

Experimental Evidence for Spatial Learning in Octopuses (*Octopus bimaculoides*)

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Octopuses forage far from temporary home dens to which they return for shelter. Spatial tasks may assess learning. Octopuses (*Octopus bimaculoides*) were placed in a novel arena, and their movements were tracked for 72 hr. Movements around the arena decreased across time, consistent with exploratory learning. Next, octopuses were given 23 hr to move around an arena; after a 24-hr delay, their memory of a burrow location was tested. Most remembered the location of the open burrow, demonstrating learning in 1 day. Finally, octopuses were trained to locate a single open escape burrow among 6 possible locations. Retention was tested after a week and was immediately followed by reversal training (location rotated 180°). Octopuses learned the original location of the burrow, remembering it for a week. Path lengths increased significantly after reversal, gradually improving and showing relearning. Octopuses show exploratory behavior, learning, and retention of spatial information.

Octopus field behavior clearly suggests spatial learning. Many species forage away from a home den that they return to repeatedly for shelter (*Octopus bimaculatus*: Ambrose, 1982; *O. briareus*: Aronson, 1986, 1989, 1991; *O. cyanea*: Forsythe & Hanlon, 1997; Van Heukelem, 1966; Yamall, 1969; *O. dofleini*: Hartwick, Ambrose, & Robinson, 1984; Hartwick, Breen, & Tulloch, 1978; Hartwick, Tulloch, & Macdonald, 1981; Mather, Resler, & Cosgrove, 1985; *O. vulgaris*: Altman, 1967; Kayes, 1974; Mather, 1988, 1991; Mather & O'Dor, 1991; see reviews in Boyle, 1983, 1988). Individual octopuses may occupy the same den continuously for anywhere from 1 day (any of the above references) to 5 months (Hartwick et al., 1984), after which they shift to a new den.

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At least some octopuses appear to be able to re-locate their dens from considerable distances and after extensive time lapses. Two *O. cyanea* traveled distances that placed them clearly out of sight from their home dens (up to 40 m; Forsythe & Hanlon, 1997); these octopuses also jet swam distances of 15 to 20 m to arrive directly back at their home dens. Foraging trips of *O. dofleini* have been reported to last up to 7 hr (Mather et al., 1985). *O. vulgaris* (Mather, 1991) and *O. cyanea* (Forsythe & Hanlon, 1997) avoid recently visited areas on subsequent hunting trips, suggesting that they remember where they foraged previously.

Chemical-trail following and short-term memory of their paths can be ruled out as explanations for orientation behavior of octopuses. Although octopus foraging is primarily tactile (see especially Forsythe & Hanlon, 1997), outbound and return travel is commonly accomplished by jet swimming through the water column rather than by crawling along the substrate (*O. vulgaris*: Mather, 1991; *O. cyanea*: Forsythe & Hanlon, 1997). Furthermore, return routes generally do not overlap outbound routes (*O. vulgaris*: Mather, 1991; *O. cyanea*: Forsythe & Hanlon, 1997). Thus, it appears that octopuses remember both where they last foraged and where their home den is located.

The field data are not conclusive on spatial learning, however. Detailed individual tracks for octopuses in the open sea are available from just two studies (*O. vulgaris*: Mather, 1991, $N = 4$; *O. cyanea*: Forsythe & Hanlon, 1997, $N = 2$). *O. dofleini* was tracked using sonic tags and was found to use several dens rather than just one (Mather et al., 1985), a finding of concern because many of the studies of octopus foraging did not involve individually recognizable octopuses. Most reported foraging trips appeared to be short, lasting less than half an hour (Mather et al., 1985; exception *O. cyanea*: Forsythe & Hanlon, 1997) and extending less than 10 m from the den (Mather, 1991; Mather & O'Dor, 1991; Mather et al.,

1985; water clarity not reported). Octopuses that were deliberately displaced by experimenters appeared to remain oriented (Mather, 1991); however, displacements were less than 4 m. Learning beyond visual den recognition may not have been required.

