

## COGNITIVE MAPPING IN THE HONEYBEE?

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### Abstract

Psychologists and neuroscientists have shown considerable interest in honeybees in recent years due to the claims for high level cognitive ability, in particular the suggestion that honeybees employ the use of a 'cognitive map' of their environment (GOULD 1990). The ideas behind cognitive mapping will be briefly reviewed and an experiment described which substitutes a barren field for GOULD's lake on the grounds that the lake is an unfeasible location for forage. In direct contrast to the results of the lake experiment, the mean number of recruits was significantly greater in the barren area than in a control area of abundant forage. This result might be expected on an optimal foraging model, although the existence of cognitive maps and insight in the honeybee remains open.

The navigation abilities of *Apis mellifera* are the most complex known among invertebrates and possibly vertebrates, excepting humans. Although it is certainly true that honey bees are able to navigate by reference to familiar landmarks, two opposing models may be used to explain the spatial representation in memory underlying this ability. The first proposal suggests that honey bees store memories for landmarks in a series of route specific 'snapshots' which are useful in a serial order for navigating along a familiar route<sup>[1]</sup>. Honeybees judge the degree of similarity or discrepancy between the current image and a 'snapshot' stored in memory from a previous trip, in order to generate a directional signal that sends the bee closer to the goal<sup>[2,3]</sup>. This matching of images can be performed no matter how the bee enters the array, for example, via novel routes<sup>[3]</sup>. The metric relations in the surrounding terrain cannot be recovered from records of this kind, because in a route specific map only colinearity information about selected sets of points is preserved, and not metric relations about distance and angles<sup>[4]</sup>. It preserves the fact, for example, that the hive falls on the straight line defined by a pair of snapshots, or more accurately, at the intersection of two such lines.

This creates a sharp dichotomy between vertebrates and invertebrates, because there is extensive evidence that vertebrates use landmarks in navigation very differently, as part of a mental map<sup>[5]</sup>. A 'cognitive map', a term coined originally by TOLMAN<sup>[6]</sup>, is the mental analogue of a topographic map, that is, a mental record encoding the relative metric positions among points, lines and surfaces in the environment which preserves all the geometric relations among the mapped entities. In operational terms, this means that an animal using such a map must be able to compute the shortest distance between two charted points without ever having travelled along that route. More generally, it must be able to determine its position, say, relative to home, or any other charted point, even when it has been displaced unexpectedly to an arbitrary place within its environment<sup>[7]</sup>. It is the remembered position of an animal's goal on their mental map that enables them to navigate towards it, rather than the current perception of goal characteristics. Some researchers, however, have argued that this invertebrate-vertebrate dichotomy does not exist, because there is evidence that invertebrates such as forager honey bees, *Apis mellifera*, can construct and store cognitive maps of their environment<sup>[8]</sup>. This view does not deny that honey bees may use a snapshot strategy under some circumstances, but is claiming that a map like strategy is available under other circumstances. Essentially, the most important evidence comes from experiments which examine the ability of bees to fly a novel route which they have never travelled before. The most recent experiments involving the displacement of trained foragers captured at one feeding site and released at another do not support the strong version of cognitive mapping ability<sup>[9]</sup>.

The full sophistication of the proposed cognitive mapping abilities of honey bees was suggested in a series of 'lake experiments'<sup>[8,9]</sup>. In the first case, bees were trained along a lake shore<sup>[11]</sup>, and the redirection technique<sup>[12]</sup> was used to manipulate the dances of the trained bees to indicate a spot in the middle of the lake. Recruits refused to explore the indicated location in the middle of the lake, although, if redirection was set to zero, large numbers arrived at the shore station.

In a modified version of the above experiment, GOULD and GOULD<sup>[10]</sup> trained one group of foragers to a feeder on a boat in the middle of a lake and another group of foragers to a feeder at the same distance from the hive, but on the shore of the lake. When the concentration of the sugar solution was increased, both groups of foragers returned to the hive and danced, but recruits arrived almost exclusively at the shore station. As a control, the experiment was repeated after the hive had been moved overnight to a different terrain, to a field with a forest/field boundary that had similar dimensions and orientation as the land/lake boundary in the experiment on the previous day. Feeders were positioned in the field in boats in the same locations relative to the hive with reference to the boundaries. When the concentration of the sugar solution was increased, fewer recruits went to the feeder that mirrored the lake station than the one that mirrored the shore station, despite equally intense dancing in both groups.

