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(Citation)
Journal of Robotics and Mechatronics,35(4):901-910

(Issue Date)
2023-08-20

(Resource Type)
journal article

(Version)
Version of Record

https://doi.org/10.20965/jrm.2023.p0901

Review:

Honey Bee Waggle Dance as a Model of Swarm Intelligence

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[Received January 24, 2023; accepted April 3, 2023]

Honey bees are social insects that form colonies (hives), which often consist of more than 10,000 individuals. In a colony, bees allocate jobs (division of labor) and work cooperatively and intelligently to maintain the colony's activity, such as nursing broods, cleaning, and guarding against enemies. Among worker bees, only forager bees collect food, and success in finding food directly influences colony survival. For more efficient foraging, honey bees share location information pertaining to profitable food sources through specific behavior called "waggle dances." During such dances, the direction and distance from the hive to the food source are encoded as body movements. Other foragers follow the dancing bees and receive location information. Some of these bees then fly to the advertised location to find the food source. Some of these "recruited bees" subsequently dance to recruit new bees. This process is then repeated. Consequently, many foragers visit the food source, and a colony can rapidly and flexibly collect large amounts of food even in foraging environment that can suddenly change (e.g., flowers disappear or nectar flux increases/decreases). To achieve effective food collection through the waggle dance, the behavior of both the dancers and followers probably contains information for an implementation of "swarm intelligence." In this review, we introduce the properties of dance behavior at the levels of dancers, followers, and colonies. We found that errors in waggle dance information play an important role in adaptive foraging in dynamically changing environments.

Keywords: social behavior, waggle dance, information transfer, collective foraging

1. Introduction

One striking feature of social animals is their ability to communicate on a range of subjects, such as mating, predator evasion, and foraging [1]. Precise and effective communication is a goal of modern robotics to gain insights into more efficient and adaptive systems in which many agents work cooperatively. Looking to nature is a promising way to achieve such goals, and foraging behavior of honey bee is one of the best models of cooperative animal behavior. The honey bee *Apis mellifera* is a social insect and forms colonies consisting of several to tens of thousands of individuals [2, 3]. To maintain the health and ensure the survival of colonies, honey bees work in a cooperative manner that leads to highly adaptive colony behaviors. It seems very intelligent. Honey bees allocate the colony's jobs (division of labor) to different workers. The queen and male bees are fertile, and their activities are mostly only involved in mating. Worker bees are females other than the queen and engage in jobs, as determined by their age (days after eclosion), such as nursing broods, building combs, cleaning inside the nest, guarding the colony from enemies, and collecting food [2, 3]. Among worker bees, only forager bees collect food, and as foraging success strongly influences colony survival, forager bees are integral to the health of the colony.

Karl von Frisch, a Nobel Prize winner in 1973, discovered that honey bees can transfer location information pertaining to profitable food sources to their nestmates through symbolic communication [4]. This type of communication behavior improves the efficiency of foraging and is referred to as "dance" because the bees move as if they are dancing [2, 5, 6]. Once a bee (called a scout bee) has found a profitable food source and flown back to the hive, it will perform a dance (round dance and waggle dance for short- and long-distance food sources, respectively). In addition to locating food sources, the waggle dance is also used for finding a suitable habitat for the new hive site in the swarming season [2, 5].

For the waggle dance, the dancing bee walks in a figure-of-eight pattern (**Fig. 1**). On the straight parts of this path, the bee wags its body forcefully from side to side and beats its wings vigorously (waggle run). On the circular parts of the path, the bee walks without wagging or wing-beating (return run) until it reaches the starting point. At this point, the bee restarts the waggle run and returns to the starting point. The dancers repeat this sequence many times. After the bee returns from the left side, the next time around, the bee will return from the

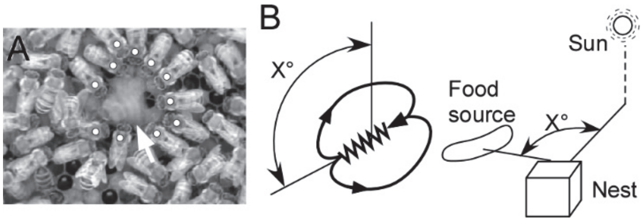

Fig. 1. Waggle dance. (A) A dancer (white arrow) walks straight with its body wagging. Many bees congregate around the dancer (open circles), and some of them may be recruited to a food source that the dancer advertises. (B) Dance information encoded in a waggle run. The direction and duration of a waggle run (left) represent the direction and distance of a food source from the hive (right), respectively.

opposite side. Thus, the trajectory of the bee draws a figure of eight. The number of waggle runs varies greatly but generally increases at both the individual [7, 8] and colony levels [9] as the profitability of a food source increases (e.g., nectar richness).

