

Performance of honeybees in analogues of the rodent radial maze

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The performance of individual honeybees pretrained to forage at a laboratory window was studied in three rudimentary analogues of the radial maze designed for the study of short-term spatial memory in rats. A linear arrangement of three targets was used in Experiment 1, a triangular arrangement of three targets in Experiment 2, and a rectangular arrangement of four targets in Experiment 3, with reward only for the first response to each of the targets presented on any given trial. Several systematic patterns of responding were observed, with no indication that the choices made by the animals were influenced by memory of targets recently visited.

Trace conditioning of both color and odor has been found in honeybees (Menzel, 1968; Menzel & Bitterman, 1983), but discriminative control of their behavior by transient residual effects of prior stimuli, commonly referred to as control by "short-term memory" or "working memory," has yet to be demonstrated convincingly. In a recent experiment, Greggers and Menzel (1993) trained foragers with four feeders that yielded sucrose solution at different rates of flow. The authors were unable to model the choices of their animals on the simple assumption that the associative strength of each feeder approached an asymptotic value determined by the flow-rate, but found it useful to think in terms of two "memories," one "feeder specific" and the other "feeder independent"—the associative strength of the entire "patch." The patch memory was characterized as "short-term working memory" and the feeder-specific memory as "long-term reference memory"—a distinction difficult to understand, given that both memories were assumed to be "updated" by reward according to equations of the same form and independently of time. Exactly the opposite usage would have been no less meaningful. Control of performance by short-term memory in the conventional sense was reported more recently by Brown and Demas (1994), who used an analogue of the radial maze designed for rats (Olton & Samuelson, 1976). Confronted on each trial with an array of six baited targets, honeybees showed a significantly greater-than-chance tendency to avoid targets chosen earlier on the trial, but the effect was small and the method (for reasons sub-

sequently to be considered) highly unsatisfactory. Nevertheless, the line of investigation begun by Brown and Demas is worth pursuing further.

The key to the impressive performance of rats in the radial maze appears to be a reluctance to return to places recently visited that was discovered in work on spontaneous alternation in simpler mazes (Glanzer, 1953; Montgomery, 1952; Wingfield & Dennis, 1934). As to the source of the reluctance, there was some engaging early speculation. For example, Heathers (1940) considered and then rejected the possibility that rats rewarded for choosing either arm of a T-maze alternate their choices because the food cup visited most recently is remembered as empty; removing the animals from cups that still contained some food was without effect. The possibility that alternation reflects a persistent search for the shortest possible route to food was rejected by Jackson (1941) on the ground that alternation in an elevated Y-maze quickly gave way to position preference when a gap was introduced between the stem and each of the pathways. Subsequent experiments showed alternation in training without food or water reward and even without deprivation (Glanzer, 1953; Montgomery, 1951; Walker, 1956). Whatever the source of the reluctance of rats to return to places recently visited, the fact that they tend not to do so points clearly, as Dennis (1939) appreciated, to the discriminative control of their performance by short-term memory, and the work of Brown and Demas (1994) raises the interesting question of whether a similar reluctance is to be found in honeybees.

EXPERIMENT 1

In this experiment, the simplest possible analogue of the radial maze was used. On each trial, the subject found a set of three baited targets, the smallest number suitable for the purpose. With three targets, the first two choices on any trial are necessarily correct, and only then can the animal make an error, going to the target first visited and already depleted of food rather than to the target not yet visited on that trial. The three-target situation is not only the easiest to analyze,

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but makes the least demand on short-term memory, requiring the animal leaving the second target to remember only the previously depleted one. Adding even one more target complicates matters substantially; the chance probability of a correct third choice increases from .5 to .67, but on leaving the third target the animal is required to remember both of the targets previously depleted, and the chance probability of correct choice declines to .33.

Method

Subjects. The subjects were 16 foraging honeybees (*Apis mellifera*) from our own hives situated near the laboratory. All were experimentally naive.

