Landmark knowledge overrides optic flow in honeybee waggle dance distance estimation

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Summary statement

The distance code in the honeybee waggle dance is embedded in the landscape memory that bees establish during their exploratory and their foraging flights.

Abstract

Honeybees encode in their waggle dances the vector (distance and direction) of an outbound flight to a food source or a new nest site. Optic flow has been identified as the major source of information in the distance estimation. Additional components of distance estimation were also identified, e.g. the sequence of experienced landmarks. Here we address the question of whether bees also use the landscape memory developed during exploratory orientation flights to estimate distance. We took advantage of the fact that flights in a narrow tunnel lead to further distance measures due to higher optic flow. We find that this effect is lost when bees had explored the area in which the tunnel is located and when they have somewhat restricted visual access to the surrounding environment through the mesh on top of the tunnel. These data are interpreted in the context of other findings about the structure of navigational memory in bees that develops during exploratory orientation flights. In particular, the data suggest that bees embed distance measures into a representation of navigational space that stores previously experienced landscape features.

Keywords: honeybees, waggle dance, optic flow, distance code, landscape memory, exploratory learning

Introduction

The waggle dance of honeybees encodes the distance and direction of the flight from the hive to a food source or to a new nest site (von Frisch, 1967). A most important discovery about the symbolic encoding of distance is the finding that the odometer of bees relies on optic flow during the outbound flight (Esch and Burns, 1995; 1996; Srinivasan et al., 2000). This was discovered by training bees in narrow tunnels that create higher optic flow than what is experienced during flight in the open environment. Increased optic flow leads to higher values of the distance code. In most experiments the distance measured by the bee was determined by the duration of the waggle run during the bees' dances within the hive. Additional and supportive information comes from experiments in which a feeder was located inside the tunnel and bees were videotaped during their search flight when the feeder was removed (Srinivasan et al., 1997). Combining these experimental approaches, it was possible to exclude alternative measures of flown distance, e.g. energy consumption (Heran, 1956; Heran, 1963), duration of flight, measuring and integrating airspeed, or some yet unknown measure of wing movement. Accumulating all this rich and supporting evidence (review: Srinivasan, 2011) it appears to be a well-established conclusion that the bee's odometer receives its information only or predominantly from optic flow.

However, several observations indicate that additional or even alternative processes may also contribute to distance estimation. (1) Bees trained along serially placed landmarks fly to both the real distance of the feeder and the serially correct location if the distances between the landmarks were either increased or decreased (Chittka and Geiger, 1995; Menzel et al., 2010). Similar "counting " effects of serially arranged marks were found when these marks were shown inside a tunnel (Dacke and Srinivasan, 2008a), indicating that both outside and inside the tunnel landmarks provide additional refence points for distance estimation. (2) Arranging a 6 m long tunnel in the open field at an angle of 90° to the direction of the approach flight did not lead to an accompanying shift of the danced waggle direction, rejecting the possibility that the flight in the tunnel contributes to a global vector based on a path integration process only (De Marco and Menzel, 2005). (3) Interestingly, such a global vector resulting from path integration was demonstrated by performing tunnel experiments in which the bees flew in the first half-length under a transversely oriented polarization filter (simulating a solar position that was directly ahead or behind the direction of flight), and the second half-length under an axially oriented polarization filter (simulating a solar position that was 90 deg to the left or the right of the flight direction) (Evangelista et al., 2014). These bees signaled a food source direction of 45 deg in their waggle dances, indicating an L-shaped

flight with equal arm length, and thus integration of two paths under 90° direction. The waggle run duration of around 230 ms was found to be within the range of the results of (Srinivasan et al., 2000). Other than in the experiments of De Marco et al. (2008), the bees performed their outbound and inbound flights inside the tunnel and had most likely no access to external landmarks. (4) Srinivasan et al. (1997) found in experiments with the tunnel that a landmark inside the tunnel enhances the accuracy with which the bees searched for food, thus leading to a reduction of the error accumulation process in optic flow measures. (5) It is known that feeders closer to the hive are more attractive than more distant feeders of similar quality (e.g. sucrose concentration). Shafir and Barron (2010) arranged two tunnels such that one was shorter than the other tunnel but induced higher optic flow (and thus should appear longer). Bees attributed more value to the shorter tunnel in their dances although it was associated with higher optic flow. (6) Dacke and Srinivasan (2008b) concluded from their data that bees appear to have two odometers, one that drives waggle dance communication and one they use to estimate the total distance in their flights to a feeder they had visited before.

In all of these studies bees were trained to fly to a feeder in such a way that additional parameters besides optic flow competed with the distance estimation.

Here, we have taken a different approach: we ask how the information from optic flow is integrated into what bees have learned during their previous exploratory flights at the beginning of their lives as foragers. Exploration of the environment is essential for bees before they start foraging (Capaldi et al., 2000; Degen et al., 2015). Sequential learning flights increasing to distances > 100 m and varying in direction lead to a knowledge of the environment surrounding the hive that allows them to find home from anywhere within the explored area via direct flights (Degen et al., 2016). The memory established during exploration is best understood as integrating egocentric, allocentric and compass information including local as well as global guiding cues (Menzel, 2023). Such a memory would potentially allow extracting a flown distance from this highly integrated form of spatial memory.

One may ask, therefore, how these different reference systems for distance estimation interact and under which conditions one dominates the other or whether compromises are made when information is inconsistent and bees have to communicate distance in the waggle dance. We address this question by setting up tunnel experiments under conditions in which the bees were differently familiar with the terrain in which the experiments were performed. For most of the experiments the colonies were positioned in the environment more than 4 weeks before

the experiments started, ensuring that the foragers tested had explored the environment outside of the tunnel. The surroundings were characterized by rich landmarks (trees, bushes, houses). In one experiment they had explored a different environment and were relocated just before the experiment. We found that the familiarity with the environment resulting from exploratory flights (and possibly additionally from foraging flights to natural food sources), rather than optic flow information, dominated the distance communicated in the waggle dance.

Materials and methods

The experiments were performed with observation hives (containing approximately 3,000 bees each, *Apis mellifera carnica*) in the summers 2022 and 2023. An IR camera (Raspberry Pi) monitored the dance area close to the entrance/exit of the hive. The experimental site was a highly structured domestic area in the village Amöneburg (Germany, 50°47'35.7"N 8°55'36.9"E) with trees, bushes, houses, roads.

The flight tunnels were rather similar to those used by Srinivasan et al. (2000), with length varying between 0.5 m and 6 m (in the preliminary experiment) and 6 m (in the main experiments 1 to 7) with an inner width of 11 cm, and a height of 30 cm. The top of the tunnel was covered with an insect-screen (Fig. 1). Bees saw the sky above them and rising landmarks in the surrounding within an angle approx. up to 60° during their flights in the tunnel. In the main experiment bees saw the surrounding environment only during the flight in the tunnel and not at all when they were feeding at the feeder F, because a light tight box was mounted at the end of the tunnel containing the feeder allowing to observe and monitor the marked bees (Fig. 1). The floor and the sides of the tunnel were covered with a black and white random texture with pixel size of 1 cm by 1 cm. Bees were trained to a feeder located outside, at the entrance of the tunnel or the end of the tunnel depending on experimental design (Fig. 2, 3).

Two sets of experiments were run. In the first set (preliminary experiments, Fig. 2) the tunnels were of different length (0.5, 1, 2, 4 or 6 m) and attached to the entrance/exit of the hive such that the end of the tunnel was always at the same location relative to the external landmarks. The length of the tunnel was changed several times by moving the colony accordingly. A feeder was always located at the end of the tunnel. The far end of the tunnel was open to allow foraging bees not taking part in the experiment to fly in and out freely. Bees visiting the feeder were marked with a white dot at the abdomen. Within the hive, dances of the marked

bees were visually observed via a video camera. A monitor displaying the images of these recordings was set up behind the hive. The colony in the observation hive had long term experience (at least 4 weeks) with their environment.

In the main experiments the location of the tunnel, the location of the feeder and the far end of the tunnel (open or closed) varied according to the individual design of the different experiments (experiments 1 – 7, Fig. 3). Bees visiting the feeder were individually marked with dual digit black and white number tags (or only pre-marked for experiment 1). The number range for differently marked bees was enhanced by positioning the tags in 4 different directions on the thorax. The dances on the dance floor were video-taped using an IR Raspberry Pi camera. The videos were analyzed off-line with the help of a custom written video analysis script in Python that detected the location and the time of a waggle run, stopped the video and opened a window that allowed to mark the start and the end of the waggle run as detected by the first and the last frame in which the bee was unsharp due to her fast-waggling movement. The video was recorded with 50 frames per second, and bees appeared somewhat unsharp during the waggle run but not during normal walking or return runs, allowing to set the frames for start and end of the waggle run accurately. The video frame was calibrated for space and time and the following data were noted in the pop-up window of the program and saved to file: duration of the waggle run, its length and the number of waggles performed, and the direction of the waggle run relative to gravity. The latter was used by the script to derive the angle to north in reference to the location of the hive, the date and the time of the day. This procedure led to efficient and precise measurements of large numbers of waggle runs. Furthermore, these data allowed to compare the variance and the correlation of two possible codes of distance: the duration and the number of waggles per waggle run. We found that number of waggles per waggle run varied less than waggle duration, and therefore used this metric (see results section, Fig. 4). The correlation between number of waggles and duration of the waggle run allowed us to relate our data to published data that used duration as the distance code.

