Jürgen Tautz

Communication Between Honeybees

More than Just a Dance in the Dark

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Preface

What It's About

An old joke tells of a man in a dark alley searching for his house keys beneath a street lamp, helped by a friendly passer-by. After an unsuccessful search, the passer-by asked the unfortunate man where he had lost his keys. The man replied that he had lost them somewhere on the way but here there was finally enough light to look for them.

In Science too, from time to time and in the absence of appropriate research methods, early explanations and solutions are not necessarily sought where true answers are hidden. If early incomplete explanations are attractive, they can persist for a very long time.

Bee research over the past hundred years has provided us with a deep insight into the homes of honeybees. We have learned a great deal about how they live and how they survive in their world. The study of honeybees has had a strong influence on the development of modern behavioural research and concepts. Communication biology in particular has significantly profited from an increased interest, and the so-called dance language of the honeybee is still accepted. In well over one thousand scientific publications about the dance language, insights have been won and concepts developed that are incorporated in countless school and learning texts and Internet contributions.

The function and importance of the waggle dance are overvalued. If a bee enters a hive and dances, so the classic story goes, she communicates with her colleagues and passes on information that will lead them directly to a food source. The second half of the story, namely the communication between bees outside the hive, continues to remain practically ignored. It plays a minor role in concepts and models of the complex communicative behaviour of the honeybee and constitutes a blind spot in bee research. Honeybees are not social insects only within their hives—if one takes this into account, it would appear that the emphasis in bee communication research has so far been particularly one-sided.

The renowned insect researcher Edward O Wilson wrote in 1971.

"Furthermore, the waggle dance had become something of a sacred cow and it needed a critical examination by an independent group of investigators." (287, p. 267)

And further:

"Also, there is a scarcity of measurements of the amount of information added to the waggle dance by additional cues, in particular the assembly pheromones of the Nasanov glands released in the vicinity of the new finds and the sight of flying workers." (287, p. 268)

Here, it concerns the communication between foraging bees in the field.

With the award of a Nobel Prize to Karl von Frisch in 1973, this "sacred cow" became firmly established and Wilson's criticism went unheard. The attention he drew at the time to the missing second half of research on the recruitment of foragers is valid to this day.

In the literature, one can indeed find the consideration that in addition to the dance bees do obtain help from other sources to guide them to a goal. However, such comments remain without consequence because they are neither included in the concept of how recruitment of foragers proceeds, nor followed up experimentally.

This book analyses the state of our knowledge from published studies of the bee dance, orders essential elements from these into a conceptual overview, and develops a program for necessary research to eventually complete the picture of one of the most remarkable behavioural achievements in the animal kingdom.

This book does NOT take into account how important, in general, the advertisement for a food source is for a bee colony, when information from the dance is ignored, and how this can change with the circumstances.

Bees that follow a dance have many options for the associated flight—nevertheless, based on information from the dance alone, they would not find the desired goal.

This book examines the mechanisms about how a goal for which a dancer advertises is nevertheless found. It illuminates the core of the dance language. If this is critically exposed, many thoughts and publications about the dance really being a language are irrelevant. The book focuses, more modestly, merely on how new recruits get to a food source for which a forager advertises in her dance.

Waldbrunn, Germany Jürgen Tautz

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About the Author

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1 The Struggle for Insight

> Those who have treated the sciences have been either empirics or dogmatical. The former like ants only heap up and use their store, and the latter like spiders spin out their webs. The bee, a mean between both, extracts matter from flowers of the garden and the field, but works and fashions by its own efforts. Sir Francis Bacon (1620)

New data does not always bring change in science, but instead new perspectives—in keeping with the parable of Francis Bacon. A new objective view of known facts can lead to completely new interpretations and understanding.

A wonderful example is the discovery of how to split the atom. Otto Hahn experimented with uranium in his Berlin laboratory and stayed in contact with his colleague, Lisa Meitner, who had fled to Sweden to avoid persecution from the National Socialists, through the exchange of letters about his research. Doubt surfaced frequently in his communications about his difficulty in reconciling his findings with the basic ideas that prevailed at the time. Lisa Meitner thought about the problem, calculated, and concluded that it must be possible to shatter the atomic nucleus. The view beyond the notion of indivisible atoms led to completely new ideas and the discovery of the fissionable atom.