Procedure. The subjects were trained individually and sequentially, each of them in a single training session less than 3 h long. The training situation was a resined plywood enclosure, 58 cm wide, 58 cm high, and 46 cm deep, set into a laboratory window as diagrammed in Figure 1a. The enclosure was open to the outside, and on the inside it was fitted with a pair of sliding Plexiglas doors through which the observer had access to the situation. A forager was selected at

random from a group of foragers at a feeding station providing 10%–15% sucrose solution, carried to the laboratory, and set down at a 100- μ l drop of 50% sucrose solution in a conical orange target at position B of the diagram. A sketch of the target, 6.2 cm in its widest diameter, 2 cm high, and 28 ml in volume, is shown in Figure 2. The animal was marked with a spot of colored lacquer as it fed to repletion, after which it was permitted to leave for the hive. Now the animal was adapted to 50% sucrose and, finding the lower concentration at the feeder less acceptable, usually would come back to the laboratory after a few minutes, continuing thereafter to shuttle back and forth between hive and laboratory, where 50% sucrose continued to be available. If the marked animal did not come back after its first placement, it was carried from the feeding station, where it could be found again, to a target containing 100 μ l of the 50% sucrose solution at position B. When the animal did return to the window of its own accord, it found a target containing 100 μ l of sucrose at position B. On its second return, it found a target containing 100 μ l of sucrose at position A, and on its third return—the final pretraining visit—a target containing 100 μ l of sucrose at position C. Throughout the experiment, the targets used on each visit were drawn from a large set of identical orange targets to which they were returned after being washed with water at the conclusion of the visit; the purpose of the procedure, which is a standard one in this laboratory, was to randomize extraneous stimuli.

On each of 20 subsequent training visits, the animal arrived from the hive to find a row of three targets that were 23 cm apart, center-to-center, at positions A, B, and C, as shown in Figure 1a. Each target contained 10 μ l of 50% sucrose solution. The animal would choose a target, take the sucrose, go on to a second target, whereupon, while it was taking the sucrose in the second target, the experimenter replaced the first target with a fresh target containing about 50 μ l of water, unacceptable to the animal and distinguishable from sucrose solution only by taste. The purpose of the exchange was to rule out the possibility that return to the first target would be influenced by scent marking; foragers have been known to mark rich sources of nectar with an attractive odor (Frisch, 1967), but more to the point here would be their tendency to mark depleted flowers with an aversive odor (Giurfa & Núñez, 1992; Núñez, 1967). At the same time, the third target was replaced with a fresh target containing 50 μ l of the sucrose solution, a quantity more than enough to permit feeding to repletion and thus to end the visit. Each trial, which began with the arrival of the animal from the hive and ended with its return to the hive, was a single foraging trip. The geometry of the targets and the movements of the experimenter were such that the replacement of the first and third targets, which required only a few seconds, could not be seen by the animal feeding at the bottom of the second target.

As already noted, error was possible only on the third choice, the animal going either to the third target, which contained sucrose, or to the target first chosen, which now contained water. If an error was made, the animal was free at once to correct its choice. Response was defined as leaving one target and going to another, landing fully on its inside surface; breaking contact with a target and returning to it before leaving it for another, a common feature of foraging behavior, was not counted. Repetitive errors could be made; on leaving the second target, the animal might, for example, go to the first target, then to the second, and then again to the first before choosing the third, which would count as two repetitive errors. Given, however, that there was no opportunity out of view of the animal to replace each target erroneously chosen, and thus to rule out the possible influence of scent marking, only the initial choice could provide uncontaminated evidence of short-term memory. Our primary interest was in whether or not, upon leaving the second target, the animal would choose correctly—that is, go to the third—as it would be expected to do on the assumption of short-term memory.