The tunnels of the main experiment were close to the hive in the experiments 1 – 4 and at a further distance (321 m, coordinates: 50°47'46.1"N 8°55'35.5"E) in the experiments 5 – 7. As mentioned above the bees flying in the tunnel could see the external environment within an angle of approximately 60° during their flights in the tunnel because they always flew close underneath the mesh. They did not see the environment during feeding. In experiment 1, the colony was located first in an area about 4.5 kilometers from the experimental area behind a hill (50°48'52.3"N 8°52'20.7"E) for 3 weeks. Many foraging bees were marked with a white

dot at the abdomen before the colony was moved. Then they were moved over night into the experimental area, the 6 m long tunnel was attached to the hive and the far end closed. Thus, the colony was naïve to the environment because it was moved into the test environment shortly before the experiment started and the bees had not explored the test area yet. The feeder could be inserted and refilled without allowing bees to fly out or to approach it from the outside.

Thus, foragers feeding at the end of the tunnel in experiment 1 had only experience with the tunnel and not with the environment around the tunnel. This was different in experiments 2 to 7. The foragers in these experiments had explored the environment. They could reach the feeder only by flying through the tunnel. Experiments 2 and 5 were control experiments with a feeder at 10 m distance from the hive (experiment 2) or at 321 m distance (experiment 5) and no tunnel flight. In experiment 3 the entrance of the 6 m tunnel was at a distance of 10 m and the feeder was located at the end of the tunnel. In experiment 4 the tunnel was attached to the hive. The difference to experiment 1 was that the bees had experience with the surroundings before flying through the tunnel to the feeder at the end of the tunnel. In experiment 6, bees visited the feeder at the end of the tunnel. In experiment 7, two screens (2.5 m high) tightly attached to the right and left of the tunnel excluded the view of landmarks outside the tunnel but left the view to the sky. The experiments 2 -7 were performed in sequence. Dance data were recorded after the foragers experienced the new test conditions for at least 3 days. A longer interval was between experiment 4 and 5 due to the training to the remote feeding site (4 days for stepwise training to the feeding site, and 3 days for familiarizing the bees to the new test conditions).

Statistics and plotting were done using *Python* 3.9.15, *Pandas* 2.1.4, *Seaborn* 0.13.2, *Statsmodel* 0.14.0, *SciPy* 1.11.3. Boxplots show quartiles, whiskers the full distribution, except for outliers that are determined using a method in *Seaborn* that is a function of the inter-quartile range. All code and data will be provided upon reasonable request. All ethical regulations have been complied with.

Results

Number of waggles per waggle run as a code for distance

Our initial objective was to compare various parameters of the waggle run to identify which of them had the least variation, and thus which would deliver the most accurate distance code (recent review: Kohl and Rutschmann, 2021). The number of dance rounds in 15 seconds, commonly utilized by Karl von Frisch (von Frisch, 1967) in many experiments, exhibited

high variability; the length of the waggle run varied also considerably (data not shown). Consequently, both measures were excluded from our analysis. Instead, we concentrated on two parameters for the same waggle runs: the number of waggles per run and the duration of a run. Both parameters were measured for the same waggle runs through video analysis in a subset of our data, as described above. The duration of the waggle run displayed slightly more variability than the number of waggles per run ($p<0.01$, Levene Test). It is noteworthy that the frequency distribution of the durations was close to a single Gaussian distribution and did not show any indication of a double peaked distribution (Fig. 4, right histogram), while the frequency distribution of waggle count/run showed two distinct peaks, one for experiments 1 and 6, and another one for experiment 7 (Fig. 4, top histogram), revealing that the lower variability in this metric kept the two distinct distributions visible. Therefore, for the bulk of our measurements, we evaluated the waggle count metric. A linear regression gave a slope of 0.086 s per waggle.

Dances during the preliminary experiments

The design of the preliminary experiment allowed us to distinguish between round dances and waggle dances. The observation hive was positioned on a trolley, allowing for quick mobility of the hive while the entrance/exit of the tunnel and the feeder at the end of the tunnel remained stationary. This is a necessary requirement because bees learn the surroundings of the hive very accurately, and in these experiments all bees accessed the hive via the tunnel irrespective of its length and whether they were trained to a feeder at the end of the tunnel or flew to natural food sources. Outbound and inbound bees not feeding at the feeder accommodated very quickly to the changing length of the tunnel. Thus, the entrance/exit to the observation hive via the tunnel remained stable, while the length of the tunnel varied (see Fig. 2). These test conditions facilitated the alteration of tunnel length, ensuring that bees encountered the access to the hive via the tunnel while maintaining rather constant spatial relations to the environment. Based on the literature we expected waggle runs in 4 of the 5 test conditions (i.e. in all conditions with the tunnels longer than 0.5 m).

Prior to the start of the preliminary experiments, foragers from the colony experienced a condition with a short tunnel (0.5 m) for several weeks. A feeder was positioned 10 cm from the entrance/exit within the tunnel, and bees visiting the feeder were identified by marking them with a white dot on the abdomen. The tunnel's length was modified once at least 50 dances were observed. Multiple rounds of semi-random insertions of tunnels with varying lengths were conducted, and the feeder was always 10 cm from the entrance/exit of the tunnel

irrespective of its length. Only round dances, and no waggle dances, were observed in marked bees for all 5 test conditions. This is an important and rather surprising finding because one would have expected that under the conditions of this experiment either only waggle dances were performed in four of the five test conditions, or an increasing number of waggle runs with increasing tunnel lengths. Thus, our results falsified the hypothesis we had in mind when we started this experiment (see above).

A substantial difference to the experiments of Srinivasan et al. (2000) was that in our tunnel flying bees could see the surrounding environment which they had learned before during their exploratory orientation flights. Furthermore, although the bees feeding at the feeder inside the tunnel and close to its far end predominantly shuttled between the feeder and the access to the hive at the other end of the tunnel, some of them may have flown out of the tunnel from time to time since the far end of the tunnel was not closed. These considerations lead to designing the main experiment in which the potential effects of the exploratory experience with the natural environment prior to the tunnel flights were systematically tested.

Dances during experiments 1 – 7 in the main experiment

Seven experiments were run in the main experiment (Fig. 3). In experiment 1, the colony in the observation hive was first located for 5 weeks in an area approximately 4.5 km away from the experimental area (50°48'52.3"N 8°52'20.7"E). The landscape here (agricultural fields, grass land) was very different from that of the experimental area (domestic area in the village). In the last week before moving the hive, many foragers were marked with a white dot on the abdomen. The foragers were not trained to a feeder, and the natural food supply was scattered over larger distances (> 200 m) and rather scarce. Before the experiment, the hive was moved during the night, a 6 m tunnel was attached to the entrance/exit, and the tunnel was closed at the far end. A feeder was placed at the far end within the tunnel, and a small shelter allowed to examine the feeder and refill it. Videos of the dance floor were recorded with an IR camera and the dances analyzed off-line using the procedure described in the Method section. In experiment 2 – 7 the colony in the observation hive was located in the experimental area for 3 weeks before the experiment started.

In experiment 1 three sessions of 30 minutes recording each were analyzed. The marked bees predominantly performed waggle dances (n=298, waggles/run mean±std: 4.1±1.1, Fig. 5); 2 round dances were observed. Thus, flights in the 6 m tunnel with view to an unexplored environment led to waggle runs, indicating that the optic flow in the tunnel elicited a long-distance dance (see below for calibration).

No tunnel was used in experiment 2, and the feeder was located 10 m from the hive in the direction of 351° to N. Four sessions of 30 minutes each were video recorded. We observed only round dances but no waggle runs, in accordance to the short distance flown (n=112 dances evaluated). However, the same result was found also for experiments 3 and 4: only round dances (n=105 dances for experiment 3, n=124 dances for experiment 4). In experiment 3 the entrance/exit to the 6 m tunnel was at distance of 10 m from the hive, direction 354° to N, feeder at the end of the tunnel, and in experiment 4, the 6 m tunnel was attached to the hive and the feeder at the end of the tunnel. This latter experiment required a different colony because a new colony had to be brought into the experimental area, and the foragers learned to access the hive through the tunnel. Therefore, experiment 4 was carried out at the time when colony 1 was exposed to a different environment (experiment 1). The results show that in experiments 3 and 4, bees danced for a location in the immediate vicinity, despite having flown through the tunnel (which simulated long-distance in experiment 1). Therefore, in the next experiments 5-7, we asked under which conditions does a tunnel simulate a long-distance, and when does it not.

In experiments 5 – 7, foragers familiar with the landscape were trained to a distant location (321 m, direction 354° to N). In experiment 5 the feeder was at the entrance of the 6 m tunnel (bees did not fly through the tunnel) and in experiment 6 at the end of the 6 m tunnel. In experiment 7 the feeder was also at the end of the tunnel but two screens (2.5 m high) excluded the view of landmarks outside the tunnel and left the view to the sky. As expected, foragers performed waggle dances in all these conditions (Fig. 5).