A honey bee nest consists of several sheets of vertical combs that are hung from a substrate, such as a tree branch. In most cases, dances are performed on the vertical comb. The direction of the food source from the hive relative to the azimuth of the sun is encoded as the angle between the upward direction and the waggle run direction, and the distance from the hive to the food source is related to the duration of the waggle run (**Fig. 1(B)**, [5]).

In most cases, a dancer is surrounded by other bees (known as follower bees) that face the dancer to receive the information which the dancer is imparting (**Fig. 1(A)**). Once receiving the location information, some follower bees will be recruited to the food source, and finally, many foragers may visit this site (**Fig. 2(A)**, [10]). Some of the recruited bees may perform dances and recruit new bees to that place. Consequently, a bee colony can quickly collect abundant food.

For effective communication, both the information sender (dancer) and the receiver (follower) must work actively and precisely. In this review, we will introduce the characteristics of dance behavior at the levels of dancers, followers, and colonies focusing on the waggle dance.

2. Effect of Waggle Dance

2.1. Food Collection at the Colony Level

Bees sometimes fly more than 6 km from the hive to forage [13], so it is unlikely that bees can quickly find a food source through random foraging. Thus, dance communication is considered crucial for successful foraging. To date, many studies have reported the occurrence of dance behavior for improved food collection (e.g., [14–16]). However, most of these studies were conducted under controlled conditions where artificial feeders containing sucrose solutions of controlled concentrations were placed in a restricted experimental area as a flower patch. In contrast, only a few studies have examined the importance of dance behavior to food collection under natural conditions, where bees can freely forage on natural food sources. Sherman and Visscher [17] prepared colonies that performed two types of dances by changing the light conditions because bees dance in random directions when diffused light is provided from above the colony: dances whose directional information was intact (oriented dance) without diffused light and dances whose directional information was disrupted by diffused light (disoriented dance). Colonies were placed around the natural food sources and allowed to forage freely. They measured the hive mass of each colony for eight months, where they switched the light conditions every 11 days. A comparison of the hive mass revealed that oriented dances led to increased food collection compared with disoriented dances. Importantly, a significant difference was found only in winter (not in summer or fall). Dornhaus and Chittka [18] compared the mass of bee hives located in different habitats. They found that foraging efficiency was substantially impaired in a tropical forest but was not significantly impaired in temperate habitats when dance information was obscured. Additional analysis suggested that there were few patches with abundant resources in the tropical forest compared to the other habitats. Instead of removing dance information, Okada et al. [11] physically prevented bees from communicating through dance. This experiment was conducted in three cities (Sapporo, Himeji, and Sanuki) for three years from mid-September to early October under natural conditions. During this period, flowers are not expected to be randomly distributed in the foraging area, and it should not be as easy to find food as in the flowering season (spring). In addition, during that season in Japan, bee hives ordinarily lose mass because bees consume nectar in the hive rather than collecting more because of the lower nectar in flowers at this time of year. In all three cities, dance disruption increased the loss of colony weight (**Fig. 2(B)**), indicating that dance behavior reduces the loss of colony weight. These three studies strongly suggested that dance behavior is an effective means of communicating information that can improve the efficiency of food collection, particularly in environments (habitats and seasons) in which food is scarce. Indeed, bees seem to dance less in spring when there are plenty of flowers around the hive (personal observation). On this point, it will be interesting to assess the most effective distance and density of feeders for eliciting dancing. It was reported previously that communication systems are beneficial in resource-poor environments [19, 20]. Although the outcomes of bee activities, including food collection, vary widely among areas, seasons, years, and colonies, the validity of the dance for improving food collection is well established [21].