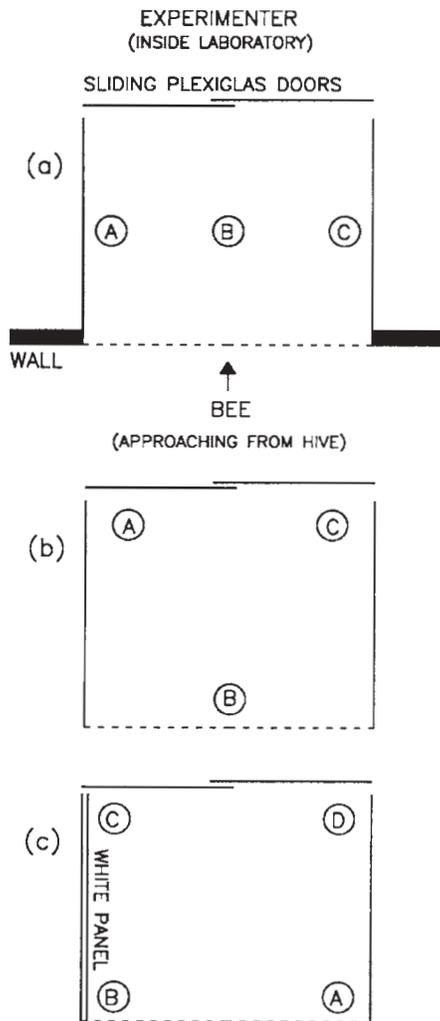


Figure 1. Diagram of the experimental situation showing (a) the linear array of targets used in Experiment 1, (b) the triangular array used in Experiment 2, and (c) the rectangular array used in Experiment 3. Width of the enclosure is 58 cm.

Results

In Figure 3, the performance of the 16 animals is plotted in terms of the proportion of correct third choices on

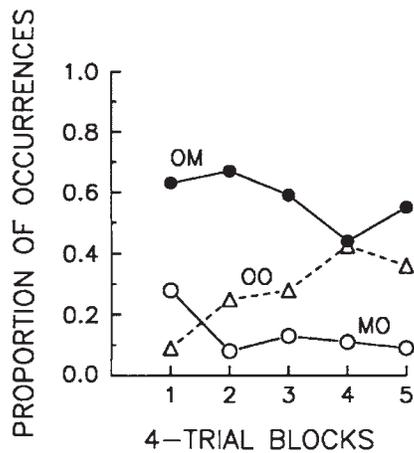


Figure 4. The proportion of occurrences of each of the three patterns over five blocks of four training trials in Experiment 1. OM, an outside target chosen first and then the middle one; OO, an outside target chosen first and then the other outside one; MO, the middle target chosen first and then one of the outside targets.

tablished with continued training is an empirical question, but it seems clear that this situation is not very useful for the study of short-term memory in honeybees; if the animals do remember at each target where they have been at least just before, there are too many other determinants of choice to demonstrate an effect of memory on subsequent choice.

EXPERIMENT 2

In this experiment, three targets were used again, but they were arrayed at the apices of an equilateral triangle rather than in a straight line. The main purpose of the triangular arrangement was to eliminate the contiguity bias that played so prominent a role in Experiment 1, the three targets now being equidistant from each other. It was hoped, too, that the triangular arrangement would produce a more balanced distribution of initial choices over the three targets.

Method

Subjects. The subjects were 8 foragers, all experimentally naive, from our own hives.

Procedure. The triangular arrangement of the targets, which were 41 cm apart, center-to-center, is diagrammed in Figure 1b. In the pretraining, each animal was placed, marked, and permitted to feed to repletion in a target placed at position B. On its first return, it found a target at the same position; on its second return, a target at position A; and on its third return, a target at position C. On the 25 training trials that followed, the procedure was exactly the same as in Experiment 1, except for the spatial arrangement of the three targets.

Results

The only nonrandom outcome of this experiment was a significant pattern-bias [$\chi^2(2) = 17.84, p < .01$]. If, in conformity with the designations used in Experiment 1, tar-