In experiment 5, bees danced about 5 waggles/run to indicate the 321 m distance (n=227, mean±std: 5.1±1.5); in experiment 6, with the added 6 m tunnel, the waggles did not increase (n=547, mean±std: 4.2±1.2); in experiment 7, when shielding the 6 m tunnel from the surroundings, the waggles increased (n=456, mean±std: 7.6±2.2; Fig. 5). A generalized linear model analysis (Poisson model family, log link function, IRLS method with post-hoc testing) showed no significant difference between the results in experiment 1 and 6. Experiment 5 and experiment 7 differed significantly ($p < 0.001$). Even though the difference between experiments 5 against 1 and 6 is significantly different, the ranges are strongly overlapping (see Fig. 5), suggesting that this difference may not have a biological relevance. However, the distribution ranges of experiment 7 are clearly distinct (Fig. 5): here flying through the tunnel led to a highly relevant and significant increased distance as signaled in the waggle dance. We used the data from experiment 5 to calibrate the distance code for number of waggles: each waggle/run indicated a 63.3 m distance (approx. 5 waggles/run for the known 321 m

distance, see Fig.5). Applying this calibration, bees indicated a fictive distance for the 6 m tunnel of 262 m in experiment 1. A similar distance was danced in experiment 6 (265 m, short of the really flown distance of 321+6 m). In experiment 7, bees danced 481 m. If we subtract the open distance of 321 m, this indicates a danced tunnel length of 220 m, i.e., slightly shorter than in experiment 1 (see right ordinate scale in Fig. 5). This experiment also shows that bees add up distance in free flight with the distance within the tunnel, when flying both sequentially. Taken together, these data suggest that the environment surrounding the tunnel provides information for distance coding if the dancer is familiar with the environment (in experiment 6 the bees did not experience the tunnel as a long distance, while in experiment 7, with no view of the environment, the tunnel was experienced as a long distance).

The observations in the preliminary experiments (Fig. 3) and the video analyses of experiments 2, 3, 4 and 6 showed clearly that the input from the environment dominated the distance coding when the dancers had explored the environment. However, it could be that the average values of waggles per run in these experiments may have resulted from some sort of switching between the competing inputs. We plotted the distribution of waggles/run for each experiment in order to investigate whether there was any evidence for independent dual information (Fig. 7). We found that the frequency distribution was close to Gaussian with no indication of double peaked distributions in any of the experiments.

Marking individual bees with number tags allowed us to further address the question whether individual dancers exposed to competing conditions may differ in coping with this situation. We had marked 368 foragers with number tags and hoped that they would forage in both experiments 6 and 7 allowing us to see at the individual level whether they would deal with the test conditions differently (Fig. 7). Unfortunately, no tagged dancers were seen in our videos that were exposed to both test conditions. However, calculating the average of waggles per waggle run for each of the individuals separately for the two test conditions allowed us to reject the possibility that some individuals may have weighted the two inputs differently.

Discussion

The flight through the 6 m tunnel simulated a flight distance of 262 m (experiment 1, tunnel close to the hive) or a distance of 220 m (experiment 7, tunnel further away from the hive) if environmental information at the test site was excluded, thus confirming the finding that optic flow is a major factor for bees to estimate flight distance. The data reported in Srinivasan et al. (2000) (their Fig. 2, experiments 2 and 4) indicated optic-flow induced distances of a

similar 6 m tunnel of 184 m (close to the hive) and 230 m (further away from the hive). These results are rather close to the result reported here given the condition that different colonies were used and the tunnels had different heights. Our tunnel was 30 cm high and their tunnel 20 cm high. The corresponding durations of waggle runs in Srinivasan et al. (2000) were 441 ms for the tunnel close to the hive and 529 ms for the tunnel further away from the hive, which is in the same order as the results found here: applying the conversion of number of waggles to duration of 0.086 s per waggle (Fig. 4) we obtained 356 ms waggle run duration for the close tunnel (experiment 1) and 408 ms for experiment 7 (Fig. 6).

We note that distance conversion rate was different in experiments 6 and experiments 5. This observation suggests that distance calibration may change over time or in different conditions, which may include time of the year, or the amount of previous experience. We are currently doing experiments in that direction.

The data presented here add an important component to distance estimation in honeybees that goes beyond the measurement and the encoding/decoding of distance in the waggle dance. We show that knowledge of the environment surrounding the tunnel can override the optic flow effect. This partly corroborates findings cited in the introduction with respect of effects of serial landmark learning (Chittka et al., 1995; Menzel et al., 2010), "counting" phenomena (Dacke and Srinivasan, 2008a), reduced error accumulation through serial landmarks (Srinivasan et al., 1997), and importantly the discovery of two odometers in bees (Dacke and Srinivasan, 2008b). In addition, the study by De Marco and Menzel (2005) showed that large range path integration collapses when bees fly out of the tunnel that was arranged 90° to the access flight to the feeder. Interestingly, unlike the results presented here, the optic flow effect was not overridden in that study when the bees continued flying the same direction inside of the tunnel as in the access flight, even though the view of the environment was not blocked. This can be explained by the special conditions of the environment around the tunnel in their study. The experiments were carried out in a large, flat and horizontal grassland without rising objects and a flat horizon. The bees saw the environment only in the moment when they left the tunnel, and in that moment their knowledge of the environment took over. The differences between Evangelista et al. (2014) and De Marco and Menzel (2005) on path integration can also be resolved on the basis of our data reported here. Flights only inside the tunnel with little or no view of the environment as in the case of the Evangelista et al. (2014) study restrict the distance measure to optic flow, whereas the moment the bees leave the tunnel and return back to the hive in flight through the open they will refer their distance measure to the landscape memory.

What we have termed "knowledge of the environment" and "landscape memory" here should be understood as a technical term catching the consequences of exploratory learning. Conceptually, this memory could have two forms within the bees' neural networks: either, each point of the known environment is elementally associated to a homing vector, or, different points of the known environment are connected in a navigational map. While the experiments in this paper cannot distinguish between these two memory forms, their discussion is important in order to understand what information is conveyed by a dancing bee when coming back from a tunnel flight. An elemental form of memory used for navigation generally assumes that the animal forms an association between a location, the visual snapshot of the environment at that location, and the associated homing vector, and assumes that the same information is memorized for all subsequent locations along the homing flight. Conversely, a navigational map exploits the advantage of the honeybee being a flying insect. Visual snapshots memorized from arial images, and sequential images on a homing flight, naturally create a visual map of the known surroundings of the bee. We propose that such a navigational map is parsimonious, and offers the necessary flexibility in natural environments with all their daily and seasonal changes. Exploratory learning of a navigational map differs from elemental target associative learning in several important aspects (Birke and Archer, 1983; Gallistel, 1990; Jeffery et al., 2024, Renner, 1988; Tolman, 1948). The process of exploration is an attention inducing and rewarding process in itself accompanied with active movement. Sequentially experienced and spatially separated objects are bound together leading to a representation of organized space, and multiple experiences of similar cues (both of the egocentric and allocentric domain) will make the spatial memory richer and more precise (Chen and Mou, 2024; Hilton and Wiener, 2023). It has been argued that multiple exploratory flights lead to memory storage and retrieval processes that appear to bind together separate memories through generalization process, memory updating, completion and correction (Menzel, 2023). Such a form of spatial representation in waggle dance followers would allow them to interpret the endpoint of the symbolically encoded flight vector (distance and direction) as a location in their spatial memory (Wang et al., 2023). This decoding would be performed most likely both in waggle dancers and in waggle dance followers because dancers frequently switch between foraging, dance following and dancing. Taken together, we conclude that the measure of distance as expressed in the dance is likely embedded in the global representation of the explored space. Phenomena like dancing for a food source after a detour flight (e.g. around a mountain, von Frisch, 1967, p. 174 – 178) or uphill could mean that dancers and followers estimate the true distance (further distance) by referring their flight

to the learned characteristics of the landscape. In an ecological context, trips need to be planned taking into account changing properties of the environment and weather conditions.