GOULD and GOULD (1988) tentatively suggest that this implies that bees use a cognitive map, in evaluating the message contained in the dance of the returning forager. "Instead of simply taking that dance as a set of flying instructions, they take it as the specification of a point on a terrain map that the foragers share. When the point specified is not in terrain where forage could be found, the message is ignored." Two major conclusions, can be drawn from the lake experiment. The first is that bees are able to place the location indicated by a dance on a cognitive map. The second is that bees have some sort of insight which allows them to make an informed decision about the feasibility of the communicated source of forage. They may or may not then use their map based knowledge to navigate to the food.

The current experiment is a modified version of Gould's lake experiments, but without the inherent problems of training bees to forage across water. It aims to assess whether honey bees are able to use a cognitive map to identify a location indicated by a waggle dance, and whether bees are able to assess the indicated location and decide that it is an unfeasible area for forage. Bees are trained to a feeder under two conditions. In the experimental condition bees are trained to the middle of an entirely blank field, ploughed and sown with a rye grass mono-culture. Just as in the lake experiment, bees that are familiar with the local terrain would 'know' this to be an unfeasible area for forage, since in their lifetime the ground bore no forage. However, unlike an area of water, potential recruits would be unlikely to be put off by adverse odours and would not get lost or drown on their way to investigate the advertised food location. In the control condition bees are trained to a feeder in a similar field but full of natural forage. The hive is positioned on the boundary between a blank area and an area rich in natural forage.

### Training Procedures

A series of transects was taken to assess the forage available to honey bees in the terrain surrounding the hive. Atmospheric pressure, humidity, temperature, percentage of cloud cover and wind speed were recorded.

Bees were trained into the barren area of no forage, sown with a rye grass mono-culture. The training procedure was based on techniques devised by von FRISCH<sup>[13]</sup> and extended by GOULD and GOULD (1988). A few drops of concentrated sugar solution (2M) were placed on the flight board using a pipette. The sugar solution was scented with clove essential oil, by adding one drop per litre. More drops were placed a few centimetres from the first, and then gradually further along a plank extending horizontally from the flight board. The plank was painted with a white line down the centre to guide the bees.

At about 10 centimetres from the flight board the feeder was introduced onto the plank. The feeder was a petri dish (diameter 8 cm and depth 1.5 cm), surrounded by bright yellow card, known to be a visual aid used by bees in locating a food source. It was necessary to ensure that the feeding dish was full at all times in order to minimise any concentration effects which could arise due to evaporation of the solution.

The feeding dish was gradually moved to the end of the 60 centimetre plank, then placed onto a tripod at the same height. When it was established that bees had adapted to this transition, bees visiting the feeder on the tripod were marked with a coloured spot on the thorax using a commercially available queen bee marker.

When the marked forager force reached 30 the sugar solution was changed to a more dilute version (approximately 0.375 M) with just a tiny amount of scent so that no more bees were recruited<sup>[13]</sup>. For a smooth transition between the different concentration dishes, bees were forced to leave the food site using a smoker. When the bees had started feeding again, the tripod was gradually moved further from the hive, about 25% further at each stage. The tripod was never left more than 20 minutes in any one spot, to avoid bees becoming 'stuck' at a certain distance (GOULD and GOULD, 1988). When foragers were visiting the required feeding station, 80 metres from the hive, more of the concentrated, scented solution was placed in the feeder so that bees would perform waggle dances back at the hive. An observer checked that these dances were indeed performed by the marked bees.

A video camera was positioned directly above the final feeding station, so that all activity at the station could be recorded, from the moment the concentrated solution was given to the trained bees for a period of 75 minutes. Each unmarked recruit arriving at the feeding station was marked with a different colour than the original trained bees. At the same time, back at the hive, for a one minute period in every five minute interval, the wooden boards were removed from the side of the hive and the number of marked bees observed dancing on the comb was noted. The wooden boards were replaced for the four minute interval between observations.

Exactly the same procedures were repeated in almost identical weather conditions for the control site in the area of natural forage directly behind the hive. Numbers of new recruits, recruit bee and trained bee visits to the feeder per minute were counted from the video recordings.

### Results

In direct contrast to the GOULDS' (1988) lake experiment, honey bee recruitment was found to be very successful in an unfeasible barren area of no forage. Many more bees were recruited in the experimental condition than in the control area of abundant forage (86 and 39 bees respectively).