get B is referred to as M, and targets A and C—although now set farther back in the window—as “outside” targets, O, the three possible two-choice patterns can be designated as M–O, O–M, and O–O. The M–O pattern occurred on 20% of trials, the O–M pattern on 38% of trials, and the O–O pattern on 42% of trials. Here again, then, there were relatively few initial choices of the “middle” target, B, although somewhat more than in Experiment 1. An analysis of variance based only on the two most frequent patterns, O–M and O–O—again because inclusion of the third pattern would violate the independence assumption—yields neither a significant pattern effect ($F < 1$) nor a significant block effect [$F(4,28) = 2.35, p > .05$], nor a significant pattern \times block interaction ($F < 1$). The critical third choice was only 45% correct, although not significantly less than 50% [$t(7) = 1.08, p > .05$], nor did the accuracy of the third choice vary significantly either with pattern ($F < 1$) or over blocks of trials [$F(4,28) = 1.98, p > .05$]. The number of repetitive errors averaged less than one per trial and did not decline significantly over blocks of trials [$F(4,28) = 2.71, p > .05$]. There is no indication whatever in these results of the control of performance by short-term memory.

EXPERIMENT 3

In this experiment, four well-separated targets were presented in a rectangular arrangement, each of them laterally situated in the enclosure; there was no target centrally situated as were the middle targets of Experiments 1 and 2 that were relatively unlikely to be chosen at the start of each visit. Another change was that the enclosure was differentiated by a white panel intended to enhance discrimination of the positions of the targets. Adding a fourth target increased the number of critical choices from one to two, providing an additional opportunity to look for evidence of short-term memory.

Method

Subjects. The subjects were 8 foragers, all experimentally naive, from our own hives.

Procedure. The rectangular arrangement of the targets is diagrammed in Figure 1c, which shows also a white panel on one of the sidewalls that was introduced to enhance spatial differentiation. Targets at positions A and B were 45 cm apart, center to center, as were targets at positions C and D; the distance between targets at positions A and D and between targets at positions B and C was 36 cm in each case. The pretraining in this experiment was somewhat less extensive than in the preceding ones. The animal was placed, marked, and fed to repletion in a target positioned centrally and then permitted only a single return to a target in the same central position. The first of 25 training trials with four targets in the rectangular arrangement began with the animal's second return to the window from the hive.

At the outset of each trial, each target contained a 10- μ l drop of 50% sucrose solution. The animal chose one of the targets, then a second, and as it took sucrose in the second target, the first was replaced, out of view of the animal as in the previous experiments, with a fresh target containing 50 μ l of water. As the animal took sucrose in the third target, the second was replaced with a fresh target containing 50 μ l of water, and the as-yet-unchosen fourth target was replaced with a fresh target containing 50 μ l of the sucrose solution from which the

animal eventually fed to repletion and returned to the hive. Here both third and fourth initial choices were critical for the question of short-term memory; the chance probability of correct choice was .67 for the third and .33 for the fourth.

Results

In Figure 5, the performance of the animals is plotted in terms of the proportions of correct third and fourth choices on each of the 25 training trials. In neither case was there significant variation over 5-trial blocks ($F < 1$). The mean accuracy of the third choice was 56%, significantly less than the 67% expected by chance [$t(7) = 3.86, p < .01$]. The mean accuracy of the fourth choice was 59%, significantly greater than the 33% expected by chance [$t(7) = 7.47, p < .01$]. The number of repetitive errors averaged 1.3 per trial and did not change significantly over blocks [$F(2,28) = 1.43, p > .05$].

At the outset of each trial, the front targets were preferred to the back targets; 75% of the 200 first choices (8 subjects \times 25 trials) were to one of the front targets. Of the second choices, 62% were on the same side as the first, front to back or back to front; 32% were on opposite sides, front to front or back to back; and only 6% were diagonal. For all choices combined, the percentage of same-side choices was 61; of opposite-side choices, 30; and of diagonal choices, 9. The three patterns differed signifi-

cantly in frequency of occurrence [$\chi^2(2) = 82.20, p < .01$]. Analysis of variance based on the two most frequent patterns, same side and opposite side, yielded a significant pattern effect [$F(1,7) = 21.08, p = .0025$], but neither a significant block effect [$F(4,28) = 1.94, p > .05$] nor a significant pattern \times block interaction ($F < 1$). As a result of the same-side preference and the fact that a front target was more likely than a back target to be chosen first, the second choice was more likely to be that of a back target. For example, with A as the first choice, the animal was more likely to go to D than to B. Given the reluctance of the animals to move diagonally, the third choice was primarily the target chosen first—for example, A—and the nondiagonally situated of the novel alternatives, C, which explains why the level of accuracy on the third choice, 56%, was less than the 67% expected by chance rather than the greater accuracy expected on the assumption of short-term memory.