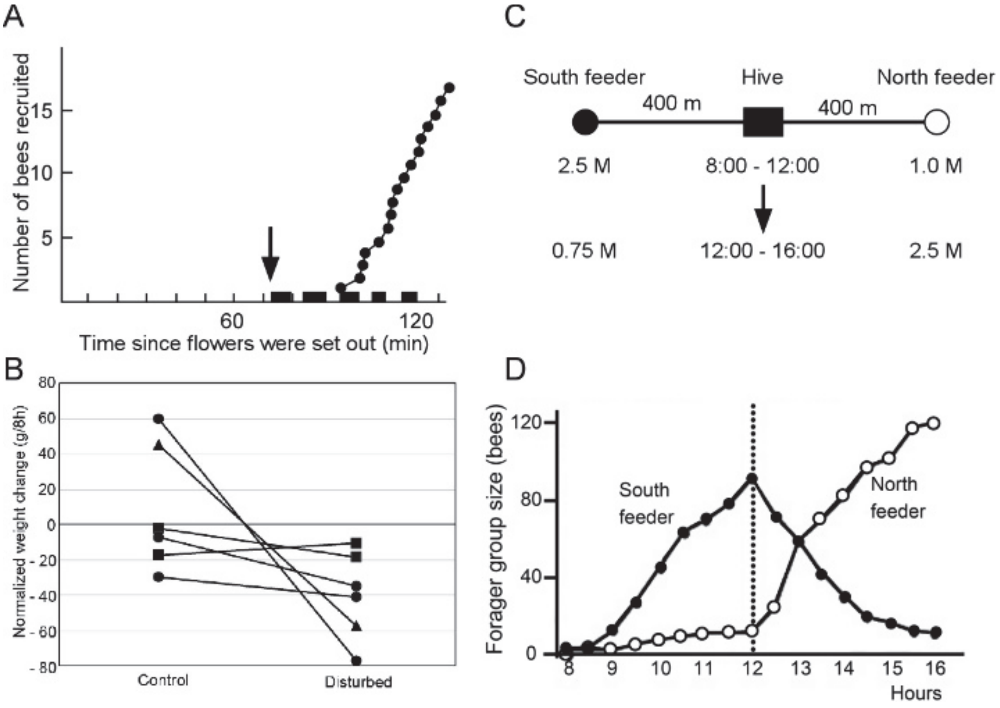

Fig. 2. Dance effect on food collection. (A) Colony-level recruitment. The recording time started immediately after the flowers were placed. The arrow and black rectangles represent times when a scout bee discovered the flowers and when this bee re-visited the flowers, respectively. Black circles represent the cumulative number of bees that visited the flower. (B) The hive weight. Daily hive weight of six colonies in three cities (circle: Himeji, rectangle: Sapporo, triangle: Sanuki) were compared between non-disturbed (control) and disturbed days. Dots connected by each line represent each colony. (C) Feeder conditions for the experiment in (D). (D) The size of the recruited bee group in the south and north feeders (modified from [10] for (A), from [11] for (B), and from [9,12] for (D)).

2.2. Adaptability to Environmental Change Through Dancing

In most experiments conducted under controlled conditions, it is possible to determine the number and distance of feeders and the concentration of sucrose solution and change them anytime during the experiment. This reflects an artificial foraging environment; however, such experiments can extract the biological characteristics of bee dance behavior more precisely. In a controlled environment, Seeley et al. [9] showed the high adaptability of honey bees at the colony level against changes in the foraging environment (**Fig. 2(C)**). They placed feeders 400 m in the south and north of the hive and only changed the concentration of the sucrose solutions. In the morning (8:00–12:00), the south and north feeders contained 2.5 mol/L and 1.0 mol/L, respectively. In the afternoon (12:00–16:00), the concentrations were changed to 0.75 mol/L for the south feeder and 2.5 mol/L for the north feeder. They counted the number of bees that visited each feeder and found that the colony quickly responded to changes in the concentration of sucrose solution as a larger number of bees visited the feeder with the higher concentration. In addition, this behavior was simulated in a mathematical model [12]. The model suggested that such adaptive colony-level decision-making can be achieved by rules implemented at the individual level and did not require a central command system. Okada et al. [22] created another mathematical model and showed that the dance is beneficial in terms of food collection under dynamically changing environments, such as those tested by Seeley et al. [9]. Okada et al. compared four types of colonies: a random-search colony in which bees did not memorize the location of the feeders or perform dances; a no-communication colony in which bees memorized the location of the visited feeder but did not communicate with each other (no dance was performed); a random-information dance colony in which bees memorized the feeder location and danced but transferred meaningless directional information about the feeder; and a normal dance communication colony in which the correct waggle dance was performed, and they found that the advantage of the dance depended on the conditions of the foraging environment [23].

