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The honeybee waggle dance: can we follow the steps?

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The honeybee (*Apis mellifera*) waggle dance, whereby dancing bees communicate the location of profitable food sources to other bees in the hive, is one of the most celebrated communication behaviours in the animal world. Dance followers, however, often appear to ignore this location information, the so-called dance language, after leaving the nest. Here we consider why foragers follow dances and discuss the function of the dance as a multicomponent signal. We argue that the 'dance language' is just one information component of the waggle dance and that the two terms should not be used synonymously. We propose that location information is often backup information to be used in case information acquired directly from the environment about food sources is not available, is of poor quality or is associated with unprofitable food sources.

Introduction

The so-called 'dance language' of foraging honeybees (*Apis mellifera*) was first decoded over 60 years ago by Karl von Frisch, who trained foraging honeybees to artificial food sources and discovered that foragers could communicate the location of distant food sources to other foragers by means of a stereotyped behaviour [1]. Foragers perform this figure-of-eight-shaped dance on the vertical wax combs inside the hive [1,2] (Figure 1), conveying information to fellow nestmates about the distance of a food source, based on the duration of the waggle phase of the dance circuit, and information about the direction of the food, based on the orientation of the body of the dancer relative to gravity [1–5]. In this way, honeybees advertise nectar, pollen and water sources or even potential nest sites. This discovery highlighted the sophistication of insect communication and remains one of the most remarkable discoveries in the study of animal behaviour.

Given that foraging bees dance only if the recently visited food source is profitable, other foragers following these dances should be able to find out where the richest food sources are [2,6]. If the food source becomes depleted or reduces in quality, foragers cease dancing and recruitment stops, thus enabling a colony to exploit the best resources in an ever-changing environment [6]. The regulation of foraging by means of dancing has been used as an illustrative example of self-organisation of a collective activity [6,7].

The 'dance language' (see Glossary) has often been considered key to honeybee foraging success (e.g. [6,8]). Thus, theoretical work has focussed mainly on this location information provided by dancers to explain the ultimate function of dancing and dance following [9–11]. By contrast, recently published studies [12,13], as well as experiments performed during the late 1960s [14], suggest that the importance of location information for honeybee foraging success is overestimated. Here we discuss the importance of the dance language for honeybee foraging and explore additional reasons why foragers follow dances.

How important is location information?

Although the location information encoded in the waggle dance can be deciphered by dance followers [4,5,15], they often ignore this information. Here we explore why these foragers follow dances despite then appearing to ignore the information that the dances contain.

Glossary

Dance language:: a term used by von Frisch [2] ('Tanzsprache') to denote a series of repetitive waggle movements performed by successful foragers conveying information about the direction and distance of food sources or nest sites (Figure 1). Here, the word 'language' does not imply the use of a set of symbols and a system of grammar.

Multicomponent (or composite) signal:: a signal comprising more than one informational component. The components can be redundant (i.e. lead to the same or an enhanced response) or nonredundant (i.e. provide multiple messages that lead to particular responses each); examples are given in Refs [47,48].

Multimodal (or multisensory) signal:: a multicomponent signal that transfers information in more than one sensory modality, for example, sound and olfaction [47,48].

Private information:: information acquired via direct interaction with the environment, as opposed to social information.

Scout–recruit concept:: traditionally, the terms used to characterise two different types of forager; the differentiation can be based on different tasks (searching for food versus collecting food), on information-use strategies (searching independently versus using social information) or on whether bees follow dances before leaving the hive (discussed in Ref. [49]). The two main problems with this concept in honeybees are (i) the different definitions of the terms used, and (ii) the limited informational content of a dichotomous concept given the variety of decision-making strategies of foragers.

Signal:: information-bearing actions or structures that have been shaped by natural selection specifically to convey information [6,50].

Social information:: any information acquired through the actions (e.g. waggle dance), body structures (e.g. shapes or colours) or products (e.g. pheromones) of other individuals.

Sugar response threshold:: this threshold is usually determined by applying solutions of increasing sucrose concentrations to the antennae of retained bees. When the antenna of a bee is touched with a sucrose solution of sufficient concentration, the bee reflexively extends its proboscis (e.g. [21]).

