

## Can honey bees count landmarks?

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**Abstract.** Honey bees, *Apis mellifera*, were trained along a row of four identical landmarks (tetrahedral tents 3.46 m high) which were equally spaced in a set-up 300 m long, the feeder being placed between the third and fourth landmarks. In the tests, the number of tents between hive and feeder was altered. Even though many bees continued to search for food at the correct distance, the distance estimation of the bees as a group depended notably on the number of landmarks. If they encountered more landmarks on their way from the hive to the feeder than they had during training, significantly more bees landed at a shorter distance than during control tests with the training landmark set-up. If they encountered fewer landmarks, they flew significantly further. This behaviour meets the basic criteria in most definitions of true counting. Since, however, a transfer of the counting performance on different objects is unlikely to occur, the observed behaviour should be referred to as protocounting (Davis & Pérusse 1988, *Behav. Brain Sci.*, **114**, 561–615). Landmark (proto-) counting is considered here a special application of a sequential memory for landmarks.

How do bees measure the distance to a goal? It has been proposed that bees estimate distance by evaluating their energy investment during flight (Heran 1956; von Frisch 1967). This view has been recently challenged by Esch et al. (1994), and it is clear that such a system of distance estimation can be insufficient, because flying animals are subject to the influences of wind. An animal as light as a bee has only very little motion inertia and is thus susceptible to changes in wind velocity.

Bees will fly at wind speeds that equal their own flight speed under calm conditions (30 km/h; von Frisch & Lindauer 1955; Heran 1956; von Frisch 1967). Without reference to the environment, they might end up hovering in a fixed position in the air if winds of such velocity come from the front. However, bees compensate partially for head wind by raising their energy investment (i.e. they increase their own relative speed). In tail winds, their relative speed is diminished (Heran 1955, 1956). These corrections are not possible by measuring energy investment alone. Flying animals have no means to estimate the wind speed without reference marks in the environment. To judge distance correctly, they have to compare their energy investment with a measure of apparent

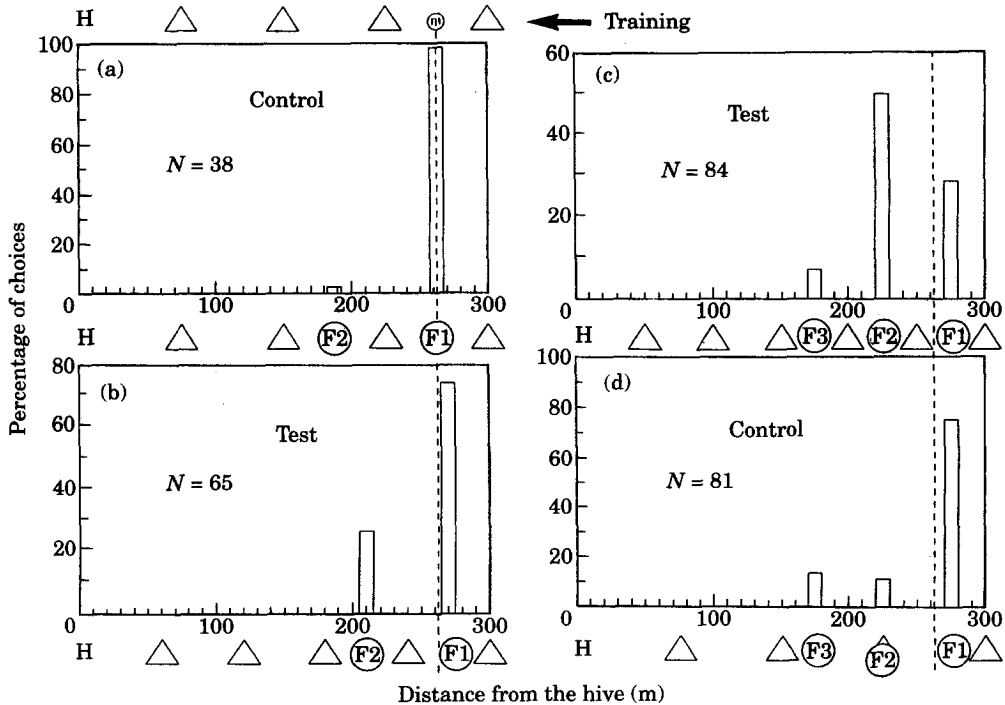
image motion (Heran & Lindauer 1963; Kirchner & Srinivasan 1989; Srinivasan et al. 1991) and/or refer to motion parallax cues (Srinivasan et al. 1990). They may also memorize specific landmarks together with a vector encoding the distance and direction from the hive (Cartwright & Collett 1987) and use these memories to update their estimation of distance during flight from time to time (Collett 1992).