Another well-known example of a change of viewpoint with far-reaching consequences was the recognition of our heliocentric planetary system. The Greek astronomer Ptolemy collected exact data on the movement of planets because very complicated assumptions and explanations were proposed why, at times, they travelled backwards. He had no other alternative possibilities other than to contribute further assumptions, as long as he held to the basic premise that the earth was the centre of the Universe. When Nikolaus Kopernicus examined Ptolemy's

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data from a different viewpoint and considered the revolutionary idea that the earth circled the sun instead, a much simpler explanation suddenly arose for the motion of planets and a new concept of the Universe.

The living world lies between the smallest and largest elements of the physical world that man has explored. Here too, the viewpoint taken when observing data and phenomena can be critical.

Over the last decades, a discovery in the life sciences with significant consequences was the molecular structure of genes. Maurice Wilkins and Rosalind Franklin had obtained X-ray crystallographic information on deoxyribonucleic acid from the cell nucleus of living organisms, but did not view their data from the same point of view as their colleagues, James Watson and Francis Crick. Their new view of available results and a little work with scissors, paper, and glue led to the idea of a double helix as the basic structure of hereditary material. With this, they created the basis of modern molecular genetics and in 1962 were together with New Zealander Maurice Wilkins awarded the Nobel Prize for medicine.

A different viewpoint of the dance language of honey bees is also possible and this is taken here. A new ordering of old data and cognisance of gaps in our knowledge accompany this book throughout as a constant reminder during the review of observations, experiments, and interpretations that have decisively led to the present picture of bee communication.

Why Half-Truths Are Practical

The bee dance is a form of communication between honeybees. A classic formulation of this probably best-known form of communication in the animal world found in every text about the bee dance is as follows: “In their dance, honeybees provide the direction and the distance to a goal.” Why is this strict statement a half-truth? In fact, bees do not communicate information about the position of the food source in their dance. Correct is that the dance provides a rough indication of the direction of and the distance to a geographical area.

Formally and correctly expressed, although sounding somewhat affected, is that through the dance the bees communicate a suggestion that outside the hive a new recruit will receive goal orienting signals and cues to a food source that can be found at a particular angle and distance in relation to the hive.

In the language of communication science, the bee dance takes the first step to reduce the uncertainty about where in the field the dance follower will have a high possibility to meet connecting signals and cues. These stimuli offer the new recruit the second step and the essential information that lead to the goal. This dry description of the communication biological meaning of the bee dance is the theme for the design of this book. A description of the complicated dance information is as follows: “Through the dance information honeybees reduce the uncertainty about where in the field recruits will meet with orienting signals and cues that will lead them to the goal.” This does not sound as elegant as the classical explanation of the bee dance but it is correct.

The classical formulation is simple, graphic, and easy to understand. That makes it attractive, but it is a conceptual model of reality and carries the inherent danger that the model, in our minds, becomes reality. Is it hair-splitting to be so exact in formulating what the bee dance achieves? What are the consequences of not being exact? Where did the half-truth statement come from? Why are they so persistent? This book will provide the answers.

So How Does a Forager Find the Goal?

There are abbreviated statements about factual issues that no one would think about taking literally. If one took the statement that the world is 4.6 million years old, one could calculate the exact date and day of the week of its coming into being. Clearly absurd and obvious to all is that this estimate of its age only establishes an approximation.

In what way is the statement “Honeybees provide the direction and the distance to the food source in their dances” (in the dance language) any different? Is the statement taken seriously?

Implicit is the idea that dancers not only convey the direction and the distance to the goal but also that the recruited forager can find a previously unknown food source given the information contained in the dance. Research on the dance language of the honeybees and also this book are concerned with exactly this aspect: How does a forager find its way to a goal to which she was recruited by a dancer?

Over the last 2000 years, there have been essentially three suggestions:

1. The recruits are LED to the goal (Aristotle).
2. The recruits are SENT to the goal (Karl von Frisch = dance language).
3. The recruits are ATTRACTED to the goal (Adrian Wenner).