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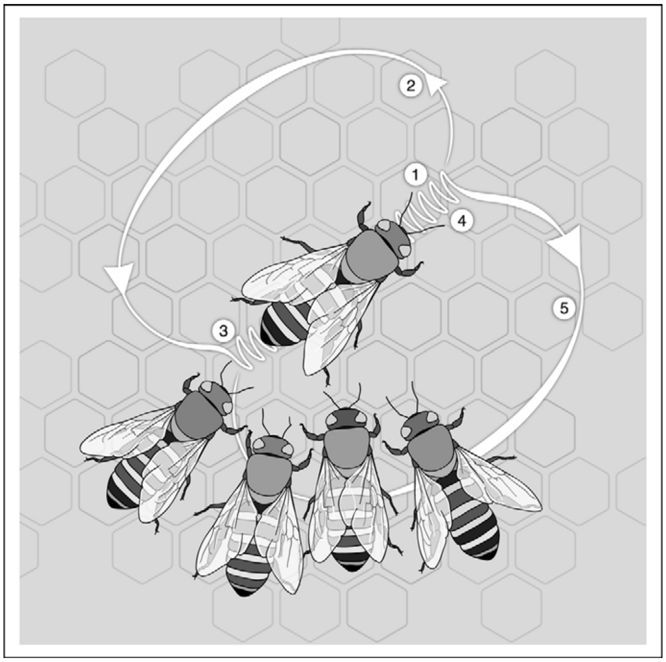

Figure 1. The honeybee waggle dance and follower bees. The dancer performs a waggle run (1) followed by a turn to one side (2) to circle back to the starting point of the waggle run (3), then she starts another waggle run (4) and usually turns to the other side (5) and so on. The better the food source, the more waggle runs she performs. During the waggle run, the dancer produces airborne sounds, airflows and vibrations in the comb, as well as releasing chemicals [19,33,52]. Followers touch the dancer directly with their antennae during the dance. However, the importance of the different stimuli for location information transfer from dancer to follower is not yet well understood. As well as providing location information, these components might have an important psychological function for surrounding bees. Multicomponent signalling can enhance the detection of the signal and improve learning of the information [48].

The low efficiency of the dance language

Several researchers have noted that the dance language appears to be less efficient at recruiting new foragers than was originally proposed by von Frisch [4,16–18]. Theoretical and empirical works suggest that followers only need 5–6 waggle runs to decode the location information [3,16,17]. However, many recruits that are successful in locating the food source do so after following many more waggle runs of several dances and subsequent search trips [16,17,19,20]. Some foragers follow >50 waggle runs without ever reaching the indicated food source [17]. Seeley [6] reported an experiment in which dancers performed a total of 8722 waggle runs and recruited 153 bees. This corresponds to 58 waggle runs per successful recruit, indicating that the transfer of location information is either inefficient or that the dance language is being decoded only by a small proportion of the bees interacting with a dancer.

It is still unclear why some recruits locate the food source successfully after following only a few waggle runs, whereas others follow dozens of waggle runs without being successful. We speculate that some bees might need more arousal and stimulation via dancing until they are motivated to start foraging, whereas others might simply be bad learners. It would be interesting to test whether the responsiveness of followers to rewards, such as sugar, is related to the number of waggle runs that they follow and the probability that they would discover the advertised food source. In honeybees, the sugar response threshold (see Glossary) is related to the individual evaluation of a reward, learning performance and several other behavioural traits (reviewed in Ref. [21]).

Olfactory information as an additional factor

Recruits can learn the odours of the collected food during their interactions with dancing bees [2,22]. There is, however, disagreement about how important odours are for honeybee recruitment (e.g. [14,23,24]). In an experiment performed by Wenner *et al.* [23], most of the recruits were observed at a location 140 m away from those indicated by the dancers (a ratio of 6.8:1, respectively). Although the indicated food sources where the dancers had been collecting food were scentless, the food source that was not advertised contained a scent that had been collected by foragers from the study colony in the days before the experiment. The authors suggested that, although the dancers successfully recruited bees to forage, recruits relied mainly on olfactory information to locate the food, rather than on the location information of the waggle dance (Box 1). Lindauer [24] later repeated this experiment with a few alterations, without finding the same exclusive effect of odour (1:1.9 ratio of recruits at nonindicated food sources versus indicated food sources). First, the colony in Lindauer's experiment had less experience with the food odour (i.e. a shorter exposure to scented food than in Ref. [23]) than was later used during the recruitment experiment; and second, the food sources advertised by dancers were also scented. Thus, although the dance language affected the recruitment pattern in Lindauer's experiment, many bees were found at the food source that was not indicated by the foragers but that did contain the same scent. The discrepancy between the results of the studies has not yet been resolved, but suggests that even small changes in experimental design can lead to very different recruitment patterns (discussed in Refs [14,24]). Thus, differences in recruiting behaviour, depending on whether the food sources are scented, require further study.