Here we show that a sequence of identical landmarks is used by bees to estimate the distance to a goal. If the number of landmarks that they pass between hive and food source is altered relative to the training situation, significant numbers of the bees land at locations that differ markedly from the trained distance.

## METHODS

Our experiments were set in a large level meadow (2 km<sup>2</sup>) practically devoid of natural orientation cues (near Wittenberge, Brandenburg, Germany). A hive was set up in the centre of this meadow. Honey bee, *Apis mellifera*, workers were trained to collect sucrose solution at a site 262.5 m from the hive. Between 20 and 30 bees were continuously flying back and forth between the hive and the feeder.

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**Figure 1.** The training set-up is shown above (a). The positions of the landmarks (tents) are marked by triangles, the test feeders are indicated by circles. H indicates the hive site. The dashed line marks the distance of the training feeder (262.5 m) from the hive. (a) The control test with the unchanged number of landmarks. (b) The test in which the number of landmarks was increased to five. (c) The test in which the number of landmarks was raised to six. (d) Control test for (c) with the original (training) landmark set-up, but the test feeder positions as in (c). F2 was placed directly in front of the third tent.

The flight path was marked by a line of four yellow tents of tetrahedral shape (height 3.46 m). They stood at distances of 75, 150, 225 and 300 m from the hive (Fig. 1). The feeding site was thus halfway between the third and the fourth landmarks.

The distances between tents were chosen so that the arrangement of landmarks could not be judged as a compound, but, instead, was experienced as a sequence. Hence, the spatial resolution of the bee's eye should set a limit as to how many landmarks can be seen at a time.

The first tent (at 75 m) appeared under a visual angle of  $\alpha_{75} = 2.64^\circ$  as seen from the hive. The respective angles for the other tents were:  $\alpha_{150} = 1.32^\circ$ ;  $\alpha_{225} = 0.88^\circ$ ;  $\alpha_{300} = 0.66^\circ$ .

The visual acuity of honey bees is approximately  $2.5^\circ$  (e.g. Eheim & Wehner 1972). It is unlikely that a bee can extract information about the spatial arrangement of objects that merely

reduce the effective light flux in single photoreceptors to different degrees. Thus, we assume that bees, from the hive or any of the landmarks, can detect only the next (or previous) landmark, but have no access to information about the spatial relationship of further landmarks.

Before the arrangement of landmarks was changed, we performed a control experiment to test how precisely the bees had learned the trained distance of the food source. Bees were simply tested in the original landmark set-up. One test feeder was placed at the training distance (262.5 m from the hive) between the third and the fourth tent and another midway between the second and the third at 187.5 m from the hive.