3. Behavioral Properties of Dancers

A waggle dance generally consists of more than one pair of waggle and return runs. Therefore, each waggle run contains a certain range of errors from the mean, even in a series of waggle runs by the same individual. **Fig. 3** shows examples of the variation in the directional and distance information of three bees. For direction, Bees 11 and 12 performed 26 and 29 waggle runs, respectively.

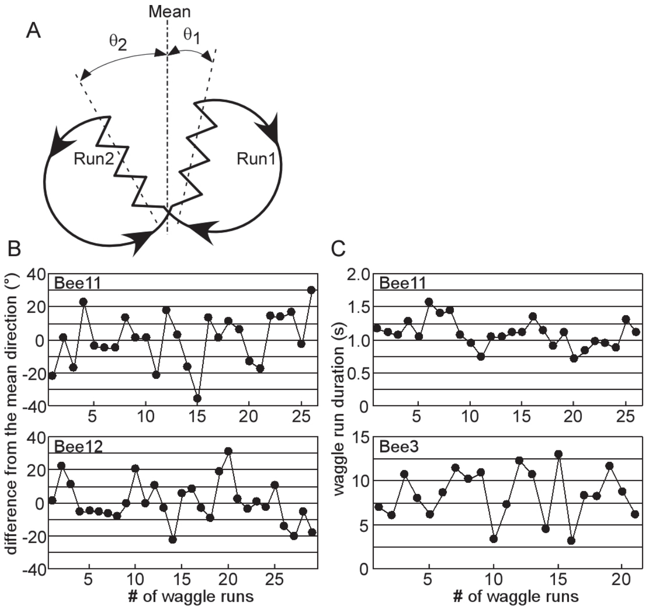

Fig. 3. Fluctuations in dance information. (A): Error of directional information encoded by waggle runs. Each run had a certain degree of variation from the mean waggle-run direction. (B): Examples of a sequence of directional errors in consecutive waggle runs of two dancers (Bees 11 and 12). (C): The duration of a sequence of consecutive waggle runs of two bees. Note that Bee 11 performed short (about 1.1 s) runs, and Bee 3 performed long (about 8.4 s) runs (modified from [24] for (A) and (B), and [25] for (C)).

When directional information differed from the mean direction of all waggle runs performed by a dancer (error), the largest negative and positive differences of Bee 11 were approximately $-45°$ (left from the mean) and approximately $+30°$ (right from the mean), although the variation seemed to concentrate around zero. In Bee 12, the differences seemed to be more concentrated around zero but still greatly varied. The distribution of the variation showed that more than 80% of the waggle runs were conducted within $\pm 15°$ (**Fig. 4(A)**). Interestingly, the error range decreased as the distance to the food source increased [26, 27]. Furthermore, dance information was more precise when the dances indicated a candidate place for the next hive site rather than a food source [28]. The error range depends on the orientation of the dance to the direction of gravity [29], being small when the waggle run direction is consistent with the direction of gravity and increasing as the waggle run direction becomes more perpendicular to the direction of gravity (i.e., parallel to the ground). Therefore, whether this variation results from a physical constraint or evolutionary adaptation remains controversial [30, 31].

The duration of the waggle runs varied among runs. The error range appears to be larger compared with that for directional information. For example, the mean duration of the waggle run by Bee 11 was 1.08 ± 0.21 s (mean ± SD), and the longest and shortest durations were 1.56 s and 0.7 s, respectively. These were approximately

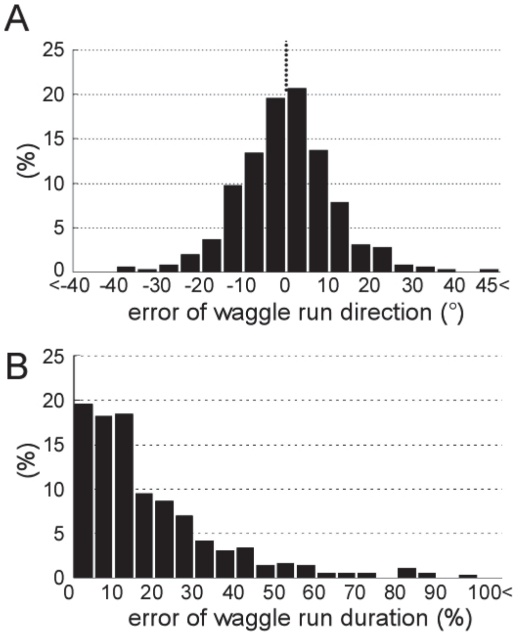

Fig. 4. Distributions of error in waggle run directions (A) and durations (B). $n = 358$ runs of 20 dancers (modified from [25]).