Private information as an additional factor

Active foragers rely on their own memories to find particular locations when visiting food patches repeatedly. After an interruption in foraging (e.g. after nightfall), these memories can be triggered by encountering the odour of the corresponding food source inside the hive [2,14,25–27]. This so-called private location information also affects the way in which foragers use the waggle dance.

Two recent studies suggest that, once they have left the hive, dance followers with foraging experience (which, during the spring and summer, includes most foragers [28]) often do not rely on social location information [20,28]. Biesmeijer and Seeley [28] reported that 12–25% of all interactions with dancers accounted for attempts to discover food. In the remaining interactions (75–88%), dance following was observed in the context of reactivation and confirmation of experienced foragers that might have already known the food source that they later visited. Most of these bees followed dances only briefly (<5 waggle runs) [28].

Biesmeijer and Seeley [28] also assumed that bees following <5–10 waggle runs did so for reactivation and otherwise followed dances to discover new food sources.

Box 1. How foragers can find a food source

Honeybee foragers can use many different strategies to find food. They can rely on private information and different kinds of social information, with and without following dances. If a forager is initially unsuccessful in finding a food source, she could begin a random search in the field, search for food sources with a known odour or fly back to the nest to get more information about food sources. Below we detail possible foraging strategies; however, there is little information about the relative importance of these different strategies for food source discoveries in honeybees under natural conditions, mainly because it is difficult to track the flight paths of most foragers.

Without following dances

Without using private information

- By random search
- By searching for plants with odours that were learned socially inside the nest

Using private information initially

- Inspecting a food source that has reappeared
- Inspecting an empty food source, subsequently searching another food source of known scent nearby
- Inspecting an empty food source, searching randomly for another food source nearby
- Reactivation by olfaction, flying to a familiar food patch
- Reactivation by olfaction to a still-empty food source, then searching another food source of familiar scent nearby
- Reactivation by olfaction to a still-empty food source, then searching another food source of novel characteristics nearby

After following dances

Without using private information

- Using location information plus olfactory information and searching the indicated food patch
- Using location information plus olfactory information, but then finding another food patch with the same scent
- Using location information plus olfactory information, but then finding another food patch by random search
- Ignoring location information, searching for plants with known scent
- Ignoring location information and olfactory information, searching randomly for good food sources in the field

Using private information initially

- Reactivation by dance, flying to a familiar food source
- Reactivation by dance, flying to an empty food patch, then finding another food patch with a familiar scent nearby
- Reactivation by dance, flying to an empty food patch and then finding another food patch nearby by random search

However, in a second study [20], foragers following as many as 17 waggle runs were reactivated to resume foraging at already visited food sources. Overall, 93% of all foragers with private information about the location of a good food source ignored the dance language [20]. This suggests that the importance of the waggle dance for reactivation under natural circumstances was underestimated in Ref. [28]. The waggle dance often triggers navigational memories about food sources known to the dance follower, irrespective of the location indicated by the dancer [20]. This could also partly explain why the dance language appears to be inefficient, in that many foragers do not find the indicated food source after following a dance [4,16–18]. In studies of dance efficiency, it is often unclear whether ‘unsuccessful’ recruits made any attempt to fly to the indicated location or, instead, inspected known food sources.

Little effect of waggle orientation on overall colony foraging success

When looking at the overall importance of location information for colony foraging success, two studies found that there is often no positive effect [12,13]. These studies compared the foraging success of colonies having correctly dancing bees with colonies having only disoriented dances, created by tilting the combs into a horizontal position. Unless the bees have a direct view of the sun or a polarised skylight, they perform dances in random direction, because they lose gravity as a reference. The studies found that, in temperate habitats, there was no difference between colonies during the spring and summer, when most nectar and pollen are harvested. The dance language did have a positive effect, however, when food sources were scarce [10,12] or appeared clumped, as in some tropical habitats [13]. Yet, even relatively small benefits of location information could be important for colony survival in such ecological situations.

In summary, studies suggest that the spatial information encoded in the dance affects the behaviour of individual bees and the overall foraging success of a colony only under certain circumstances. However, as we discuss below, the waggle dance does more than just provide spatial information.