In the training situation, the bees had passed three tents on their way from the home site to the feeder, while the fourth tent was 37.5 m beyond the food site. To test whether bees were able to use the set-up of landmarks that they had passed

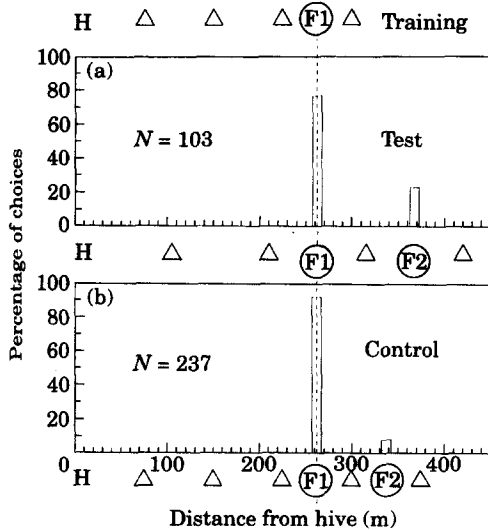


Figure 2. The experiment in which the number of landmarks per unit distance was reduced relative to the training situation. The training situation was the same as in Fig. 1. (a) The test with four landmarks, two before and two after the trained distance of 262.5 m. (b) Control test. Original training set-up, plus an additional landmark at 375 m. Test feeders were at 262.5 m (training distance) and 337.5 m (midway between landmarks 4 and 5).

during flight to estimate how far they had travelled, we systematically changed the number of landmarks between hive and food source. In this way, we produced a contradiction between the distance at which the bees had been rewarded (262.5 m) and the distance indicated by the arrangement of landmarks. Our question was whether bees would continue to fly the distance they had experienced during training, or whether the altered number of landmarks might guide them to choose a compromise between the trained distance and the trained landmark number.

During training, the distance between every two tents measured 75 m, such that the last tent was placed 300 m from the hive. In the following tests, we increased the number of landmarks in this set-up from four to either five (distance between tents: 60 m) or six (distance between tents: 50 m). In the first case (five landmarks; Fig. 1b), we placed one test feeder midway between the third and fourth tents (distance from hive: 210 m) and the second between the fourth and the fifth tents (distance from hive: 270 m). In the second case (six landmarks; Fig. 1c), we performed triple

choice tests. Three test feeders were set up between the third and the fourth, the fourth and the fifth, and the fifth and the sixth tents. These test feeders thus stood at distances of 175, 225 and 275 m from the hive. A control experiment with the landmark configuration of the training situation and the feeders placed as in the experiment with six landmarks was also performed (Fig. 1d; see Results).

Next, we proceeded to extend the landmark set-up, that is, the number of landmarks encountered between the hive and the training distance was reduced. The tents were placed at 105, 210, 315 and 420 m from the hive (Fig. 2a). Thus, the distance between the landmarks was raised from 75 to 105 m. One test feeder was halfway between the second and third tents, that is, at the original training distance of 262.5 m. The alternative test feeder was positioned midway between the third and fourth tents (367.5 m from the hive), thus marking the position at which bees should land if they preferred the correct number of landmarks over the correct distance. We then performed a control experiment with the original training set-up and an additional fifth tent at 375 m, so that all distances between tents measured 75 m. The first test feeder was placed at 262.5 m (training distance) and the second midway between the last two tents at 337.5 m (Fig. 2b).

The distances in the set-up were measured with a theodolite in combination with an infrared laser telemeter (Distomat Di4, Theodolith T1, Wild company, Heerbrugg, Switzerland).

All tests were prepared by blowing all bees off the feeder and closing the hive entrance. Hence, while the landmarks were being altered, no bees could leave the hive, and all bees that had been removed from the feeder would gather in front of the hive entrance. Displacing the landmarks took about 10–15 min.

Afterwards, the hive entrance was opened again, and the choice behaviour of the bees searching for a feeder was recorded. A choice was counted only when a test animal actually landed on one of the test feeders. Bees were captured on arrival and kept in a box until the end of the test. We chose this procedure for two reasons. (1) The bees should not learn anything during the tests. This means they should not be rewarded at a place that differed from the training site. They should also not be rewarded at the training site when it was not surrounded by the original landmark

setting. (2) Individual bees should not be allowed to make multiple choices at the feeders.