150% and 70% of the mean duration, respectively. The range of variation increased when the mean run duration increased. Bee 3 performed 21 long runs (mean ± SD = 8.37 ± 2.85). In 16 of 21 runs, the difference in each run from the mean duration was greater than 1 s. This difference corresponds to more than 200 m. Dividing the difference in duration of each single waggle run from the mean duration by the mean duration of the corresponding series of waggle runs, we found that about 56% of waggle runs ranged within a mean duration of ±15%, that is, the waggle dance for a food source 1,000 m away indicates a distance of 850–1,150 m, and approximately 80% of them were within ±30% (**Fig. 4(B)**). Considering the range of error in the direction, a waggle dance may not point to a place to visit as precisely as expected. Indeed, a rough calculation based on the information errors revealed that a waggle dance indicates a 22-fold area of a standard football ground for a food source 1,000 m away [25]. Therefore, to reduce the influence of inaccurate information on successful foraging, dance followers are expected to follow multiple runs.

4. Behavioral Properties of Followers

Followers go out to forage after attending the waggle runs. However, to the best of our knowledge, few studies have focused specifically on the followers rather than the dancers. Therefore, we have limited knowledge of the followers and their specific behaviors. Nonetheless, recent video analyses of follower behavior in the hive combined with observations of foraging behavior have revealed important characteristics. For example, it was

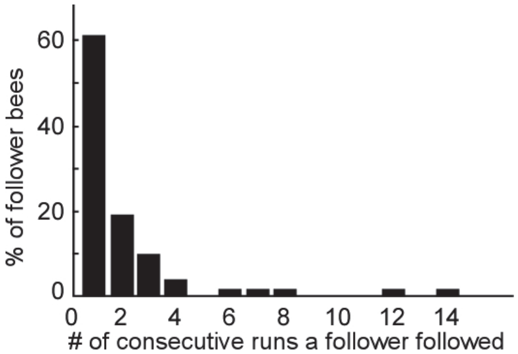

Fig. 5. Distributions of the number of runs that a follower bee followed consecutively before turning away from a dancer (modified from [25]).

found that only 9% of novice foragers successfully arrived at the food source advertised by the dance [32]. A follower averages the directional information received via multiple dances [33] and must follow, on average, approximately eight consecutive waggle runs before successfully locating a food source [34]. Detailed observations of the following behavior at the individual level revealed that even in a series of waggle runs by the same individual, some runs attracted no followers, while others attracted up to 10 bees [25]. Some followers turned away from the dancer after attending only one of their waggle runs, whereas others followed the dancing bee for more than 10 runs. Quantitative analysis of individual tracking found that about 80% or more followers turned away from dancers after following one or two waggle runs (**Fig. 5**) [25, 35]. Few bees (approximately 1%) followed more than five consecutive waggle runs (**Fig. 5**). Our observations showed that 80% of followers attended only one or two sessions of a waggle dance [25, 35], while Judd [34] observed that almost all the bees followed the dancers more than twice. This difference might be due to differences in the analyses. We used 62 followers of five dancers, and Judd used 28 followers of a single dancer. Therefore, Judd's observation might reflect a particular case, such as a dancer-specific or dance-event-specific case.

5. Interaction Among Bees in the Hive: Spatial Separation

Studies on imprecision in dance information and the quick abandonment of following a dancer imply that a colony must maintain a high encounter rate for dancers and followers to communicate dances. Individual dancing bees tend to often change their dancing location after performing several runs in a single waggle dance [7]. The locations where waggle runs were performed appeared in clusters (**Fig. 6(A)**) [25, 35]. Bee 10 performed 20 waggle runs in a dance in two distinctly different places (clusters 1 and 2). Until the 13th run, this bee performed waggle runs in cluster 1 and then moved to cluster 2 where it performed seven runs (**Fig. 6(A)**). Bee 11 performed 26 runs, 23 in three clusters and three in non-cluster locations. Although each dancer changes dancing location locally, the dancing itself is performed in a restricted area on the comb close to the entrance, called the "dance floor" [36]. Among 1,339 waggle runs (632 in the morning and 707 in the afternoon), 86.3% (1,155 out of 1,339) of waggle runs were observed in a specific area of 20 cm width × 10 cm height from the entrance (**Fig. 6(B)**) [24]. Hence, for communication, the dance floor might be a special area to facilitate interactions between followers and dancers.