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Figures

Fig. 1. Left: view from within the tunnel as used during the preliminary experiments and the experiments 1 – 6 of the main experiment. Right: view of the tunnel from outside. Note the concealed ending: the feeder was in the dark, and the experimenter could enter the cover.
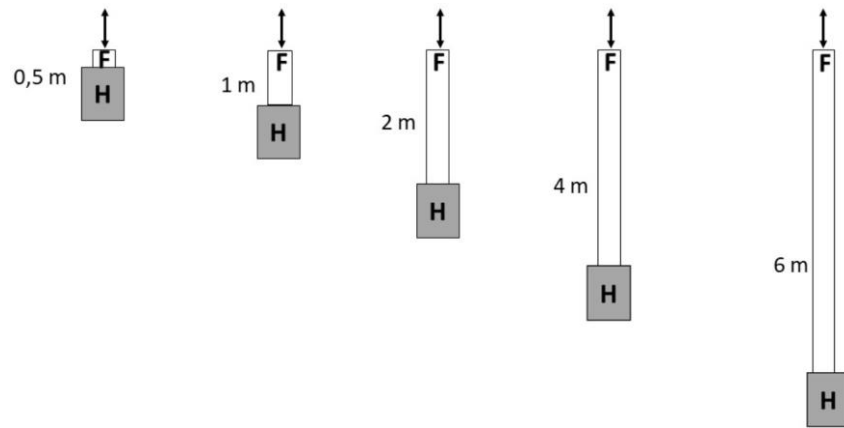
Fig. 2. Preliminary experiments. The colony in the observation hive had long time experience with the environment. Tunnels of different length (0.5, 1, 2, 4 or 6 m) were attached to the front of the hive with the entrance hole such that the entrance/exit to the tunnel was always at the same location. The feeder was close to the end inside the tunnel. The length of the tunnel was changed several times by moving the colony accordingly. Bees visiting the feeder were marked with a white dot at the abdomen. A monitor displaying the images of the IR video camera recording the bees' dances within the hive was set up behind the hive, and dances of the marked bees were visually observed and evaluated. Bees not trained to the feeder (thus not marked) were free to move in and out at the end of the tunnel and were not included in the on-line evaluated dances.
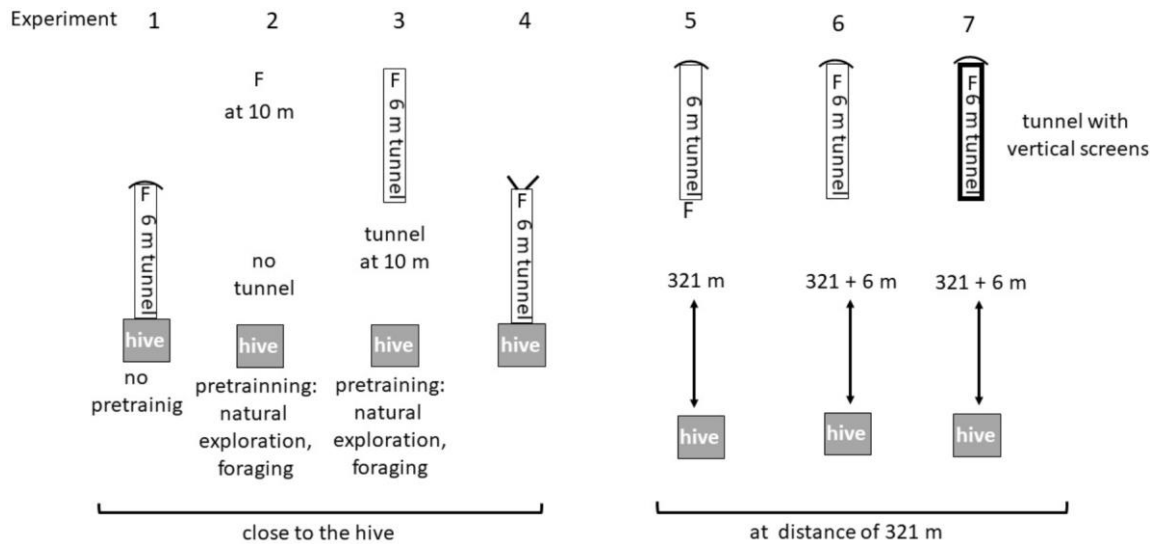
Fig. 3. Design of the experiments in the main experiment. Experiment 1: The tunnel was attached to the entrance of the hive prior to any exploratory flights, foraging flights or feeder (F) training. Experiment 2: The foraging bees were trained to a feeder at a distance of 10 m from the hive. Experiment 3: Experienced foragers were trained to the end of the 6 m tunnel. The entrance to the tunnel was at 10 m from the hive. Experiment 4: The tunnel was attached to the entrance of the hive after the bees had explored the environment and foraged at natural food sources. Experiment 5: experienced foragers were trained to a feeder (F) at a distance of 321 m and subsequently fed at this location. Experiment 6: bees from experiment 5 were trained to a feeder (F) at the end of the 6 m tunnel. Experiment 7: The animals from experiment 5 and 6 were further trained to the feeder of the tunnel but two screens (2.5 m high) were attached to the side walls of the tunnel. In this situation the animals could see the sky but no landmarks surrounding the feeder. ∨ in experiment 4 indicates that the entrance/exit to the hive via the tunnel is open for other foragers not feeding at F, ⌒ marks the closed end of the tunnel that is covered with a box allowing access to the feeder and blocking the view of the surrounding during feeding at F.
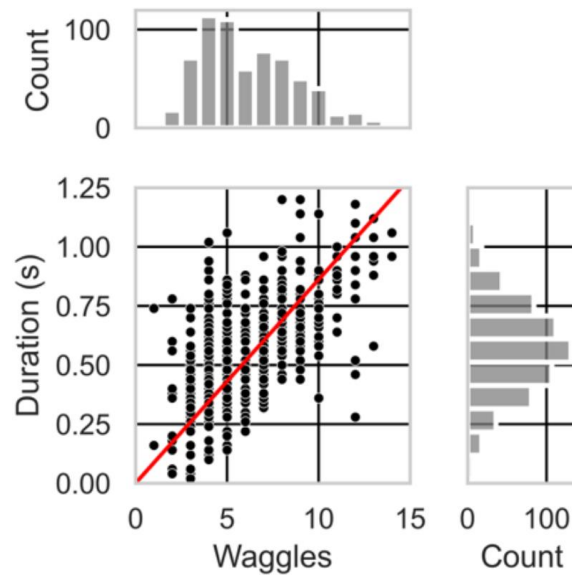
Fig. 4. Plot of waggles/run against duration/run, for experiments 1, 6 and 7 of the main experiment group, with histograms for both at the side. Note that the histogram for waggles has two peaks: at 5 waggles/run corresponding to experiments 1 (n=84, mean±std: 4.1±1.1) and 6 (n=233, mean±std: 4.3±1.3), and at 7 waggles/run corresponding to experiment 7 (n=337, mean±std: 8.1±2.1). The higher variability in duration smears the distribution to a single peak (mean±std for duration, experiment 1, 6, 7: 0.43±0.18, 0.48±0.19, 0.67±0.18).
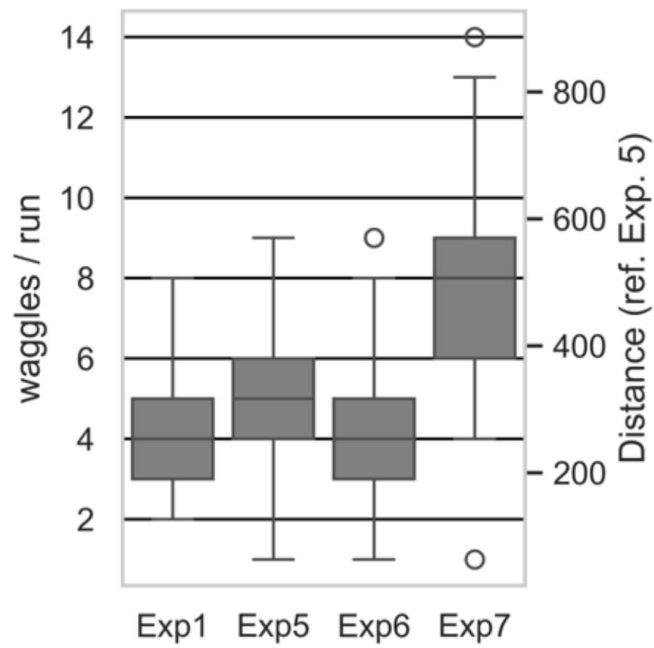
Fig. 5. Distribution of waggles/run in experiments 1, 5, 6 and 7. Boxes show quartiles, whiskers rest of distributions, except for outliers (see methods). Right ordinate axis shows distances in meters indicated by the waggle dance, calibrated with experiment 5 (no tunnel). (see S2 for data and statistics).
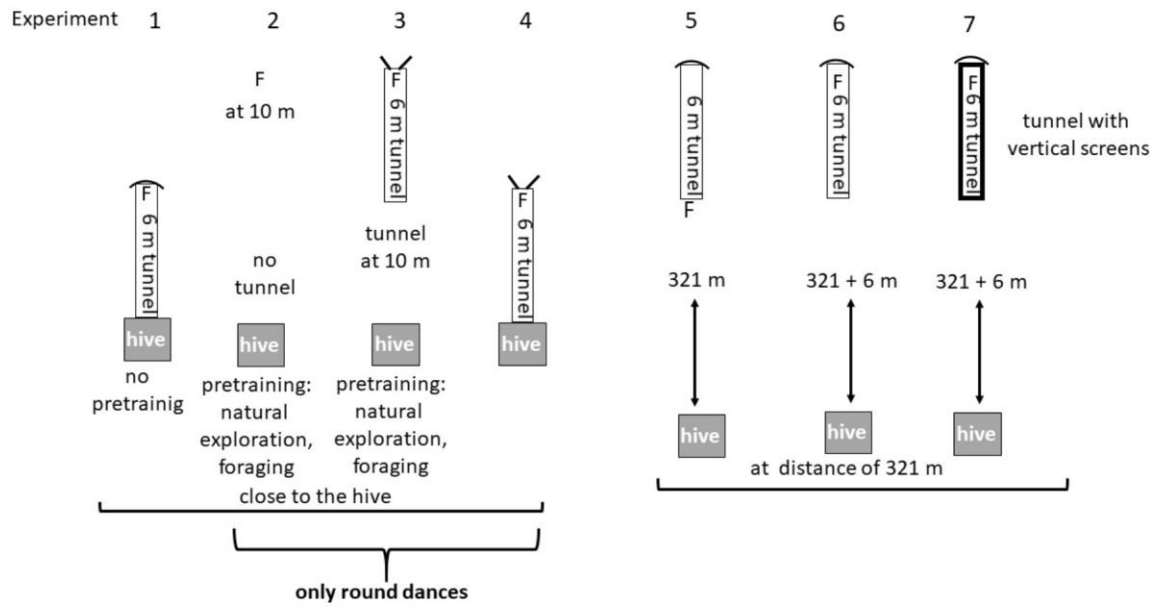
Exp. 1		Exp. 5	Exp. 6	Exp. 7
4.1 ± 1.1	waggles	5.1 ± 1.5	4.2 ± 1.2	7.6 ± 2.2
298	n (waggle runs)	227	547	456
0.356 s	duration (calc)	0.437 s	0.360 s	0.655 s
	m/waggle	63.3 m	78.1 m	
	danced distance (ref exp. 5)	321 m	265 m	481 m
262 m	danced tunnel length (5)	59 m	3 m	220 m
	danced distance (ref exp. 6)	396 m	327 m	594 m
323 m	danced tunnel length (6)	73 m	4 m	271 m