The waggle dance: a multicomponent signal

The waggle dance is a multicomponent signal in that it (i) attracts surrounding bees so that they can receive other types of information; (ii) informs bees of the presence of good food sources; (iii) activates private navigational information (if present) in followers; (iv) facilitates the acquisition of information about food odours; and (v) indicates the location of the food source. To understand how the waggle dance affects collective foraging patterns and, therefore, what its ultimate function might be, the behavioural response to the different components of this multicomponent signal should be considered.

Dancing modulates the readiness to respond to information

Before von Frisch discovered the location coding of the waggle dance, he reported that foragers could be recruited to food sources by what he called the ‘round’ dance [25], which is performed by foragers returning from nearby food sources [2,25] and is now considered to be a special version of the waggle dance [29,30]. Bees following round dances leave the hive in a random direction and search nearby for food sources [2]. von Frisch reported that dancing attracts the attention of bees in the immediate vicinity of the dancer [25]; thus, the dancer primes the readiness of surrounding bees to respond to other components of the multicomponent signal.

Chemosensory information

During their interaction with the dancer, followers can learn the odour of the food source [2,22,25], which helps them to locate other food sources with the same odour [2,14] (see also Box 2). Followers position themselves around dancing bees in ways that optimise olfactory information acquisition, for example, they preferentially

Box 2. The evolutionary origin of the waggle dance

Comparisons of recruitment systems of different social bee species have led to the suggestion that successful ancestral foragers showed some kind of excitatory movements (e.g. zig-zag runs, shaking movements, running into other foragers and/or produced buzzing noises) [51–53] that attracted the attention of other nestmates and made them leave the nest in search of food. Such recruitment behaviours can still be observed in bumblebees, stingless bees and ants [54–56]. In addition, foragers would have learned the odour of the food source in the nest during food offerings that were performed during interruptions in the excitatory movements. Thereby, these movements might have facilitated the acquisition of olfactory information. Such nest-based food odour learning can still be observed in stingless bees, bumblebees, ants and wasps [54,57–59].

These excitatory behaviours are assumed to be the origin of a dance that conveyed information about the location of the food (e.g. [51]). Interestingly, it has been suggested that stingless bee *Melipona panamica* foragers transmit spatial information to other foragers by sounds inside the nest [53]. However, the intermediate stages toward a dance that provided the direction and distance to a food source are still poorly understood [52]. There is now growing consensus that selection initially favoured the transfer of location information about new nest sites, rather than about food sources (e.g. [54,60]).

contact body parts where food odours are most intensive like the mouthparts of nectar foragers or the hind legs of pollen foragers [31]. Small nectar offerings from dancers to surrounding bees during interruptions in dancing also appear to have an important role as reinforcement for olfactory conditioning [2,22,32].

Additionally, waggle-dancing bees release chemicals (two alkanes and two alkenes of long carbon-chain length), which increase the propensity of bees to leave the hive [33]. The effect of these chemicals was confirmed by blowing a volatile mixture of the chemicals on the comb surface, where bees usually perform dances. This could partly explain von Frisch's observation that many bees following dances subsequently show an elevated probability to leave the hive and search for food [25]. In this way, the dance informs other bees that profitable food sources can be found in the surroundings of the hive. The fact that artificially injecting these chemicals into the hive encourages bees to leave the hive suggests that foragers might be recruited by dances without ever physically contacting a dancer (Box 1). It might be that bees acquire information about the amount of dancing and, therefore, the foraging conditions, by the amount of these chemicals that they perceive on the hive floor [33]. However, this needs to be tested experimentally. If it is the case, then we would expect a positive relationship between the concentration of the chemicals on the hive floor or in the hive atmosphere and the number of foragers leaving the hive.

What kind of information do dance followers use?

Researchers tend to interpret dance following as an attempt of the follower bee to decode spatial information about a food source. However, there are other reasons why dances are followed [20,28]. For example, the dance often functions as a means of reactivating inactive foragers to fly to food patches that they have already visited, but does not necessarily have to indicate a location or plant species that is already known to the follower [20,34]. Hence, some inactive foragers seem to use the dance as an indication of an increased chance of finding food at places where food has been found previously without decoding the location information of the dance. By contrast, other bees appear to rely strongly on the food odour information gained during dance following, when they search for food in the field [23].