Laboratory training experiments support the field evidence for spatial learning in octopuses. Initial training experiments using *O. vulgaris* in simple detour mazes obtained mixed results (no evidence for improvement: Bierens de Haan, 1949; Boycott, 1954; Buytendijk, 1933; some evidence for learning: Schiller, 1949; Wells, 1964, 1967, 1970). In these experiments, the researchers used visible rewards (crabs behind glass) to motivate subjects. This kind of experimental design is also challenging for many "higher" vertebrates (Pearce, 1987). In a simpler, T-shaped maze, octopuses were required to crawl along a moist surface through the maze to the goal box, where they could return to seawater (Walker, Longo, & Bitterman, 1970). On this task, five *O. maya* attained 100% success after 27 days with three trials per day and successfully mastered two reversals. This experiment demonstrated that spatial learning is definitely within the range of octopuses' abilities. Also in a training paradigm, two *O. rubescens* appeared to learn to orient to a moving landmark to obtain a food reward (Mather, 1991), a task reminiscent of the pretraining procedures used in discrimination learning experiments. There is also some preliminary evidence suggestive of play (Mather & Anderson, 1999), a possible form of exploratory learning (Eimon, 1983).

The experiments described below are the product of our efforts to develop a method for training octopuses in a way that did not depend on food for motivation. We used escape to motivate the octopuses to solve a maze problem that was comparable to a natural spatial learning problem. In Experiment 1, we asked whether octopuses would show spontaneous movements in a novel arena without any immediate, tangible rewards for doing so. In Experiment 2, we asked whether octopuses actually learned anything during their movements around the arena. Finally, in Experiment 3, we asked whether octopuses could be trained to solve a spatial problem using escape as motivation.

General Method

Unless otherwise specified, experiments were conducted at the Marine Biomedical Institute (MBI) of the University of Texas Medical Branch at Galveston. Housing and experimental tanks were interconnected on the same 13,000-L recirculating sea water system, dedicated to holding cephalopods and their live food. Water was a mixture of natural seawater from the Gulf of Mexico and artificial seawater made from Instant Ocean brand salts (Aquarium Systems, Mentor, OH); unless otherwise specified, salinity ranged from 31 to 35 ppt, and water temperatures ranged from 16 to 18 °C. In this closed system, water exiting each tank passed through mechanical, chemical, and biological filters and was treated with ultraviolet light to kill pathogens. Water flow was continuous at all times, including throughout trials. A complete description of maintaining octopuses in the laboratory can be found elsewhere (Forsythe & Hanlon, 1980; Hanlon & Forsythe, 1985).

Subjects were cultured and wild-caught *O. bimaculoides*, the California mudflat octopus. Octopuses were housed individually in holding tanks (30 × 14 × 25 cm deep) with locking tops. Each octopus was provided with a black Plexiglas box (14 × 15 × 20 cm high; Experiment 1) or a terra cotta flower pot (Experiments 2 and 3) to use as a home den. These containers also allowed experimenters to scoop up and move octopuses from one place to another with minimal disturbance (Walker et al., 1970).

Octopuses were fed a mixture of live and frozen fish, shrimp, and crabs once per day in the early evening.

One of the experiments was conducted at the Marine Resources Center of the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts. There, octopuses were housed individually in mesh-sided containers (16 × 24 × 14 cm) placed within larger tanks and were fed a mixture of live and frozen fish and shrimp and frozen squid. Water for the housing and experimental tanks consisted of partially recirculated natural seawater that was filtered and heated to 20 °C.

Data were analyzed using nonparametric statistics as specified (Siegel & Castellan, 1988).

Experiment 1

The purpose of this first experiment was to determine whether octopuses would move spontaneously within a new environment in a manner consistent with an interpretation of exploration.

Method

A single octopus ($N = 6$ wild-caught octopuses ranging from 63 to 864 g; all but 2 octopuses were between 63 and 88 g) in its rectangular plastic den was placed into an open arena and allowed to explore the maze freely. The arena consisted of a round tank (1.8 m diameter) covered with a 1-cm layer of crushed oyster shell and containing three large rocks and three clay bricks (Figure 1a). The tank was filled with water to a depth of 45 cm. Continuous water exchange was provided from an inflow pipe extending to just below the surface of the water and an outflow pipe at the bottom of one side of the tank. Black plastic curtains surrounded the arena on the north, east, and south sides to minimize disturbances during trials; the west side faced windows. A video camera was mounted directly above the tank and was connected to a remotely located monitor and videocassette recorder. Natural light was supplemented by a single, 100-W red floodlight (24 hr/day) to facilitate video recording during the night.

Each octopus received one trial that began at 1630 and extended for a continuous 72-hr period. Each octopus was fed the night before the trial began and then not again until the trial was over. Octopuses of this size do not need to feed every day. Sequential trials were spaced by at least 24 hr to allow ample water exchange. Trials were continuously videotaped.