Fig. 6. Summary of the results on dances in the main experiment. The upper part of the figure repeats the design of the 7 experiments, the lower part gives the data for the experiments 1, 5, 6 and 7 together with the calculations of distances from the number of waggles and the corresponding durations as calculated from Fig. 4.
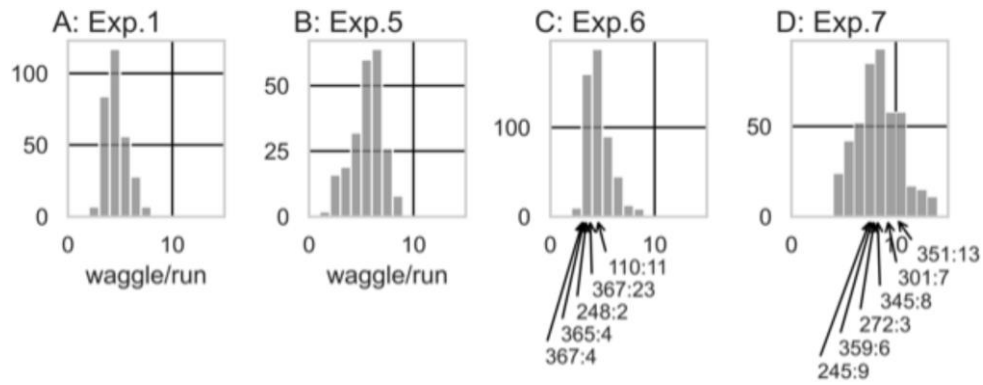
Fig. 7. Histograms of waggles/run in experiments 1, 5, 6 and 7. In each experiment, a single prominent peak is visible. Note the high values in experiment 7 as compared to experiments 1, 5 and 6. In experiments 6 and 7, the values for identified bees are indicated with arrows toward the abscissa, the label indicates the bee identity, and the number of averaged (observed) waggle dances (e.g.: bee number 110 had 11 evaluated dances in experiment 6).

Supplement 1: related to Fig. 4

Data for each experiment (column 2, values: Exp1, Exp6, Exp7),
data shows averaged waggles (column 3),
and averaged duration (column 4).

	Experiment	Waggles	Duration
0	Exp1	0.644494	0.698625
1	Exp1	0.48337	0.454106
2	Exp1	0.644494	0.873281
3	Exp1	0.644494	1.082868
4	Exp1	0.805617	0.943143
5	Exp1	0.644494	0.628762
6	Exp1	0.48337	0.5589
7	Exp1	0.48337	0.069862
8	Exp1	0.48337	0.628762
9	Exp1	0.48337	0.489037
10	Exp1	0.48337	0.5589
11	Exp1	0.644494	0.83835
12	Exp1	0.644494	0.454106
13	Exp1	0.322247	0.349312
14	Exp1	0.966741	1.152731
15	Exp1	0.805617	0.803418
16	Exp1	0.644494	0.593831
17	Exp1	0.48337	0.83835
18	Exp1	0.644494	0.803418
19	Exp1	0.322247	0.244519
20	Exp1	0.805617	0.803418
21	Exp1	0.966741	1.536974
22	Exp1	0.805617	1.013006
23	Exp1	0.644494	0.873281
24	Exp1	0.644494	1.013006
25	Exp1	0.644494	1.117799
26	Exp1	0.322247	0.104794
27	Exp1	0.48337	0.489037
28	Exp1	0.805617	0.83835
29	Exp1	0.805617	0.873281
30	Exp1	0.805617	1.152731
31	Exp1	0.48337	0.419175
32	Exp1	0.644494	0.733556
33	Exp1	0.644494	0.593831
34	Exp1	0.322247	0.244519
35	Exp1	0.644494	0.733556
36	Exp1	0.644494	0.83835
37	Exp1	0.48337	0.384244
38	Exp1	0.644494	0.489037
39	Exp1	0.805617	0.733556
40	Exp1	0.805617	0.908212
41	Exp1	0.644494	0.803418
42	Exp1	0.805617	0.768487
43	Exp1	0.644494	0.628762
44	Exp1	0.644494	0.733556
45	Exp1	0.644494	0.873281
46	Exp1	0.322247	0.244519
47	Exp1	0.322247	0.069862

48	Exp1	0.48337	0.733556
49	Exp1	1.127864	1.432181
50	Exp1	0.805617	1.117799
51	Exp1	0.644494	0.803418
52	Exp1	0.966741	1.292456
53	Exp1	0.644494	0.908212
54	Exp1	0.322247	0.314381
55	Exp1	0.805617	1.362318
56	Exp1	0.644494	0.733556
57	Exp1	0.805617	0.978075
58	Exp1	0.644494	0.908212
59	Exp1	0.48337	0.034931
60	Exp1	0.644494	1.047937
61	Exp1	0.48337	0.663693
62	Exp1	0.644494	0.733556
63	Exp1	0.644494	0.978075
64	Exp1	0.805617	0.873281
65	Exp1	0.48337	0.698625
66	Exp1	0.805617	0.978075
67	Exp1	0.644494	0.5589
68	Exp1	0.48337	0.83835
69	Exp1	0.644494	0.943143
70	Exp1	0.966741	0.978075
71	Exp1	0.805617	1.013006
72	Exp1	0.966741	1.117799
73	Exp1	0.805617	1.257524
74	Exp1	0.805617	0.628762
75	Exp1	0.966741	0.978075
76	Exp1	0.48337	0.489037
77	Exp1	0.805617	0.5589
78	Exp1	0.48337	0.489037
79	Exp1	0.805617	1.013006
80	Exp1	0.48337	0.454106
81	Exp1	0.644494	0.698625
82	Exp1	0.805617	0.978075
83	Exp1	0.805617	0.803418
674	Exp6	0.644494	1.397249
675	Exp6	0.644494	0.489037
676	Exp6	0.644494	1.502043
677	Exp6	1.127864	1.502043
678	Exp6	0.805617	1.502043
679	Exp6	0.48337	0.27945
680	Exp6	0.805617	0.978075
681	Exp6	0.805617	0.978075
682	Exp6	0.644494	1.082868
683	Exp6	0.48337	0.663693
684	Exp6	0.966741	1.047937
685	Exp6	0.805617	1.047937
686	Exp6	0.644494	1.152731

687	Exp6	0.644494	0.5589
688	Exp6	0.644494	0.83835
689	Exp6	0.966741	0.83835
690	Exp6	0.966741	1.536974
691	Exp6	0.644494	0.419175
692	Exp6	0.805617	1.362318
693	Exp6	1.127864	1.362318
694	Exp6	0.644494	1.222593
695	Exp6	0.966741	0.83835
696	Exp6	0.805617	0.978075
697	Exp6	1.127864	0.978075
698	Exp6	0.48337	1.292456
699	Exp6	0.805617	0.768487
700	Exp6	0.805617	1.117799
701	Exp6	0.644494	1.117799
702	Exp6	0.644494	1.292456
703	Exp6	0.644494	0.663693
704	Exp6	0.644494	0.873281
705	Exp6	0.644494	0.873281
706	Exp6	0.644494	1.397249
707	Exp6	0.966741	0.978075
708	Exp6	1.127864	0.803418
709	Exp6	0.644494	0.803418
710	Exp6	0.48337	0.83835
711	Exp6	0.966741	1.257524
712	Exp6	0.644494	0.943143
713	Exp6	0.805617	0.943143
714	Exp6	0.805617	1.082868
715	Exp6	0.644494	0.5589
716	Exp6	1.288987	1.152731
717	Exp6	0.805617	1.152731
718	Exp6	0.805617	1.432181
719	Exp6	0.644494	0.733556
720	Exp6	1.127864	0.978075
721	Exp6	0.805617	0.978075
722	Exp6	0.805617	1.013006
723	Exp6	0.48337	0.768487
724	Exp6	0.805617	1.047937
725	Exp6	1.127864	1.047937
726	Exp6	0.644494	1.187662
727	Exp6	0.644494	0.628762
728	Exp6	0.805617	1.362318
729	Exp6	0.805617	1.362318
730	Exp6	0.966741	0.803418
731	Exp6	0.322247	1.047937
732	Exp6	1.127864	0.978075
733	Exp6	0.644494	0.978075
734	Exp6	0.48337	0.978075
735	Exp6	0.48337	0.209587