The only result of this experiment that might be taken as evidence of short-term memory is accuracy on the fourth choice, which was 59% as compared with a chance value of 33%, but that result follows directly from the patterns evident in the first two choices. When the first two choices were same-side choices, the correct third choice was of necessity on the opposite side, and the correct fourth choice was on the same side as the correct third choice. Since the animals were reluctant to change sides, the fourth choice was likely to be correct; the mean percentage of correct fourth choices in this case was 78. When the first two choices were on opposite sides, the correct third choice was most likely to be on the same side as the second; a correct fourth choice therefore was unlikely because it was of necessity on the side opposite that of the correct third choice; the mean percentage of correct fourth choices in this case was 33. In the few instances in which the first two choices were on a diagonal, the correct fourth choice was diagonally situated with respect to the correct third choice; the mean percentage of correct fourth choices was 8. The overall accuracy of the fourth choice, like that of the third, can be accounted for entirely in terms of response bias.

DISCUSSION

The results of these experiments give no indication of the discriminative control of the behavior of honeybees by short-term memory. A few negative results are hardly definitive, of course, but the positive results reported by Brown and Demas (1994) give added importance to an account of our negative results and the experiments in which they were obtained, if only to provide some methodological perspective for future work.

An important constraint in work with free-flying foragers is that they come to the experimental situation of their own accord and, after feeding to repletion—which normally requires about 50 μ l of sucrose solution—leave for the hive of their own accord, continuing to shuttle regularly between the hive and the laboratory every 4–5 min as long as sucrose is available. Brown and Demas (1994)

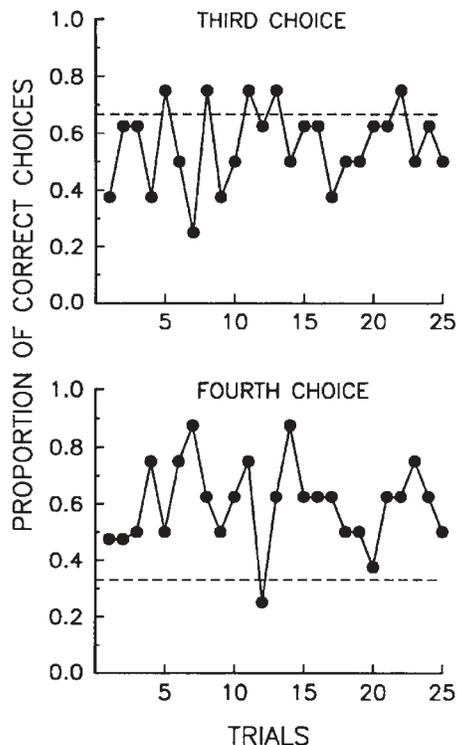


Figure 5. The proportion of correct third choices (upper panel) and fourth choices (lower panel) on each of the 25 training trials in Experiment 3. While the animal was feeding in any target, previously visited targets were replaced with fresh ones; the chance probabilities of correct choice were .67 for the third and .33 for the fourth (dashed lines).

provided much less sucrose than was required for feeding to repletion on each trial, and when the trial ended the subject was simply barred from the situation for a period of time, which means that trials were given under different motivational conditions and at different points in the subject's foraging cycle, or, if the excluded subject went off to forage elsewhere, at widely different intertrial intervals. Brown and Demas report that the intertrial interval "typically" was 5 min, but they also report that to complete "at least 26 trials" required 2 days on the average; the two values are difficult to reconcile. Our own procedure, standard in this laboratory, was to provide enough sucrose for feeding to repletion on each visit, so that each trial began with the subject's arrival from the hive 4–5 min after the preceding trial and ended with the replete subject's voluntary return to the hive following the final choice.