In the following, it will be shown that all three of these ideas are valid but not alternatives. Instead, the sending, leading, and attraction are interwoven links in a complex communicative chain beginning in the hive and ending in the goal. All three together are necessary to bring the recruits to the geographical location of the goal.

The special area of behavioural science concerned with the orientation abilities of animals has developed a number of general concepts and definitions that apply to the honeybee’s search for a goal. Research into orientation over long distance, where animals achieve an impressively high performance, presents a particular challenge. These reach a spatial goal they are unable to see at the start nor directly perceive on the first leg of their journey. The goal at the beginning is not seen, nor smelled, heard, or perceived in some other way. There is no natural connection with the destination.

The analysis of typical characteristics of navigation was researched in early studies of homing in birds, several years before the beginning of modern research on communication in honeybees [222, 277].

Maximally three sequential phases are involved in which an animal can find its way to a distant goal. To begin, a direction is chosen and maintained over a certain distance, which then gives way to a search phase, followed by a directed orientation that leads the animal to its goal.

An explanation of how the new bee recruits arrive at a goal, to which they have no sensory connection at the start from the hive, will become ever clearer with the passage of this book and in relation to the model ornithologists introduced very early for bird migration. The concept "In their dance, honeybees provide the direction and the distance to a goal" contains no differentiation into the three phases of distant orientation because, it is supposed, the dance follower can derive the position of the goal from the dance.

In fact, the dance does not achieve this. Instead, its contribution is only the first phase of distant goal orientation, not the second and third phases. The dance sends the recruit on its first phase to a region where the second phase of distant goal orientation begins. There, recruits search for leading signals and cues such as the scent of flowers and communication with experienced foragers (Fig. 1.1).

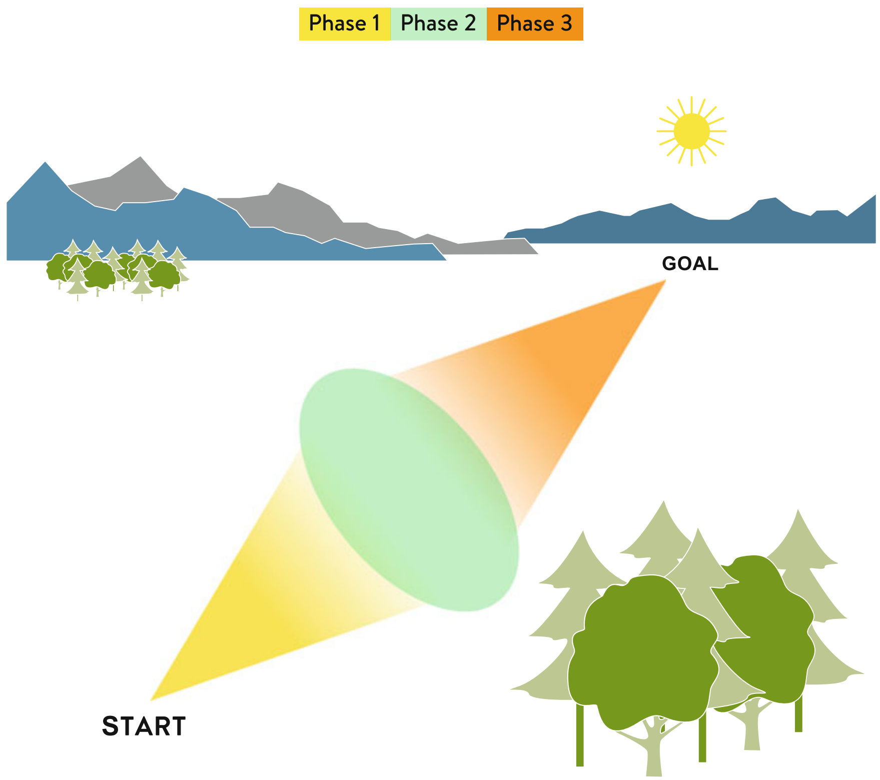

Fig. 1.1 Distant goal orientation leads a bee over three phases from the start to the goal. Phase 1, fly off in a chosen direction (SEND—yellow sector), until Phase 2, when the search area is reached and goal orientation stimuli are available (SEARCH—green sector), transfer to Phase 3 (ATTRACT—orange sector) follows

Initially, it may seem an exaggeration, given the stretches bees cover, to talk of distant goal orientation. This is very different from the bee´s point of view. A ten-kilometre distant goal is, roughly calculated, about one million bee body lengths away. Calculating this for the body length of a white stork would mean a distance of a thousand kilometres for the bird, a flight that deserves to be called distant.