736	Exp6	0.805617	1.082868
737	Exp6	0.805617	1.082868
738	Exp6	0.805617	1.257524
739	Exp6	0.805617	0.628762
740	Exp6	0.805617	0.628762
741	Exp6	0.644494	0.628762
742	Exp6	0.644494	1.187662
743	Exp6	0.644494	1.152731
744	Exp6	0.805617	0.628762
745	Exp6	0.48337	0.628762
746	Exp6	0.805617	1.152731
747	Exp6	0.48337	0.5589
748	Exp6	0.805617	1.152731
749	Exp6	0.805617	1.152731
750	Exp6	0.48337	1.222593
751	Exp6	0.805617	0.384244
752	Exp6	0.805617	0.593831
753	Exp6	0.48337	0.593831
754	Exp6	0.48337	1.292456
755	Exp6	0.322247	0.698625
756	Exp6	0.48337	0.663693
757	Exp6	0.644494	0.663693
758	Exp6	0.966741	1.187662
759	Exp6	0.644494	0.5589
760	Exp6	0.805617	0.733556
761	Exp6	0.805617	0.733556
762	Exp6	0.644494	1.571905
763	Exp6	0.48337	0.523968
764	Exp6	0.644494	0.978075
765	Exp6	0.805617	0.978075
766	Exp6	0.48337	0.419175
767	Exp6	0.966741	0.523968
768	Exp6	0.48337	0.803418
769	Exp6	0.805617	0.803418
770	Exp6	0.48337	0.454106
771	Exp6	0.322247	1.047937
772	Exp6	0.805617	0.663693
773	Exp6	0.322247	0.663693
774	Exp6	0.644494	1.502043
775	Exp6	0.644494	0.209587
776	Exp6	0.805617	1.117799
777	Exp6	0.966741	1.117799
778	Exp6	0.966741	1.187662
779	Exp6	0.644494	0.593831
780	Exp6	0.805617	0.523968
781	Exp6	0.805617	0.523968
782	Exp6	0.644494	1.327387
783	Exp6	0.48337	0.908212
784	Exp6	0.805617	1.327387

785	Exp6	0.805617	1.327387
786	Exp6	0.48337	0.908212
787	Exp6	0.48337	0.454106
788	Exp6	0.644494	1.013006
789	Exp6	0.805617	0.523968
790	Exp6	0.644494	0.873281
791	Exp6	0.322247	0.698625
792	Exp6	0.48337	0.978075
793	Exp6	0.48337	0.27945
794	Exp6	0.644494	1.117799
795	Exp6	0.644494	0.5589
796	Exp6	0.48337	1.117799
797	Exp6	0.644494	0.593831
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799	Exp6	0.48337	0.803418
800	Exp6	0.805617	0.908212
801	Exp6	0.48337	0.419175
802	Exp6	0.644494	1.047937
803	Exp6	0.644494	0.523968
804	Exp6	0.805617	0.663693
805	Exp6	0.644494	0.83835
806	Exp6	1.127864	0.593831
807	Exp6	0.805617	0.593831
808	Exp6	0.48337	0.943143
809	Exp6	0.644494	0.698625
810	Exp6	0.644494	0.768487
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813	Exp6	0.644494	0.174656
814	Exp6	0.644494	1.781493
815	Exp6	0.805617	0.593831
816	Exp6	1.450111	0.908212
817	Exp6	0.322247	0.978075
818	Exp6	0.48337	0.803418
819	Exp6	0.644494	0.244519
820	Exp6	0.644494	0.733556
821	Exp6	0.805617	0.873281
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823	Exp6	0.805617	0.733556
824	Exp6	0.644494	0.663693
825	Exp6	0.966741	1.397249
826	Exp6	0.644494	0.489037
827	Exp6	0.805617	0.908212
828	Exp6	0.805617	0.593831
829	Exp6	0.966741	0.83835
830	Exp6	0.644494	1.781493
831	Exp6	0.644494	0.83835
832	Exp6	0.644494	1.187662
833	Exp6	0.48337	0.523968

835	Exp6	0.805617	0.27945
836	Exp6	0.644494	0.733556
837	Exp6	0.644494	0.663693
838	Exp6	0.644494	1.641768
839	Exp6	0.322247	0.663693
840	Exp6	0.48337	0.943143
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843	Exp6	0.966741	0.523968
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848	Exp6	0.644494	0.663693
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865	Exp6	0.48337	0.104794
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867	Exp6	0.805617	0.698625
868	Exp6	0.966741	0.384244
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870	Exp6	0.48337	0.803418
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874	Exp6	1.450111	0.83835
875	Exp6	0.644494	0.83835
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877	Exp6	0.805617	0.733556
878	Exp6	0.644494	0.943143
879	Exp6	0.48337	0.5589
880	Exp6	0.48337	0.908212
881	Exp6	1.127864	0.83835
882	Exp6	0.48337	0.83835
883	Exp6	0.48337	0.384244

884	Exp6	0.644494	0.628762
885	Exp6	0.805617	0.803418
886	Exp6	0.644494	1.013006
887	Exp6	0.805617	0.244519
888	Exp6	0.48337	0.5589
889	Exp6	0.644494	0.5589
890	Exp6	0.805617	1.117799
891	Exp6	0.644494	0.523968
892	Exp6	0.644494	0.593831
893	Exp6	0.48337	0.943143
894	Exp6	0.805617	0.978075
895	Exp6	0.48337	0.768487
896	Exp6	0.48337	0.698625
897	Exp6	0.644494	0.785953
898	Exp6	0.48337	0.698625
899	Exp6	0.805617	0.349312
900	Exp6	0.644494	1.013006
901	Exp6	1.127864	0.5589
902	Exp6	0.48337	0.768487
903	Exp6	0.644494	0.768487
904	Exp6	0.805617	0.803418
905	Exp6	0.805617	0.523968
906	Exp6	0.48337	1.013006
907	Exp6	0.644494	0.943143
1011	Exp7	1.288987	1.013006
1012	Exp7	1.450111	1.257524
1013	Exp7	1.288987	1.013006
1014	Exp7	0.966741	1.082868
1015	Exp7	1.288987	1.117799
1016	Exp7	1.288987	1.082868
1017	Exp7	1.450111	0.768487
1018	Exp7	0.966741	0.83835
1019	Exp7	0.805617	0.768487
1020	Exp7	1.288987	1.117799
1021	Exp7	1.450111	1.257524
1022	Exp7	1.127864	1.117799
1023	Exp7	1.127864	0.83835
1024	Exp7	0.966741	0.83835
1025	Exp7	0.805617	0.83835
1026	Exp7	1.127864	0.943143
1027	Exp7	1.450111	1.257524
1028	Exp7	1.127864	0.943143
1029	Exp7	1.127864	1.013006
1030	Exp7	1.450111	1.257524
1031	Exp7	1.127864	1.013006
1032	Exp7	1.127864	0.943143
1033	Exp7	1.127864	0.978075
1034	Exp7	1.288987	0.943143
1035	Exp7	0.805617	0.908212

1036	Exp7	1.611234	1.397249
1037	Exp7	0.966741	0.908212
1038	Exp7	0.805617	1.502043
1039	Exp7	1.127864	0.978075
1040	Exp7	1.772358	1.502043
1041	Exp7	1.127864	1.257524
1042	Exp7	1.611234	1.397249
1043	Exp7	1.450111	1.257524
1044	Exp7	0.966741	1.502043
1045	Exp7	1.288987	1.117799
1046	Exp7	1.288987	1.502043
1047	Exp7	0.805617	0.768487
1048	Exp7	1.288987	1.117799
1049	Exp7	0.966741	0.768487
1050	Exp7	0.805617	1.432181
1051	Exp7	0.966741	0.83835
1052	Exp7	1.127864	1.432181
1053	Exp7	1.933481	0.489037
1054	Exp7	1.611234	1.397249
1055	Exp7	0.805617	0.489037
1056	Exp7	1.288987	1.187662
1057	Exp7	1.288987	1.117799
1058	Exp7	1.127864	1.187662
1059	Exp7	0.966741	1.502043
1060	Exp7	1.933481	1.676699
1061	Exp7	1.611234	1.502043
1062	Exp7	1.611234	0.628762
1063	Exp7	1.772358	1.536974
1064	Exp7	0.966741	0.628762
1065	Exp7	0.966741	1.292456
1066	Exp7	1.127864	0.978075
1067	Exp7	1.611234	1.292456
1068	Exp7	0.644494	1.362318
1069	Exp7	1.127864	0.978075
1070	Exp7	1.611234	1.362318
1071	Exp7	1.288987	1.362318
1072	Exp7	1.288987	1.117799
1073	Exp7	1.611234	1.362318
1074	Exp7	2.094605	1.536974
1075	Exp7	1.450111	1.257524
1076	Exp7	1.611234	1.536974
1077	Exp7	1.611234	1.327387
1078	Exp7	1.127864	0.978075
1079	Exp7	1.127864	1.327387
1080	Exp7	1.450111	1.152731
1081	Exp7	1.127864	0.978075
1082	Exp7	1.611234	1.152731
1083	Exp7	1.772358	1.571905
1084	Exp7	1.127864	0.978075

