The retrieval of visuo-spatial memories by honeybees

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Summary. In order to explore how honeybees manage to retrieve the right landmark-memory in the right place, we trained bees along a short foraging route which consisted of two identical huts 33 m apart. Bees entered each hut to collect a drop of sucrose on the floor. The location of the drop was defined by the same arrangement of four blue and yellow cylindrical landmarks. However, in one hut the drop was between two yellow cylinders and in two other it was to the east of the blue cylinders. On tests with the sucrose missing, bees tended to search in the appropriate area in each hut (Fig. 1), thus showing that they used cues other than the sight of the local landmarks to select the appropriate memory.

In a second experiment, the position of the sucrose was specified by yellow cylinders in one hut and by blue triangles in the other. When the arrays were swapped between huts, bees searched in the position specified by the array they encountered (Fig. 2). Thus, memories can be triggered by visual features of local landmarks.

Bees were also trained outside to collect food from two platforms 40 m apart. The location of sucrose on one platform was defined by yellow cylinders, and on the other it was defined by blue triangles. When these arrays were exchanged between platforms, bees searched on each platform as though the landmarks had not been swapped. It seems that the more distant surroundings, which fill most of the visual field, may be more potent than the local landmarks in deciding which memory should be retrieved.

It is argued that one role of distant landmarks and other contextual cues is to ensure that bees retrieve the correct memory of a constellation of local landmarks while the bees are still some distance away from their goal. Even at a short distance, a bee's current image of local landmarks may differ considerably from its stored representation of those landmarks as seen from the goal. Accurate recall of the appropriate memory will be more certain if it is primed by relatively distant landmarks which present a more constant image as a bee moves in the vicinity of its goal.

Introduction

Both bumble (Heinrich 1976) and orchid bees (詹森 1971) will follow stereotyped routes during foraging. On such foraging trips, a bee leaves its nest and visits a series of places in a fixed order, collecting nectar at each, before returning home. Honeybees can be persuaded to behave similarly; suitable training will lead them to collect sucrose in a specified order from each of four feeding stations spaced some 5 m apart (TS Collett and R Wehner, unpublished data). We have exploited the bees' ability to follow routes in an attempt to analyse how they retrieve their memories of landmarks.

The location of a single foraging station can be defined by nearby visual landmarks. Studies of ants (Wehner and Rauber 1979; Wehner et al. 1983) and bees (Cartwright and Collett 1982; Gould 1987a) suggest that these insects store an image of local landmarks as viewed from the goal they wish to retrieve. A bee visiting several stations must remember the arrangement of local landmarks seen from each station. To find a particular station, the bee needs to recall its memory of the appropriate set of landmarks. Otherwise it may...
attempt to match the scene imaged on its retina to its stored representation of quite a different scene. Moreover, the bee must retrieve its memory of those landmarks at some distance from the station, else the landmarks can be of no help in guiding the bee to its goal. This presents a problem because, away from the goal, the image of local landmarks on the bee's retina may match rather poorly the bee's memory of the same landmarks as seen from the goal. Consequently, this retinal image tends to be an unreliable cue for memory-retrieval.

This paper presents experiments which go some way to showing how bees solve this difficulty of recalling the correct landmark-memory when local cues are imperfect. We find that landmark-memories can indeed be triggered by a view of the local landmarks themselves. But memories are also primed by contextual cues, such as the more distant visual surroundings and information picked up en route to the goal. One attraction of studying memory-retrieval in bees is that it may soon be possible to translate these behavioural concepts into physiological mechanisms. But at present we can do no more than follow current theory (e.g., Rumelhart and McClelland 1986) and assume that evoking a memory means providing an input to drive a neural network towards a particular state of activity.

Methods and results

Contextual cues contribute to memory-retrieval

Our first experiment tested whether a memory of local landmarks can be primed by the context in which the landmarks are embedded. Bees were trained on a short foraging route. They flew 75 m from their hive to collect a small amount of sucrose from one hut and then a further 33 m apart to collect more sucrose from a second very similar hut before returning home. The huts were situated on a large area of grass surrounded by trees and buildings. Each hut formed a six foot cube with wooden walls and floor. It was roofed with closely woven, white cotton sheeting to provide diffuse lighting and it was painted white inside.

The bee entered each hut through a 45 cm wide door to find an array of two yellow and two blue upright cylinders (7 cm in diameter, 25 cm high) which marked out a 30 cm wide square on the floor (Fig. 1). The arrangement of cylinders was the same in both huts; all that differed was the position of the sucrose with respect to these landmarks. A small drop of sucrose was available on a micro-scope slide on the floor. In this and all the following experiments, the drop was marked with a 1 cm metal ring. The slide in one hut was placed midway between the two yellow cylinders. In the second hut, the slide was 15 cm to the east of the two blue cylinders. The arrangement of landmarks and slide was translated to a new position on the floor after every visit, so that the cylinders provided the only cue to the location of the sucrose. Once a bee is inside the hut and the door is closed, the bee has no usable visual information to tell it which hut is which. If, with the slides removed, bees search predominantly at the appropriate spot on the floor of each hut, they must have retrieved the correct landmark-memory by means of cues other than the sight of the landmarks.

It took about a day and a half to train bees to visit the two huts in sequence and to locate the slides quickly. Bees were then tested ca. every 5 training trials over the next two or three days, unless rain or a bee's disappearance curtailed the experiment. Sufficient data for analysis were obtained from 5 bees. For a test, the slide and ring were removed from one hut and the landmarks were replaced by an identical set used only for testing. A single bee was allowed to enter the hut. The door was closed and its flight-path was recorded on videotape for ca. 2 min by means of a camera suspended from the roof. At the end of the test, the training landmarks and sugar solution were replaced and training was resumed. After two tests in one hut, the videosystem was moved to the other hut and testing continued there.