Movement paths for each octopus were traced onto plastic transparencies; from these, it was apparent that the octopuses were using the den as a home base from which they moved in discrete bouts of locomotor activity. The movements of each octopus were scored in hourly blocks by noting the times the octopus exited and returned to its home den. Two variables were computed for each 1-hr time block: the number of movement bouts outside the den (bouts) and the percentage of time spent outside the den (activity). One octopus was excluded from analyses because it died shortly after the experiment; however, analyses including data on this octopus gave similar results.

Results

All octopuses moved around the entire arena throughout the 3-day period. The percentage of time spent moving outside of the home den decreased across the 3 days (Figure 2). About 55% of all activity occurred in the 1st day. Periodicity was evident in both individual and mean plots of activity, with the least amount of activity observed at 1600 and 0400. When we divided the 3 days into 12-hr blocks according to these low periods, activity averages were 74%, 38%, 38%, 24%, 14%, and 15%, suggesting that an asymptote of activity was reached after about 48 hr in this arena.

The number of movement bouts per hour ranged from 0 to 13, with a median of 1. There was a trend toward fewer bouts with

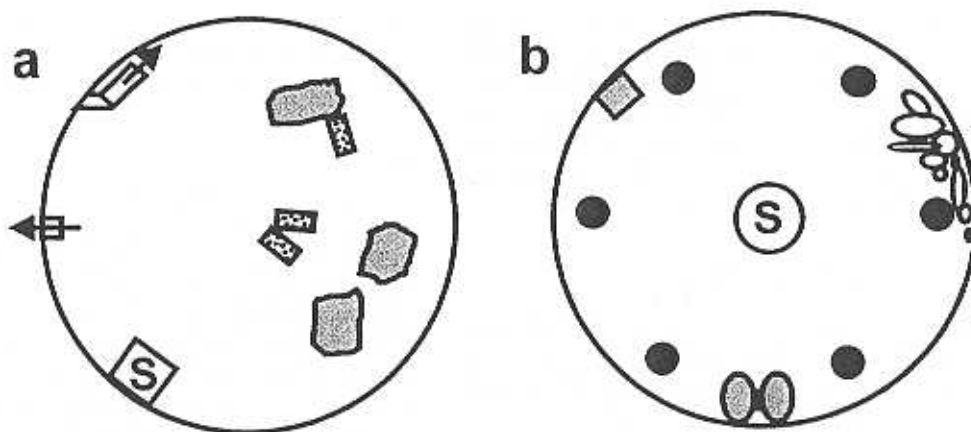


Figure 1. Diagram of experimental arenas. a: The arena in Experiment 1 (1.8 m diameter) was lit with natural light and was filled with water to a depth of 45 cm. The start location (S) and water in- and outflows (arrows) are indicated. Landmarks consisted of three large rocks (gray) and three red clay bricks (stippled). b: The arena in Experiment 3 (1.5 m diameter) was brightly lit and filled with water to a depth of just 8 cm (this experiment took place at the Marine Biological Laboratory). The octopus could escape by entering one of the burrows. The start (S) and burrow (solid circles) locations are marked. In each trial, five burrows were blocked and one remained open.

increased time in the experimental arena, although this trend was less distinct than for activity. About 49% of all bouts occurred in the 1st day. No clear periodicity in the number of bouts was detected, but using the same 12-hr blocks as with activity, the number of bouts averaged 32, 34, 20, 18, 12, and 19, suggesting that an asymptote of movement bouts was reached after 24 hr.

Discussion

The gradual decrease in activity outside the den is consistent with an interpretation of exploration. Had the octopuses moved simply to seek food, activity should have increased because octopuses were not fed during the 3 days they were in the maze (the

normal feeding schedule was once per day). Had the octopuses been motivated simply to gain exercise, one might expect similar movements on all 3 days. It is unlikely that the movements decreased because octopuses were tired; in the field, octopuses travel far greater distances on a daily basis (see above). Instead, results are consistent with the interpretation that they were exploring.