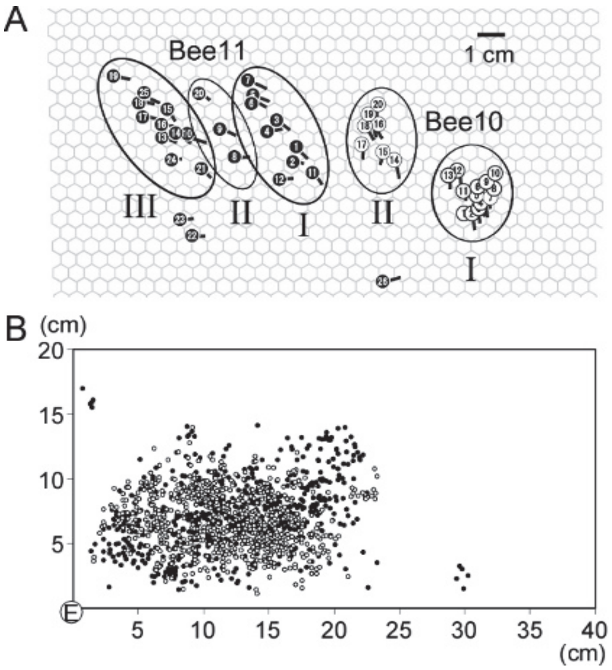

Fig. 6. Sites and orientations of waggle runs on a comb. (A) Locations and orientations of waggle runs of Bee 10 (open circle) and Bee 11 (black circle) that performed 20 and 26 runs, respectively. Circles indicate starting points. The numbers in the circles indicate the order of the waggle runs. The waggle run direction and distance are indicated by the direction and length of the line, respectively. Runs in a putative cluster are surrounded with roman numerals. For reference, positions are superimposed on honeycombs. (B) Sites where waggle runs were performed. The rectangle represents the outline of the comb. Runs concentrate on the dance floor irrespective of whether the runs were in the morning (10:36–12:11, open circles) or afternoon (12:42–14:42, black circles). "E" in the graph represents a corner closest to the entrance (modified from [25, 35] for (A), and [24] for (B)).

In a normal bee hive, several hundred bees are on one side of the comb, including nurse, comb-building, cleaning, nectar-treating, and forager bees. Some of them stayed in one place and some walked around. We measured the 10-s walk distances of 724 bees on one side of a comb at 10:40 on September 13, 2006 and found the spatial distribution of walking bees (unpublished data). Of the 724 bees (body length, ∼15 mm), 232 walked less

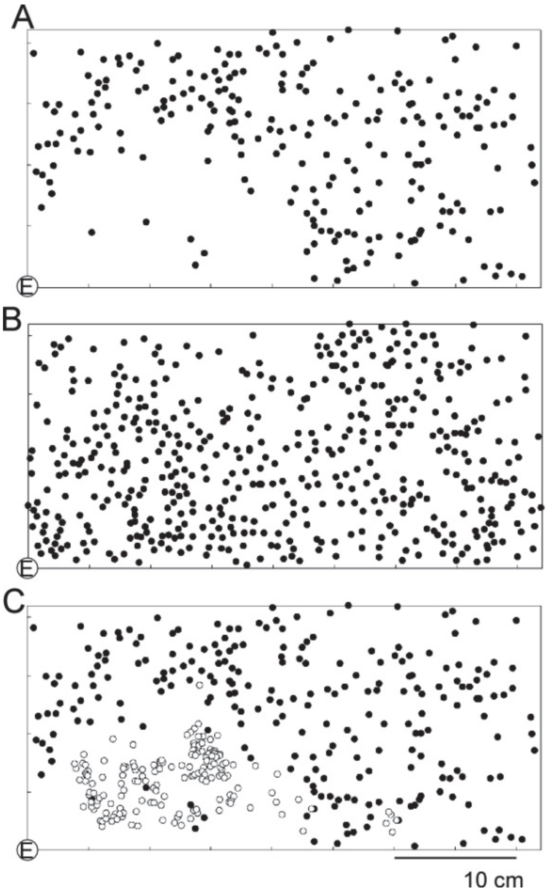

Fig. 7. Positions of bees for a 10-s wandering analysis. Initial positions of stayers (A) and movers (B) are indicated by black dots. (C) A merge of the position of stayers (black dots) and the starting points of waggle runs (open circles). A rectangle presents an outline of a comb. "E" in these graphs represents a corner closest to the entrance.