Because dance followers are often foragers that are already engaged in foraging, it has been suggested that active foragers follow dances to confirm the continued availability of the type of food that they had been collecting [28]. Most of these bees follow only a few waggles (<5 waggle runs) and, therefore, are not interested in detailed location information [28]. This kind of dance following was found to be particularly frequent in bees that had had an unsuccessful foraging trip immediately before dance following [28]. However, in such a situation, it might be beneficial to follow more waggle runs and decode the location instruction of the dance because the advertised food patch is apparently profitable. Experiments are needed to test whether dance following of active foragers does serve to confirm the availability of particular food types.

Leaving the hive without following dances

Foragers sometimes leave the hive without having followed dances (e.g. [28,35–37]). Such bees are often called 'scouts,' and it is assumed that they do not use acquired information. However, under natural conditions, bees leaving without having followed a dancer could (i) use private information after reactivation (e.g. via chemosensory cues; Box 1); (ii) use private information and inspect previously visited food sources [2]; (iii) use social information (e.g. chemosensory information acquired previously [38], or in the present [33]); or (iv) use neither private nor social information and rely on innate search behaviours. To separate the strategies, information is required about the foraging experiences of a bee, about whether she was reactivated and, most importantly, what she does after leaving the hive. However, to our knowledge, little is known about the relative frequency and importance of these strategies under natural conditions.

This array of behavioural strategies of bees either following dances or leaving the hive without doing so (Box 1) makes the classic dichotomous scout–recruit concept an arbitrary classification of little informative value. Considering more strategies of information use (Box 1) instead will lead to a better understanding of collective foraging in honeybees.

Private versus social information

Many plant species only bloom (and offer nectar or pollen) at limited periods during the day [2,39]. Honeybees can learn these times of food abundance after a few days [40] and often specialise to collect one or two different food types at particular times of the day at particular locations [41,42]. A foraging honeybee will return to the same flower patch at the same time period for many days (even her entire life) if the patch remains rewarding [42].

Private information is especially important for the organisation of collective foraging in times of good foraging conditions when food patches offer food for several days. With increasing foraging experience and, therefore, more precise private information about the location and flowering time of food sources, foragers show a decreasing interest in following dances [28,36].

Social information use is often assumed to be adaptive because the costs of individual exploration can be avoided [43]. In changing or heterogeneous environments, however, erroneous or outdated information could be obtained by relying on others. Hence, social information use is not always an adaptive strategy [43,44]. There is evidence from various taxonomic groups, including birds, fish, insects and mammals, that private information is used if it is available and reliable, whereas social information is used as a backup if private information has proven to be unreliable [43,45,46] or outdated [45] or if individuals evaluate this option as unprofitable [43]. Honeybees also appear to rely on private rather than social location information if the former is both available and reliable [20,28,36].

The impression that dance followers often use social location information could be a consequence of the fact that experiments investigating the waggle dance are normally performed after the end of the flowering season or at places where there are few alternative food sources because it is otherwise difficult to train bees to artificial feeders [6]. Under these circumstances, one would expect private information to be outdated or not available and that foragers would rely more on social location information. To explore the use of private and social information in honeybees further, controlled feeder experiments should experimentally manipulate the reliability and outdatedness of private and social information, as well as the costs and benefits associated with using information.

Conclusions and future directions

It has been convincingly shown that honeybees following a waggle dance can decipher the spatial information encoded by the dance [4,5,15]. However, followers often do not use this information. Experienced foragers usually rely on private information about food source locations after following a waggle dance, whereas other foragers appear to rely mainly on food odours learned during dance following to find food sources with the same odour [23]. This shows that the dance language is only one component of the waggle dance and that the two terms should no longer be used synonymously.

For a better understanding of the adaptive value of the waggle dance, various questions still need to be addressed, including: why do engaged foragers frequently follow dances? Which circumstances favour the use of social location information versus private location information in experienced foragers? What explains the large variation between individuals with respect to dance-following behaviour? Future theoretical and experimental work should explore communication and recruitment in honeybees as a more complex process where multiple kinds of information are available and can act together. Harmonic radar technology, which enables one to follow the flight paths of bees over distances of hundreds of meters, might help us to understand how common different foraging strategies are (e.g. [5]). Adopting an approach that does not reduce the waggle dance to a mechanism to communicate spatial information but also considers alternative strategies of information use (Box 1) will help us understand why bees follow its steps.

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