said that the performance of the worker hive bee is essentially an elementary form of map-making and map-reading, a symbolic activity in which the direction and action of gravity is a symbol of the direction and incidence of the sun's rays" (Thorpe, 1949, p. 11–12).

Conclusion

The development of thinking in animal behavior during the 20th century and well into the 21st was epitomized by the ongoing debate on the waggle dance (Menzel, 2023). Pre-cognitive-turn arguments are still put forward in abundance, ignoring or downgrading the richness of cognition in the insect brain and the role of multiple forms of learning and memory-processing. Novel experimental approaches (e.g. radar tracking, sophisticated video analyses of social behaviors) have opened new avenues that allow rich data sets of behavior to be interpreted inside and outside the colony. Early in his impressively rich oeuvre, von Frisch promised: "The bee colony is like a magic well the more you draw from it, the richer it flows" (Von Frisch, 1927). This is indeed the exciting experience of any researcher who has had the pleasure of studying bees.

Implications for the future

The cognitive turn in the behavioral and neural sciences has benefited from new empirical approaches to understanding the brain. In our context, the assumption of a cognitive map is no longer debated since it has been possible to unravel its neural bases in the mammalian brain. Nothing similar exists yet for the insect brain although a few basic neural elements are known, such as the neural mechanisms of associative learning and of the sun compass. I suspect that the debate on the cognitive dimension of the waggle dance and its embeddedness in a map-like memory will be resolved once we unravel its neural correlates.

Further information

T. Munz (2016), The dancing bees: Karl von Frisch and the discovery of the honeybee language. University of Chicago Press 2016. This book provides an excellent account of the historical conditions in which Karl von Frisch's performed his research.

Von Frisch published a booklet on his research the first time 1927 in German under the title "Aus dem Leben der Bienen" (Springer Verlag, Berlin, Heidelberg). This book was updated by him nine times, the last revision appeared 1977. Several translations were published. The English version (Karl von Frisch, Bees, Their Vision, Chemical Sense and Language) was published the first time in 1950. The last version revised by him appeared 1971. A new edition was published 2024 and contains a highly readable Foreword by Donald R. Griffin (Rockefeller University).

Multimedia for the online version

Data of flight trajectories on which the arguments are based that waggle dance communication is embedded in a cognitive map of the explored environment (Wang et al., 2023): https://osf.io/a59rs/files/?view_only=6da39e230c8d4072b27ab70ccecb06e2.

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