1085	Exp7	1.611234	1.571905
1086	Exp7	1.450111	1.571905
1087	Exp7	1.450111	1.257524
1088	Exp7	1.288987	1.571905
1089	Exp7	0.966741	1.047937
1090	Exp7	1.933481	1.676699
1091	Exp7	1.450111	1.047937
1092	Exp7	0.966741	0.593831
1093	Exp7	1.611234	1.397249
1094	Exp7	1.127864	0.593831
1095	Exp7	0.805617	0.489037
1096	Exp7	1.450111	1.257524
1097	Exp7	0.966741	0.489037
1098	Exp7	1.450111	1.641768
1099	Exp7	1.127864	0.978075
1100	Exp7	2.094605	1.641768
1101	Exp7	1.611234	1.222593
1102	Exp7	1.450111	1.257524
1103	Exp7	1.127864	1.222593
1104	Exp7	0.805617	1.397249
1105	Exp7	1.288987	1.117799
1106	Exp7	1.288987	1.397249
1107	Exp7	1.288987	1.676699
1108	Exp7	1.127864	0.978075
1109	Exp7	2.094605	1.676699
1110	Exp7	1.127864	1.676699
1111	Exp7	2.094605	1.816424
1112	Exp7	2.255728	1.676699
1113	Exp7	0.644494	1.292456
1114	Exp7	1.288987	1.117799
1115	Exp7	1.450111	1.292456
1116	Exp7	0.805617	1.152731
1117	Exp7	0.966741	0.83835
1118	Exp7	1.288987	1.152731
1119	Exp7	0.805617	1.013006
1120	Exp7	1.288987	1.117799
1121	Exp7	1.450111	1.013006
1122	Exp7	1.127864	0.768487
1123	Exp7	1.611234	1.397249
1124	Exp7	1.127864	0.768487
1125	Exp7	0.644494	1.397249
1126	Exp7	1.127864	0.978075
1127	Exp7	1.450111	1.397249
1128	Exp7	1.288987	1.676699
1129	Exp7	1.127864	0.978075
1130	Exp7	1.772358	1.676699
1131	Exp7	1.450111	1.362318
1132	Exp7	1.127864	0.978075
1133	Exp7	1.450111	1.362318

1134	Exp7	0.805617	1.432181
1135	Exp7	1.288987	1.117799
1136	Exp7	1.772358	1.432181
1137	Exp7	1.288987	0.873281
1138	Exp7	1.288987	1.117799
1139	Exp7	0.966741	0.873281
1140	Exp7	1.127864	1.082868
1141	Exp7	0.966741	0.83835
1142	Exp7	1.611234	1.082868
1143	Exp7	1.127864	1.117799
1144	Exp7	1.772358	1.536974
1145	Exp7	1.288987	1.117799
1146	Exp7	0.966741	1.502043
1147	Exp7	1.288987	1.117799
1148	Exp7	1.611234	1.502043
1149	Exp7	0.644494	0.733556
1150	Exp7	1.288987	1.117799
1151	Exp7	1.127864	0.733556
1152	Exp7	0.644494	1.117799
1153	Exp7	1.127864	0.978075
1154	Exp7	1.450111	1.117799
1155	Exp7	0.644494	0.978075
1156	Exp7	1.127864	0.978075
1157	Exp7	1.288987	0.978075
1158	Exp7	1.933481	0.803418
1159	Exp7	1.450111	1.257524
1160	Exp7	1.288987	0.803418
1161	Exp7	1.933481	0.908212
1162	Exp7	2.094605	1.816424
1163	Exp7	1.127864	0.908212
1164	Exp7	0.966741	0.628762
1165	Exp7	1.611234	1.397249
1166	Exp7	1.127864	0.628762
1167	Exp7	1.772358	1.222593
1168	Exp7	1.288987	1.117799
1169	Exp7	1.288987	1.222593
1170	Exp7	0.966741	0.663693
1171	Exp7	2.094605	1.956149
1172	Exp7	1.127864	0.663693
1173	Exp7	0.805617	1.152731
1174	Exp7	1.772358	1.536974
1175	Exp7	1.611234	1.152731
1176	Exp7	2.094605	1.013006
1177	Exp7	2.094605	1.816424
1178	Exp7	1.450111	1.013006
1179	Exp7	1.772358	1.117799
1180	Exp7	1.127864	0.978075
1181	Exp7	1.450111	1.117799
1182	Exp7	1.288987	1.047937

1183	Exp7	1.288987	1.117799
1184	Exp7	1.611234	1.047937
1185	Exp7	1.288987	1.292456
1186	Exp7	1.288987	1.117799
1187	Exp7	1.450111	1.292456
1188	Exp7	0.805617	1.187662
1189	Exp7	0.805617	0.698625
1190	Exp7	1.288987	1.187662
1191	Exp7	0.966741	1.292456
1192	Exp7	1.611234	1.397249
1193	Exp7	1.611234	1.292456
1194	Exp7	0.805617	1.187662
1195	Exp7	0.966741	0.83835
1196	Exp7	1.450111	1.187662
1197	Exp7	1.127864	1.117799
1198	Exp7	1.288987	1.117799
1199	Exp7	1.127864	1.117799
1200	Exp7	1.288987	0.768487
1201	Exp7	1.288987	1.117799
1202	Exp7	1.127864	0.768487
1203	Exp7	1.127864	1.152731
1204	Exp7	1.450111	1.257524
1205	Exp7	1.450111	1.152731
1206	Exp7	0.805617	1.047937
1207	Exp7	1.933481	1.676699
1208	Exp7	1.288987	1.047937
1209	Exp7	1.450111	1.432181
1210	Exp7	1.288987	1.117799
1211	Exp7	1.288987	1.432181
1212	Exp7	1.450111	1.571905
1213	Exp7	1.127864	0.978075
1214	Exp7	1.933481	1.571905
1215	Exp7	0.805617	1.187662
1216	Exp7	1.288987	1.117799
1217	Exp7	1.611234	1.187662
1218	Exp7	0.966741	0.978075
1219	Exp7	1.611234	1.397249
1220	Exp7	1.288987	0.978075
1221	Exp7	0.966741	0.873281
1222	Exp7	1.450111	1.257524
1223	Exp7	1.288987	0.873281
1224	Exp7	1.288987	1.222593
1225	Exp7	1.127864	0.978075
1226	Exp7	1.450111	1.222593
1227	Exp7	1.288987	1.71163
1228	Exp7	1.288987	1.117799
1229	Exp7	1.288987	1.71163
1230	Exp7	1.288987	1.082868
1231	Exp7	1.127864	0.978075

1232	Exp7	1.288987	1.082868
1233	Exp7	1.288987	2.095874
1234	Exp7	1.127864	0.978075
1235	Exp7	1.450111	2.095874
1236	Exp7	1.450111	1.99108
1237	Exp7	1.772358	1.536974
1238	Exp7	1.611234	1.99108
1239	Exp7	1.127864	0.768487
1240	Exp7	1.127864	0.978075
1241	Exp7	1.127864	0.768487
1242	Exp7	0.966741	1.187662
1243	Exp7	0.966741	0.83835
1244	Exp7	1.611234	1.187662
1245	Exp7	0.805617	0.978075
1246	Exp7	1.450111	1.257524
1247	Exp7	1.450111	0.978075
1248	Exp7	0.805617	1.467112
1249	Exp7	1.450111	1.257524
1250	Exp7	1.933481	1.467112
1251	Exp7	1.127864	1.082868
1252	Exp7	1.450111	1.257524
1253	Exp7	1.288987	1.082868
1254	Exp7	0.644494	0.733556
1255	Exp7	1.611234	1.397249
1256	Exp7	0.805617	0.733556
1257	Exp7	1.450111	1.152731
1258	Exp7	1.772358	1.536974
1259	Exp7	1.127864	1.152731
1260	Exp7	1.450111	1.082868
1261	Exp7	1.127864	0.978075
1262	Exp7	1.288987	1.082868
1263	Exp7	1.127864	0.978075
1264	Exp7	1.127864	0.873281
1265	Exp7	1.127864	0.978075
1266	Exp7	1.288987	1.152731
1267	Exp7	1.127864	0.978075
1268	Exp7	1.611234	1.082868
1269	Exp7	1.288987	1.117799
1270	Exp7	1.450111	1.152731
1271	Exp7	1.288987	1.257524
1272	Exp7	1.450111	1.816424
1273	Exp7	1.127864	0.978075
1274	Exp7	1.772358	1.746562
1275	Exp7	1.127864	0.978075
1276	Exp7	1.127864	1.047937
1277	Exp7	1.288987	1.117799
1278	Exp7	1.450111	1.152731
1279	Exp7	0.966741	0.83835
1280	Exp7	1.127864	1.013006