Trained bees visited the feeder more in the barren area than the control area (335 and 187 respectively), despite the fact that 30 bees were trained in each condition. Recruits were more keen to continue visiting the feeder in the experimental condition, with a mean of 4.58 visits per bee in the barren area and 3.72 times in the area of normal forage, such that the number of recruit visits overtook the number of trained bee visits in the experimental condition after 57 minutes. The total number of visits to the feeder in the barren field was more than twice that of the field of forage (729 and 332 respectively). The time course of arrival of both recruits and trained bees in experimental and control conditions is shown in Figures 1 and 2.

Table 1

Total Number of Visits to the Feeding Station		
	Experimental Condition	Control Condition
New Recruits	86	39
Recruit Bee Visits	394	145
Trained Bee Visits	335	187
Total Visits	729	332

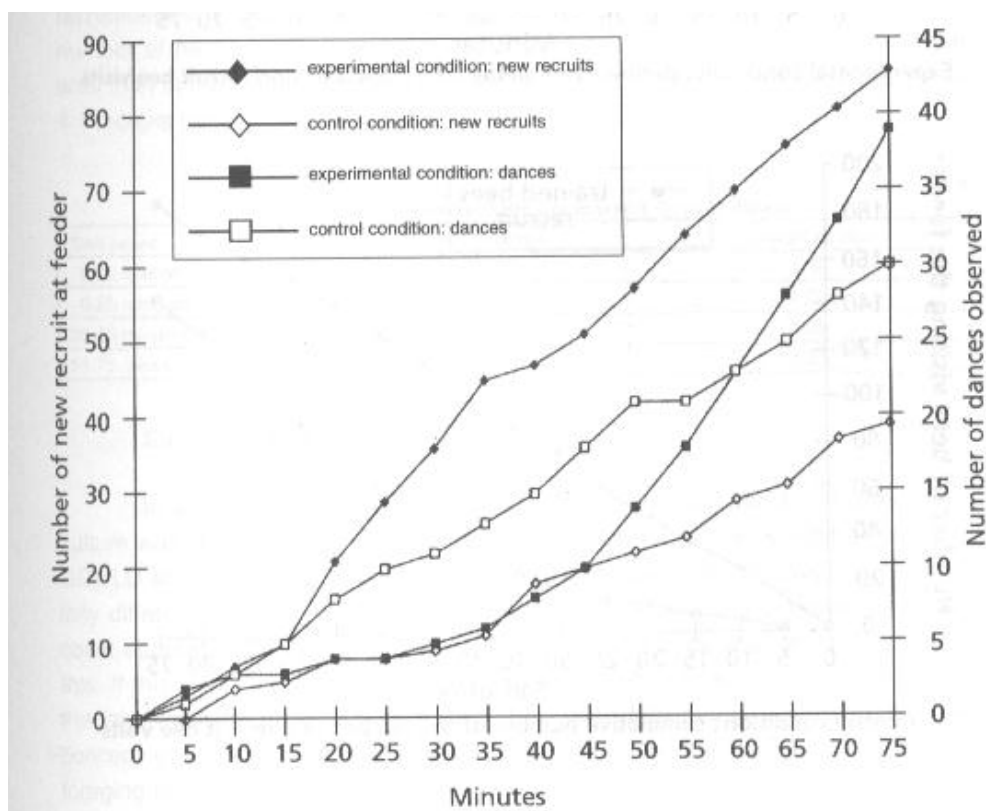


Figure 1 - Cumulative number of new recruits arriving at the feeder and number of dances observed in the hive

These results cannot be explained by suggesting that other environmental factors affected the results, because the weather conditions and location were identical for both conditions. They cannot be explained either by the suggestion that greater numbers of recruits in the experimental condition were due to more trained bees continuing to visit the feeder, because, despite this, more dances were in fact observed in the control condition during the first hour of the experiment.

The number of dances observed is only a guide to the actual number of marked bee dances, since for four minutes out of every five dancing was not observed. It was decided, however, that this would be a more accurate guide to natural dancing in the hive than would result from continual observation of the combs, because such continual exposure to light significantly affects honey bee dances<sup>[13]</sup>.