than 2.5 mm (stayer) and 492 walked for 2.5 mm or longer (mover). While movers were found on the whole comb, stayers were found outside the dance floor (**Fig. 7**). When the positions where all 161 waggle runs were observed between 10:36 and 10:41 were superimposed on the distribution of stayers, they were clearly separated (**Fig. 7(C)**). This means that only dancers and movers, but not stayers, were on the dance floor. The followers should be some of the movers but not the stayers. Thus, stayers will disturb interactions between dancers and followers if they stay on the dance floor. Performing waggle runs at multiple small areas on the dance floor and spatial separation may facilitate efficient communication.

6. Interaction Between Dancers and Followers: Information Transfer

The waggle dance contains a negligible error range (±15°) for directional information, as described in Section 3. To reduce the disadvantage caused by errors, precise information should be obtained; this can be achieved by averaging the received information. However, while a bee colony appears to produce rich opportunities for followers to encounter dancers, dance followers turn away from the dancer after attending only one or two runs, suggesting that directional information is still not precise. Although the biological significance of an error in directional information remains controversial [37], if such errors result from adaptation through natural selection, then a bee colony must gain some advantage from the error.

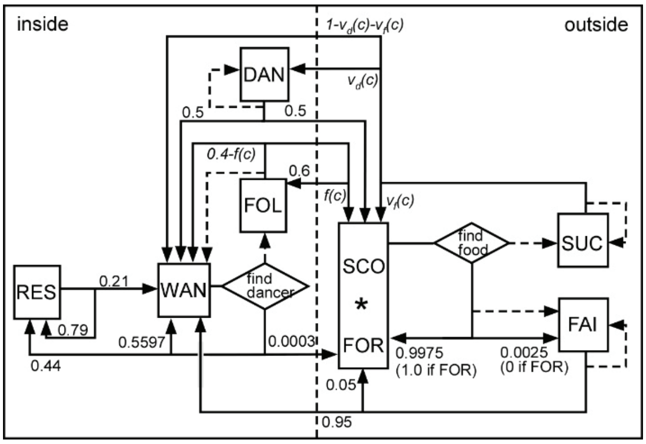

Fig. 8. Detail of iMoAD-f. Eight behavioral states are indicated that transitioned based on a specific probability and state-specific rules that are shown beside each solid arrow (see [24] for detail). DAN, dancing; FAI, failure; FOL, following; FOR, foraging; RES, resting; SCO, scouting; SUC, success; WAN, wandering (modified from [24]).

To examine the advantage from the errors, we created an individual-based Markov model for foraging (individual-based Markov model of *Apis mellifera* dance-guided foraging, iMoAD-f) [24]. Dance-guided foraging behavior was categorized into eight behavioral states: resting, walking in the hive (wandering), flying while searching for a food source (scouting), flying back to the hive with food (success), flying back to the hive without food (failure), flying to a food source with directional information (foraging), dancing, and following a dance (following). **Fig. 8** shows the transition of iMoAD-f. The biological properties of the behavioral states (e.g., flying and walking speed and searching duration), information transfer conditions (e.g., number of waggle runs and walking distance of a dancer), and transition probabilities among these states were parameterized from empirical data as much as possible. Using iMoAD-f, 1-day (8 h) foraging behavior can be simulated in various foraging environments, such as the number of feeders, location (direction and distance from the hive), and concentration of each feeder (food source). The range of directional errors in the waggle runs is also changeable. Therefore, iMoAD-f can be used to compare the error effect as 1-day foraging results (number of successful visits and energy collection [J/8 h]) among colonies with different directional error ranges.