Experiments were stopped when no further bees arrived at the test feeders (usually after about 30 min). After each test, the original set-up of landmarks was restored. Before the next test, bees were allowed to collect sucrose solution and fly regularly back and forth between hive and feeder for about 45 min.

Chi-squared goodness-of-fit tests were used to evaluate the data.

## RESULTS

In the control test with an unchanged arrangement of landmarks only one out of 38 bees chose the closer feeder; all others landed at the trained distance (Fig. 1a). Thus, the bees did not tend simply to land at the first feeder that occurs on their way from the hive.

When the number of landmarks was increased to five (Fig. 1b), the majority of bees (74%;  $N=48$  out of 65) still landed at the position closest to the training feeder (270 m), but 26% ( $N=17$  of 65) also landed at the position between the third and fourth tents (210 m). This distribution is significantly different from the control test with the unchanged number of landmarks ( $\chi^2=9.2$ ,  $df=1$ ,  $P<0.0025$ ).

With six landmarks (Fig. 1c), the majority of bees (58%;  $N=49$  of 84) chose the test feeder between the fourth and fifth tents at a distance of 225 m. The feeder closest to the training site (262.5 m) stood at 275 m between the fifth and the sixth tents and was ranked second (33%;  $N=28$  of 84). The few remaining bees (8%;  $N=7$  of 84) landed at the test feeder between the third and the fourth tents. Thus, most bees chose a compromise between the goal distance during training and the number of landmarks that they had experienced during the training situation.

To test whether this distribution was caused by the fact that the feeder F1 stood 12.5 m behind the training food site, we performed the control experiment with the unchanged landmark configuration of the training situation, that is, with four tents and the test feeders at the same positions as in the test with six landmarks (175, 225, 275 m; Fig. 1d). Under these circumstances, 75% ( $N=61$  of 81) of the bees landed at 275 m (at 225 m:  $N=9$  of 81; 175 m:  $N=11$  of 81). These

choice values are significantly different from those in the experiment carried out with six tents ( $\chi^2=40.6$ ,  $df=2$ ,  $P<0.001$ ). Hence, the bees were generally not disturbed by a feeder 12.5 m behind the training position. They were also not disturbed by the fact that the feeder was not placed centrally between the two neighbouring tents.

When the distances between landmarks were extended from 75 m to 105 m, such that only two landmarks were passed between the hive and the learned distance of 262.5 m, only 78% ( $N=80$  of 103) of the bees landed at the correct distance; 22% ( $N=23$  of 103) chose to fly more than 100 m further and landed at a distance of 367.5 m, thereby passing the correct number of three tents (Fig. 2a). In the control experiment, only 8% ( $N=18$  of 237) of the bees chose to fly beyond the fourth tent and land at 337.5 m, whereas 92% ( $N=219$  of 237) alighted at the training position (Fig. 2b). Thus, even though the second test feeder in the control test (F2 in Fig. 2b) was 30 m closer to the hive than the second feeder in the experiment with extended distances between landmarks (F2 in Fig. 2a), a significantly lower proportion of bees arrived at F2 in the control test ( $\chi^2=14.7$ ,  $df=1$ ,  $P<0.001$ ).

In essence, these results indicate that an increased number of landmarks between hive and food source relative to the training situation causes the bees (as a group) to estimate a flight distance that is shorter than the one indicated by energy investment. The reverse is true if the number of landmarks is reduced relative to the situation experienced during training.

## DISCUSSION

In the Introduction, we pointed out that it is necessary for bees to integrate landmarks into their estimation of the distance to a goal. We have shown here that bees indeed use familiar landmarks to update their distance estimation. In all tests, however, a large percentage of the bees continued to search for food at the training distance. These bees must have relied on an internal measure of distance (such as energy investment, flight time) and/or some other external cues (such as the apparent optic flow of the landscape) more heavily than on the movable landmarks.

On the other hand, the distance estimation of the bees as a group depended notably on the array of landmarks. What could have been the strategy employed by those bees that were deviated from the training site by the altered sets of landmarks?