To avoid interanimal interference, it is necessary to work sequentially with individual subjects, which Brown and Demas (1994) did not appreciate at the outset; the first 6 of the 15 subjects of their main experiment, whose data are nevertheless included in the analysis, were trained sporadically in pairs over a period of several days. It is necessary also to position the training situation in such a way as to avoid intruders, which Brown and Demas invited by working near a feeding station that, like their training situation, was painted violet. To exclude intruders as well as any unwelcome experimental animals which, after completing a trial but not yet replete, often remained in the vicinity, Brown and Demas covered their shallow experimental enclosure, which was only 18.8 cm deep, with a sheet of Plexiglas, leaving little flying room.

Another difficulty to be dealt with in these experiments, as already noted, is that foragers may mark depleted flowers with an aversive odor which for a short time discourages revisiting (Núñez, 1967). To check on the possibility that the results of their main experiment might be attributed to aversive marking, no precautions against it having been taken, Brown and Demas (1994) trained animals in two further experiments, capturing them in midtrial, after three of the targets had been depleted, and transferring them to a similar situation equipped with fresh targets—a procedure that disturbed the animals, as was evidenced by a sharp reduction in their responding. In any case, post-transfer marking still was possible, and it is difficult to understand Brown and Demas's claim to have controlled for its effects simply by ignoring revisits, which actually were rare.

Our own solution to the marking problem was to replace depleted targets with fresh ones in the course of each trial under circumstances in which the animals could not see the changes being made. A more elegant solution is suggested by the work of Giurfa and Núñez (1992), who used targets to which sucrose solution could be delivered automatically from below and from which, also from below, air could be withdrawn by a pump. Evidence both of aversive scent marking and of the efficacy of the air-extraction technique was found in the much greater rejection of depleted targets by their animals when the pump was off than when it was on. The technique is useful because it per-

mits work with a larger number of targets and in a wider field than would be practicable with our replacement procedure. Unfortunately, ventilation may not entirely eliminate marking scents, although it considerably reduces the likelihood that spurious evidence of short-term memory will be found.

Another precaution that must be taken in such experiments is against the possibility that fresh and depleted targets are discriminated on the basis of the presence or absence of sucrose solution (Walker, Lee, & Bitterman, 1990). The standard procedure in this laboratory is to bait each unrewarded alternative with a drop of water, which is distinguishable from sucrose only by taste (Couvillon & Bitterman, 1991), and our like procedure in the present experiments was to bait the replacement targets with water. Neither in their main experiment nor in the first of the two subsequent control experiments did Brown and Demas (1994) replace the sucrose taken with water, and tests made in the first control experiment led them to suspect that the baited and unbaited targets were indeed visually discriminated. In the second control experiment, the three targets in the positions chosen before the shift were baited with water, but targets chosen after the shift were not, which means that performance after the first postshift choice could have been influenced by visual as well as by olfactory cues. In the light of the many methodological shortcomings of their experiments, the claim by Brown and Demas to have demonstrated the ability of honeybees "to represent multiple locations in a flexible, dynamic manner" is not at all convincing.

It might be suggested that further work on the problem be done with a greater number of targets than we used here. Brown and Demas (1994) used six, which makes the analysis of performance extremely complex; the matrix of mean target-to-target transition probabilities that they present tells very little about what the animals actually were doing apart from their tendency to choose contiguous alternatives. Our own contrary inclination is to turn to analogues of the simple T- and Y-maze experiments—that is, the two-choice experiments—in which spontaneous alternation in rats was first discovered. Nor should future work be tied to the possible reluctance of honeybees, apart from scent marking, to return to places recently visited. Experiments on spontaneous alternation with both alternatives always rewarded would certainly be worth doing, although experiments without reward, which are feasible with rats, unfortunately are not feasible with honeybees. There should also be experiments in which delayed alternation (win–shift) or delayed persistence (win–stay) in the choice of places is differentially reinforced. Given that there still is much to be known about place learning in honeybees (Couvillon & Bitterman, 1992; Huber, Couvillon, & Bitterman, 1994), experiments of like design might profitably be done with colors and odors as well as with places.

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