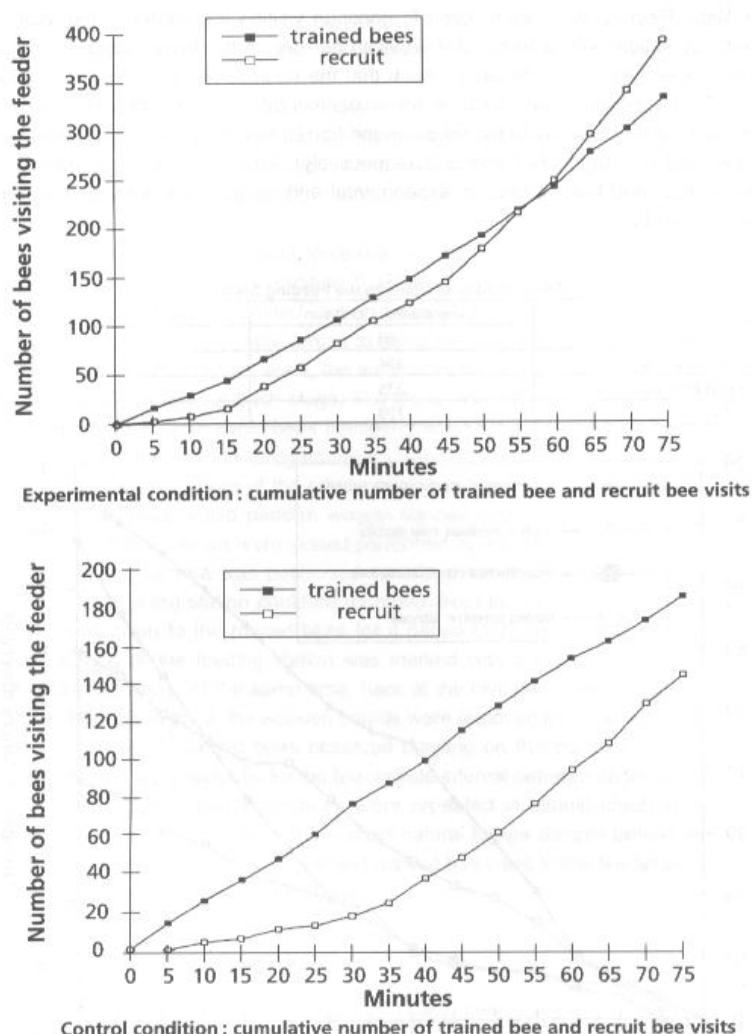


Figure 2 – Comparison between the number of recruit bee visits and trained bee visits

Pilot studies showed that dancing was severely diminished after the sides had been removed for more than about 10 minutes. It must be emphasised that recruitment is improved in the barren area, not just activity in general. The mean number of new recruits per dance (see table II) was much greater in the barren area than in the control area of abundant forage (mean 4.23 recruits per dance and 1.1 recruits per dance respectively).

Table II

Mean number of new recruits per marked forager dance

Time period	Experimental Condition	Control Condition
0-75 minutes	4.23	1.10
0-25 minutes	3.93	1.03
26-50 minutes	5.95	1.00
51-75 minutes	2.79	1.25

### Summary and Conclusions

In the present study, the entirely blank area sown with a rye grass mono-culture was chosen as a highly 'unfeasible' location for forage, similar to the lake in GOULD and GOULD's (1988) study. It may be argued that the lake is fundamentally different from the barren area because it is theoretically possible that

forage could appear on the land but not on the water and bees may instinctively 'know' this. If this is correct the present study does not provide a direct comparison with the lake experiment. However, it may be replied that this is a very sophisticated concept which vastly underestimates the importance of experience in honey bee foraging behaviour. Others have reported that past foraging experience can significantly influence resource assessment by the honey bee<sup>[14]</sup>. On this argument, the barren field and the lake are equally unfeasible to a honey bee who, in her entire lifetime, has never experienced any forage in the area.

In any case, the necessity for the honey bee to quickly adapt to a unique, and often difficult, set of foraging circumstances, makes it unlikely that any location (even a lake) is judged to be entirely unfeasible and subsequently rejected, whether due to experience or rigid biological programming. The very fact that GOULD and GOULD were able to train bees over water illustrates that bees do not entirely reject the possibility of flying over water to attain forage. Valuable sources of forage would be missed if potential recruits ignored dances referring to areas previously lacking in forage. Foraging animals encounter constantly changing distribution, abundance and quality of resources, they must contend with seasonal and regional variations and the differential effects of unpredictable weather on foraging. Forage often appears in supposedly unfeasible places, for example, on islands and lily patches in the middle of lakes, on barren moorlands when it becomes the heather season in Scotland, and in high up window boxes in the middle of concrete cities.

It is perhaps unnecessary to use the notion of honey bees making judgements concerning the feasibility of an indicated food source at all, and instead it may be suggested that bees have the innate tendency to test all new dance information indicating profitable forage wherever the communicated location may be. It is therefore likely that an 'optimal foraging' strategy can be invoked to explain the heightened activity in the barren area in the present experiment without recourse to the cognitive map explanation.

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