Exploration in this context can be defined as a combination of movement and learning (Archer & Birke, 1983); the animal gains information about its environment by moving around in space. A first indication of possible exploratory learning is a decrease in movements within a novel environment (reduced exploration) with

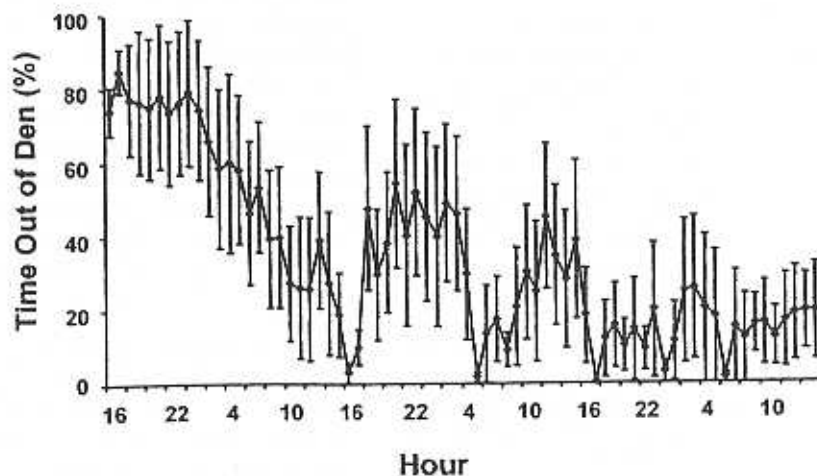


Figure 2. Plot of the percentage of time the octopuses spent outside their home den ($M \pm SE$; $N = 5$). Activity decreased gradually for the first 48 hr, thereafter remaining at a relatively constant low level. There appears to be a 12-hr cycle of activity, with lows at about 0400 and 1600. (Note that numbers on the x-axis represent time of day, e.g., 1600, 2200, 0400, etc.)

repeated or extended exposure. This is exactly what was found. The continuing activity after the initial burst of movement could be interpreted as "patrolling," or updating the knowledge base (Russell, 1983). From our observations here, however, it cannot be determined whether any learning actually took place, and if it did, whether it involved simple habituation to the novel surroundings or some more complex form of spatial learning.

Experiment 2

The purpose of this experiment was to determine whether the octopuses learned about their environment while they moved around the experimental arena, a necessary condition for their motor behavior to be accurately termed *exploration*.

Method

Thirty-nine octopuses were used in this experiment. Ten were laboratory cultured, and 29 were wild caught. Octopuses were tested in three cohorts. The cohorts were similar except that the first cohort consisted of the cultured octopuses, and the third cohort was tested under less optimal laboratory conditions (i.e., noisy laboratory, higher water temperatures, use of artificial lights, and low live-food availability).

The experimental arena consisted of a round tank (1.5 m diameter) with two burrows on opposite sides of the tank (180° apart). Burrows were constructed from sections of polyvinyl chloride (PVC) pipe (7.6 cm diameter × 15.0 cm deep). Glass jars that exactly fit into the pipe sections were used to facilitate returning octopuses to their home tanks at the end of the trial. Landmarks included bricks, odd plastic pieces, rubber bungs, shells and small rocks, an artificial plant, and patterned towels hanging over the tank sides. The start location was at the center of the tank.

In the exploratory phase, the water in the maze was approximately 20 cm deep, and the lighting was entirely supplied by indirect natural light from west-facing windows. Each octopus was placed separately in the maze and allowed to move around freely, without disturbance, for a period of exactly 23 hr. For each octopus, one burrow was open (jar facing upwards) and one burrow was blocked (jar facing downwards). Octopuses could not detect which burrow had been blocked without going right up to it. At the end of this exploratory phase, octopuses were returned to their home tank for a resting period of exactly 24 hr.

In the testing phase, the water in the maze was lowered to approximately 2 cm depth and natural lighting was supplemented with a 500-W halogen lamp aimed directly into the tank. *O. bimaculoides* is nocturnal and shy, disliking bright light and open spaces (Boal, 1993); thus, the octopuses were motivated to find their way to the open burrow. Each octopus was tested individually by inverting its home den (still containing the octopus) on a stand at the start location in the center of the arena. On the stand, the opening of the home den faced downwards and was about 4 cm above the water level. The octopus would climb down out of its den to return to the water below and then search for the open burrow. The trial ended when the octopus entered the open burrow or when 15 min had elapsed, whichever came first.

Octopuses of all three cohorts were divided into three groups. For Group 1 or the same group ($n = 12$), the open burrow was in the same location as during the exploratory phase (half on the right and half on the left). For Group 2 or the reversed group ($n = 12$), the burrows were reversed so that the open burrow was the one that had been blocked during the exploration phase (half were changed from right to left and half from left to right). For Group 3 or the control group ($n = 10$), 4 octopuses were tested after omitting the exploratory phase, and 6 octopuses were tested after an exploratory phase with both burrows open.