1281	Exp7	1.127864	0.978075
1282	Exp7	2.255728	1.851355
1283	Exp7	1.450111	1.257524
1284	Exp7	1.611234	1.571905
1285	Exp7	1.611234	1.397249
1286	Exp7	1.288987	1.467112
1287	Exp7	1.127864	0.978075
1288	Exp7	1.611234	1.397249
1289	Exp7	0.966741	0.83835
1290	Exp7	1.611234	1.013006
1291	Exp7	1.288987	1.117799
1292	Exp7	0.966741	0.454106
1293	Exp7	0.966741	0.83835
1294	Exp7	1.933481	2.060943
1295	Exp7	1.288987	1.117799
1296	Exp7	1.288987	1.362318
1297	Exp7	0.966741	0.83835
1298	Exp7	1.288987	1.432181
1299	Exp7	1.127864	0.978075
1300	Exp7	1.933481	1.921218
1301	Exp7	0.805617	0.698625
1302	Exp7	1.772358	1.397249
1303	Exp7	0.966741	0.83835
1304	Exp7	0.966741	0.978075
1305	Exp7	1.450111	1.257524
1306	Exp7	1.127864	0.908212
1307	Exp7	0.966741	0.83835
1308	Exp7	1.772358	1.432181
1309	Exp7	0.805617	0.698625
1310	Exp7	1.288987	1.187662
1311	Exp7	0.966741	0.978075
1312	Exp7	0.805617	0.908212
1313	Exp7	1.611234	1.397249
1314	Exp7	1.288987	1.362318
1315	Exp7	1.288987	1.117799
1316	Exp7	1.450111	1.047937
1317	Exp7	1.450111	1.257524
1318	Exp7	1.288987	1.222593
1319	Exp7	0.966741	0.83835
1320	Exp7	1.933481	1.571905
1321	Exp7	1.611234	1.397249
1322	Exp7	0.805617	0.628762
1323	Exp7	1.127864	0.978075
1324	Exp7	1.611234	1.222593
1325	Exp7	1.611234	1.397249
1326	Exp7	1.611234	1.292456
1327	Exp7	1.933481	1.676699
1328	Exp7	1.611234	1.502043
1329	Exp7	1.288987	1.117799

1330	Exp7	0.161123	1.292456
1331	Exp7	0.805617	0.698625
1332	Exp7	1.933481	1.362318
1333	Exp7	1.933481	1.676699
1334	Exp7	1.611234	0.943143
1335	Exp7	1.288987	1.117799
1336	Exp7	1.127864	0.978075
1337	Exp7	0.805617	0.698625
1338	Exp7	0.966741	0.83835
1339	Exp7	1.127864	0.978075
1340	Exp7	1.450111	1.257524
1341	Exp7	1.450111	1.257524
1342	Exp7	1.933481	1.676699
1343	Exp7	1.611234	1.397249
1344	Exp7	1.288987	1.257524
1345	Exp7	1.933481	1.816424
1346	Exp7	0.966741	0.83835
1347	Exp7	1.127864	0.978075

Supplement 2: related to Fig. 6

Data for each experiment (Experiments 1, 5, 6, 7),
data shows number of waggles for each experiment.

	Exp 1 all sessions	Exp 5_all nwaggles	Exp 6 all nwaggles	Exp 7 all nwaggles
1	4	6	4	8
2	3	2	6	8
3	4	6	4	5
4	4	4	3	7
5	5	5	5	5
6	4	2	5	7
7	3	3	3	7
8	3	7	5	8
9	3	4	4	6
10	3	3	5	11
11	3	2	4	9
12	4	4	4	8
13	4	6	3	6
14	2	5	5	7
15	6	5	3	5
16	5	5	3	7
17	4	5	5	10
18	3	5	3	6
19	4	5	3	10
20	2	6	3	10
21	5	2	4	10
22	6	6	5	10
23	5	2	4	7
24	4	2	4	10
25	4	2	4	10
26	4	4	4	8
27	2	4	6	9
28	3	4	4	7
29	5	6	6	6
30	5	4	4	13
31	5	5	3	7
32	3	3	3	8
33	4	6	4	13
34	4	2	3	14
35	2	1	4	9
36	4	6	3	8
37	4	4	4	9
38	3	3	3	7
39	4	6	4	9
40	5	6	6	11
41	5	6	5	9
42	4	6	4	11
43	5	3	4	6
44	4	5	3	10
45	4	5	4	8
46	4	6	3	10
47	2	6	4	7
48	2	5	6	9
49	3	5	3	8
50	7	6	3	8
51	5	6	4	7
52	4	5	3	7
53	6	4	3	8
54	4	4	5	7
55	2	6	3	10

56	5	5	4	9
57	4	5	3	9
58	5	5	4	10
59	4	5	8	9
60	3	6	4	8
61	4	5	3	10
62	3	5	4	9
63	4	2	5	7
64	4	5	4	7
65	5	5	5	9
66	3	4	3	8
67	5	3	4	8
68	4	4	4	12
69	3	5	5	10
70	4	5	4	8
71	6	3	6	8
72	5	3	6	9
73	6	3	4	8
74	5	3	5	8
75	5	3	4	9
76	6	3	4	10
77	3	5	5	7
78	5	6	4	10
79	3	2	3	9
80	5	7	3	12
81	3	7	3	8
82	4	6	4	5
83	5	5	5	7
84	5	2	4	8
85	4	6	3	5
86	4	5	5	5
87	3	5	6	5
88	3	5	6	8
89	3	5	4	9
90	4	7	4	5
91	5	4	3	4
92	6	5	5	5
93	4	4	4	6
94	4	4	3	5
95	3	6	4	4
96	4	7	6	7
97	6	6	3	5
98	4	7	6	8
99	4	6	5	5
100	4	7	5	8
101	3	7	4	7
102	3	5	3	5
103	3	8	4	4
104	3	5	6	4
105	4	6	6	8
106	3	4	5	6
107	3	2	4	6
108	5	5	9	8
109	8	5	5	8
110	5	7	5	8
111	3	5	3	4

112	4	4	5	7
113	6	6	4	8
114	6	7	4	5
115	5	5	4	7
116	3	4	5	7
117	4	6	4	5
118	4	5	4	4
119	4	5	4	11
120	4	6	4	6
121	4	4	3	6
122	4	6	4	6
123	6	1	3	10
124	4	9	3	5
125	5	6	4	4
126	4	5	3	7
127	4	5	3	8
128	3	4	6	10
129	3	5	5	8
130	3	2	3	4
131	3	8	5	6
132	3	4	3	6
133	3	5	4	8
134	5	5	4	7
135	3	5	3	6
136	3	5	4	4
137	6	4	5	5
138	4	4	3	7
139	4	5	6	5
140	3	6	4	5
141	3	4	3	10
142	3	6	4	7
143	4	6	4	5
144	3	5	4	4
145	3	5	3	7
146	4	5	3	4
147	3	6	5	6
148	4	7	4	7
149	3	6	4	8
150	3	9	3	6
151	4	7	4	4
152	3	6	3	6
153	3	7	3	5
154	3	7	4	7
155	4	3	3	5
156	4	4	3	11
157	5	4	8	6
158	4	4	3	6
159	3	8	6	6
160	3	8	5	8
161	3	4	4	6
162	5	6	4	4
163	5	6	3	9
164	5	6	4	9
165	4	6	3	5
166	4	7	4	5
167	4	6	5	4

168	4	6	4	8
169	4	5	4	10
170	4	6	4	6
171	3	8	3	4
172	4	8	4	4
173	3	6	5	10
174	4	5	3	4
175	4	6	3	7
176	3	5	3	6
177	4	7	4	4
178	5	6	3	11
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Supplement 3: related to Fig. 6

Data for each experiment (Experiments 1, 5, 6, 7), data shows number of waggles for
each experiment, separated for individual sessions.

	Exp 1_session 1	Exp 1_session 2	Exp 1_session 3	Exp 5_session 1	Exp 5 session 2	Exp 5 session 3	Exp 5 session 4	Exp 6_session 1	Exp 6_session 2	Exp 6_session 3	Exp 6_session 4	Exp 6_session 5	Exp 7 session 1	Exp 7 session 2	Exp 7 session 3	Exp 7 session 4
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Table S1.

Available for download at
https://journals.biologists.com/jeb/article-lookup/doi/10.1242/jeb.248162#supplementary-data

Table S2.

Available for download at
https://journals.biologists.com/jeb/article-lookup/doi/10.1242/jeb.248162#supplementary-data

Table S3.

Available for download at
https://journals.biologists.com/jeb/article-lookup/doi/10.1242/jeb.248162#supplementary-data