In simulation experiments, error effects were assessed

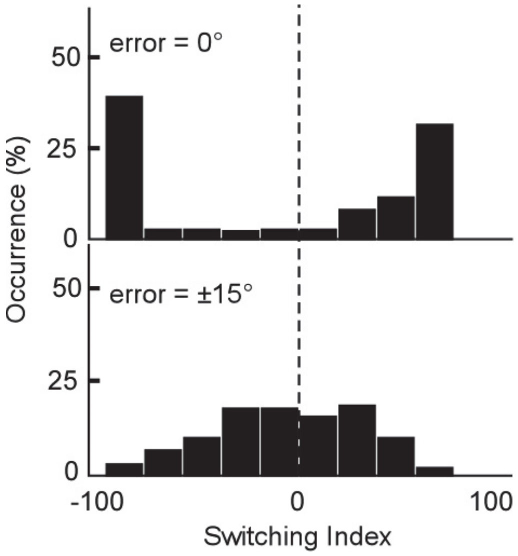

Fig. 9. Distributions of SIs under the condition that feeders were 1000 m away from the hive. When the error was 0°, two prominent peaks were found in which bees succeeded to switch feeders (SI = +60 to +80) and failed in switching completely (SI = −100 to −80), i.e., high-risk, high-return foraging (modified from [24]).

under a dynamically changing foraging environment similar to that in Seeley et al.'s experiments (**Fig. 2(C)**) [9]. Simulations showed that a colony with no error range had a significantly larger number of successful visits to the better feeder (∼12,500 visits) than a colony with a 15° error range (∼2,400 visits) when two feeders were located 400 m away from the hive. When the number and distance of feeders were changed, all simulation experiments revealed that the number of successful visits decreased as the variation in error increased. In particular, dances with errors of 30° or larger were no longer beneficial for food collection.

The foraging environment in the simulation experiment mimicked the empirical condition of Seeley et al. [9]. Therefore, it is also important to determine how well bees switch to feeders that are currently the best from the former best feeder. Detailed analyses of the time course of 1-day foraging revealed that a natural error range (10°–15°) improved flexibility in food collection against environmental change [24]. To evaluate the degree of success in switching feeders after the foraging environment has changed, a switching index (SI) was calculated based on the number of visits to each feeder during the last 30 min. If the bees visited only the current best feeder, the SI was +100. In contrast, if the bees visited only the former best feeder, the SI would have been −100. When the number of visits to the former and current best feeders were equal, the SI was 0. Thus, the SI would be positive if the bees switched feeders correctly. When the error range was 0°–5°, a colony achieved great success in finding and collecting food but also failed to locate a new profitable feeder when the environment changed. This is a high-risk, but high-return foraging strategy (**Fig. 9**). A colony with an error of 10°–15° was able to successfully visit a new feeder when the environment changed. This strategy seemed to balance successful and risky foraging.

7. Conclusion

7.1. Recent Studies on the Honey Bee Waggle Dance

Although there is no doubt that a waggle dance helps honey bees collect food, recent studies have suggested the importance of odors [38–41] and the instant availability of dance information when a forager flies out from the hive [42, 43]. These studies suggested that bees do not follow the information provided in dances blindly but also use information from their private memory based on their experience of foraging places. That is, bees flexibly use different sources of information [44, 45]. Taken together, recent advances in the understanding of dance behavior imply that dancing may have two different functions: transferring food location information and increasing the number of bees that fly out to forage. Recent technological developments have facilitated the tracking of behaviors of individual bees inside [46–49] and outside [50–53] the hive, performing accurate simulations through more precise modelling [24, 54–57] and analyzing dance behavior using a robot [58, 59]. Such analyses lead to a better understanding of honey bee waggle dances.

7.2. From Bee Waggle Dance to Swarm Intelligence

The honey bee waggle dance is achieved by local interactions between bees (not a centrally controlled system but a parallel and distributed system) and takes place in a special area that seems appropriate for interactions between dancers and followers. Although dance information contains a negligible range of errors (10°–15° in directional information and 15% in distance information), this error improves the flexibility of foraging adaptability in a dynamically changing environment.

We believe that understanding the principles of honey bee dance will facilitate progress in finding the principle mechanisms underlying swarm intelligence. Appropriate functioning of three factors, signal senders, recipients, and circumstances for signal exchange, should be important for keeping a swarm functionally active.

Acknowledgments

This work was supported by JSPS KAKENHI (grant numbers: 18K06345, 19K06765, and 22K06314 to R.O.) and Narishige Zoological Science Award to R.O.

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