One conjecture is that these bees learn to land after a landmark that occurs at 225 m (the third tent) independently of how many landmarks they have passed before this particular landmark. In the tests, these bees might have chosen some kind of compromise that best matches the situation they have memorized. There are three hypotheses for the bees' behaviour in a test in which there is no landmark at 225 m. (1) The bees land after the landmark nearest to 225 m. (2) The bees land after the first landmark encountered after 225 m. (3) They choose a site after the closest landmark before 225 m.

Hypotheses 1 and 3 may be rejected on account of the test with an extended set of landmarks (Fig. 2), because they cannot explain why more bees should be deviated to 100 m behind the training site than in the control test. Hypothesis 2 might explain the data. Can it explain the results in the other two tests?

In the test with six landmarks (Fig. 1c) there were tents at 200 and 250 m (i.e. equal distance from 225 m). The majority of the bees landed after the tent at 200 m in this test; this hints that hypothesis 2 is not valid here. Hypothesis 1 can be excluded because one would expect equal choice values after both the tents at 200 and 250 m. Hypothesis 3 could be valid here.

Hypothesis 3 might also explain the data in the test with five landmarks (Fig. 1b), where the bees had a choice between landing after a tent at 180 and at 240 m, and more than in the control test chose the former. However, hypotheses 1 and 2 do not hold here either.

Thus, none of these hypotheses holds true in all three tests. The only remaining possibility is thus that those bees that did not land at the training distance in the tests must have had a representation of the number of landmarks to be passed between hive and food source. Does this mean that bees can count? To establish counting, one must exclude other number-related processes, such as 'relative numerosness judgments' and 'subitizing' (Piaget 1952; Gelman & Gallistel 1978; Davis & Memmott 1982; Davis & Pérusse 1988). Relative numerosness judgments are broad relative judgments of inequality, such as many versus

few. Inherent to such judgments is the relatively poor precision. Our results, however, show significant differences in the behaviour of the bees (as a group) when the number of landmarks was increased or decreased by one. Subitizing is a rapid assessment of simultaneously presented items. It can be precluded in the present context because of the sequential nature of the training and test set-ups.

In the sense of Davis & Memmott (1982), the observed behaviour of the bees fulfils the criteria of counting. However, Gelman & Gallistel (1978) and Davis & Pérusse (1988) incorporated another requirement into their definition of true counting, the 'abstraction principle'. This principle purports that after having learned to perform a given behavioural unit assigned to a certain number of objects counted, the subject should be able to transfer this knowledge onto a set of objects of a different quality.

Obviously, we have not tested whether the bees are capable of such a transfer, but we consider it as unlikely to occur. According to Davis & Pérusse (1988), if the basic criteria listed above are fulfilled, but a transfer of the counting performance has not been shown, the respective animal's behaviour should be referred to as 'protocounting'.

Cooper (1984) and Davis & Bradford (1986) argued that 'numerical learning may be a special case of spatial learning'. There might be a relationship between the observed protocounting behaviour and a special kind of insect navigation: the application of a serial memory for landmarks (Collett 1992, 1993). During natural foraging bouts, insects often visit a sequence of plants in fixed stable order (e.g. Heinrich 1976). Bees memorize a given mark along a flight trajectory together with the information about the next target to be expected (Collett & Kelber 1988; Collett et al. 1993).

If bees can store information of the sort: B follows A, C follows B, and after C follows the feeder, then one might expect that the variables in this memory can also be filled with identical contents, i.e. A follows A, then follows A again, and then one should land. Operating a serial memory on items that differ in quality is obviously not counting. However, the landmarks in our experiments cannot be distinguished without using their ordinal position, simply because they are exactly alike.

So, we suggest that the observed behaviour of the bees is an instance of protocounting, but not in the sense of some abstract cognitive capacity without biological significance. Instead, the bees might use a kind of memory that is applied during normal foraging, that is, a memory of the sequence of landmarks to be passed.

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