The behavior of the octopuses in the testing phase was recorded using an overhead video camera connected to a remotely located monitor and video

recorder. This permitted the experimenter to view trials without being seen by the octopuses. Behavior was scored by recording the first burrow contacted and the time taken to enter the open burrow.

Results

Evidence for exploratory learning was mixed. During their single escape trial, 16 of 24 octopuses contacted the burrow that had been open during the exploratory phase. Eight of 12 octopuses in the same group contacted the open burrow first (4 on the right and 4 on the left), and 8 of 12 octopuses in the reversed group contacted the blocked burrow first (4 on the right and 4 on the left). This result is not statistically significant (binomial test, $p = .10$), but the trend is consistent with an interpretation of exploratory learning. There was no difference between the two groups in average time to find the open burrow (174 and 171 s).

Laboratory-cultured octopuses performed similarly to the wild-caught octopuses. The second cohort, all wild-caught and tested under the best of laboratory conditions, showed excellent spatial learning. All 9 octopuses from the same group and the reversed group went first to the burrow that had been open during the exploratory phase (binomial test, $p = .002$). The same group also took significantly less time to find the open burrow than did the reversed group: Wilcoxon-Mann-Whitney test, $W_x = 10$, $n_1 = 4$, $n_2 = 5$, $p = .01$.

For the control group, 6 octopuses contacted the burrow on the right side initially, 3 contacted the burrow on the left side initially, and 1 never left the starting area. The mean time to find an open burrow was not significantly different for naïve and experienced octopuses in this group: $M = 88$ s ($SE = \pm 27$) and $M = 63$ s ($SE = \pm 12$), respectively, with 1 octopus in each category failing to find an open burrow.

Discussion

This study revealed some evidence for exploratory learning. The first burrow the octopuses contacted was usually the one that had been open during the exploratory phase. The second cohort, in particular, performed exactly as would be predicted from a hypothesis of exploratory learning.

We were surprised that the time taken to locate the open burrow did not differ between the same and reversed groups. This result could be due to the small size of the experimental arena. It is also possible that performances were compromised by the difference in the appearance of visual cues when the water level was changed. During the testing phase, the water was only about 2 cm deep. In water this shallow, the octopus's head and eyes protrude above the water level, and it is not known how good their visual acuity is through air.

We assumed that a 23-hr exploration period would be sufficient for learning. Results from Experiment 1 indicate that about half of all movements occurred in the first 24 hr in this kind of arena, so this seemed a fair assumption, although it is possible that more time in the arena would have resulted in stronger evidence for learning. We also assumed that a 24-hr retention of learning was reasonable. Certainly this duration seems consistent with memory requirements for octopuses when they forage in their natural habitat (see references above), but it is possible that results would have been stronger after a shorter retention period.

Experiment 3

The purpose of this experiment was to test the feasibility of training octopuses to solve a spatial problem that represents a natural problem of re-locating a previously used shelter when adverse conditions occur (e.g., tidal change or predator appearance).

Method

Five of the 15 octopuses used in this experiment were tested at the MBL. Twice each day, morning and evening, we placed individual octopuses in the center of a brightly lit, round arena (diameter = 1.5 m) and permitted them to explore the maze for up to 20 min. Equally spaced around the periphery of the maze were six terra cotta flowerpots, set into the bottom of the arena so that they formed burrows. The saucers for the pots were set in a standard position partially covering each burrow; the octopuses could see the saucers but not the burrows. The substrate consisted of 1 cm crushed oyster shell, which was raked between trials to ensure that octopuses could not follow any potential chemical cues from previous trials. A rock pile, shells, and an unused air stone were placed around the periphery of the maze to provide landmarks (Figure 1b). The maze was filled with seawater to a depth of approximately 8 cm.

The remaining 10 octopuses were tested at the MBI. Training was conducted as above with the following exceptions. The burrows were constructed of glass jars set into holes, as described in Experiment 2. Terra cotta saucers were placed so as to partially cover each burrow. The crushed oyster shell substrate was omitted; the bottom of the tank consisted of dark gray PVC. A rock pile, artificial plants, and a coiled piece of rope were placed around the periphery of the maze to provide landmarks. The maze was filled with seawater to a depth of about 3 cm.