How Research Explains the Phenomenon

In addition to the dance language, a second hypothesis has been proposed to explain how a recruit reaches a goal for which a dancer has advertised. This hypothesis (scent of the goal alone attracts bees) also does not differentiate between consecutive orientation phases. It assumes the first phase does not exist and that recruits search for and then simply follow scent trails that lead to the goal.

Dictionaries bring the state of research on recruitment of foragers, slightly modified and always back to the same point, for example in the Cambridge Dictionary (1995):

> There are two main hypotheses to explain how foragers recruit other workers—the waggle dance or dance language theory and the odour plume theory.

In fact, neither of the two hypotheses is correct.

Neither approach resulted in a research program in which all three phases of distant goal orientation (initial stretch, search step, and orientation step) that a new recruit takes to reach the goal receive the same attention and are investigated.

It is interesting to examine the observations, thoughts, and experiments from which the researchers derive their conclusions. Different standpoints are established not only through individual intellectual dead ends, but also through the power of terms used and lack of preparedness to accept and integrate results and data that do not “fit.”

To make a theme or area lively and transparent in this book, which is as complex as the research and ideas surrounding the bee dance, the individual researchers should speak for themselves. Experiments and their results are presented and the conclusions researchers derived (or did not derive) are described.

The suspected record number of scientific publications about the bee dance makes a selection of available publications unavoidable. However, care has been taken to represent each standpoint with its central experiments, data, and implications.

It is illuminating, when reading publications that are concerned with the bee dance, to see which follow the central issue of this book and if the aspect of communication between bees in the field takes place are mentioned in the study or even given attention in practice.

It seems an irony in the history of bee research that systematic research of honeybee behaviour began more than a hundred years ago with the discovery of communication between foragers in the field. This discovery was, although not corrected, simply overridden.

As in every science, next to the fantasy and observational skills of researchers, there are available methods appropriate to the state of knowledge and ideas that constitute a phenomenon. See the old joke in the Preface.

To investigate communication between honeybees means the methods must be appropriate for the study of bees both in their nest and also out in the field.

Next to technical observational methods that are continually expanding, the ability of honeybees to learn opens the way for research possibilities found in very few other insect species. In learning experiments, bees allow themselves to be directly "questioned" about the perceptive world they live in. Karl von Frisch was the first to recognise and exploit this.

Thus equipped, bee research worked its way ever deeper into the world of the honeybee. One of the most stimulating fields is the communication biology of these insects. A few animals and no other insects have been the subject of as many behavioural studies as the honeybee.

Honeybees Make No Clear Statements in Their Dances

The particular interest of science in honeybees and the fascination they evoke are reasons why the so-called dance language is more popular than any other animal behaviour. When reading or learning school texts or consulting the Internet about the dance language, one is immediately confronted with the formulation provided at the beginning of this book—it is set in stone.

This would not be hard to accept if the formulation was understood for what it is, namely an oversimplified and strongly reduced model that does not represent biological reality.

Bohr's model of the atom with a central nucleus and electrons that circle in shells around it is a good start into the world of the atom with unquestioned didactic value and therefore popular to this day. For modern atomic physics, this model with its half-truths that do not represent the reality of the atom is merely of historical importance. Will the half-truths of the bee dance also end in that way?

An area of mathematics, fuzzy logic, is concerned with the treatment of unclear statements [139]. The roots of fuzzy logic go back to the Greek philosopher Plato who expressed the thought that between the statements "true" and "false" lay a third possibility, the "half-true." In contrast, his colleague Aristotle was of the opinion that the precision of mathematics and science was only possible if statements were either "true" or "false."

Honeybees with half-true statements in their dance are clearly on Plato's side. Half-truths in the bee dance are not untruths.