For each octopus, five of the burrows were plugged with either a rubber bung (MBL) or by inverting the glass jar (MBI) so that no entry was possible. The location of the open burrow varied randomly between octopuses but was consistent between trials for any 1 octopus. Octopuses could not see which burrows were plugged without going right up to them. Once the octopus found the open burrow, it would enter and pull the saucer over its head to block the light.

At the start of a trial, the octopus den (in all cases, terra cotta flower pots that still contained the octopus) was inverted on a stand in the center of the experimental arena, as described in Experiment 2. A trial was considered to have begun once the octopus left the center start location. Octopuses at MBL received two trials per day, one in the morning and one in the afternoon. Octopuses at MBI received one trial per day between 0900 and 1500. The order in which the octopuses were tested was randomized within each session.

There were three stages to the experiment that followed immediately one after another. In Stage 1 or the training stage, each octopus received 20 trials (MBL) or 24 trials (MBI) with a single burrow open. In Stage 2 or the retention stage, no trials were given for a period of 1 week. Then each octopus received 2 more trials (MBL) or 3 more trials (MBI) with the original maze configuration. In Stage 3 or the reversal stage, each octopus received 10 trials (MBL) or 18 trials (MBI) with the open burrow placed opposite (180°) to the location it had been during Stage 1.

All trials were videotaped using a video camera mounted above the experimental arena and connected to a remotely located video recorder and monitor. This arrangement ensured that the experimenter remained out of sight of the octopuses during trials and permitted later scoring of octopus performances.

Trials were initially scored for initial heading, distance traveled before entering the open burrow, and time taken to enter the open burrow (MBL octopuses). Initial headings were completely erratic; this variable was subsequently dropped. Plots of distance and time were so similar as to be redundant. Because of unavoidable temperature fluctuations at the MBI

during this experiment (15 to 21 °C) that could have affected metabolism and thus movement rates of the octopuses, the variable chosen for full analysis was distance traveled.

Performances varied widely both within and between octopuses. Not all octopuses responded in every trial; sometimes they never left the center of the tank. If an octopus never found the open burrow in the allotted time, its distance score was arbitrarily set to equal its maximum distance plus one standard deviation, computed from all of its completed trials. MBL and MBI octopuses had been given slightly different numbers of trials in each stage. To combine results, individual performances were aligned at the beginning of each stage; thus, individuals varied in how many trials they completed within each stage.

To evaluate learning, we used median performance for each octopus within each three-trial block. This procedure reduced our data by two thirds; however, it allowed us to see patterns in highly variable performances without fear of bias in our data trimming.

Results

There were no notable differences in octopuses trained at MBL and at MBI. The performances of all 15 octopuses are plotted in Figure 3. There was a marked decrease in distance traveled to find the open burrow between Blocks 1 and 2, with no evidence for improvement thereafter. Performances on the retention trials (Block 9) were as good as asymptotic performances before the week with no trials. When the location of the open burrow was reversed 180° (Block 10), distance traveled to find the open burrow initially increased substantially but then gradually dropped to former, asymptotic levels.

To determine whether learning had occurred, performances of octopuses in their first block of three trials (median performance in the first three-trial block) were compared with performances on subsequent blocks of training trials in Stage 1 (Blocks 2–8). Twelve octopuses provided data for at least six blocks of trials and were included in this analysis. Nine of these 12 octopuses performed better in Blocks 2–8 than in Block 1. The other 3 appeared to have found the open burrow quickly by chance, initially, and

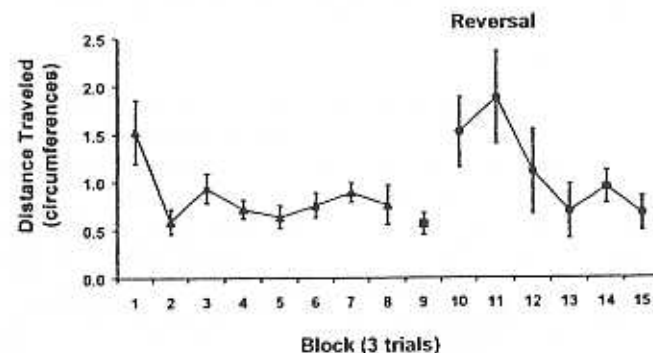


Figure 3. Plot of distance in circumferences that the octopuses traveled to reach the open burrow ($M \pm SE$; $N = 15$). Performances on the initial task of locating a single open burrow improved after the first block of three trials and remained stable thereafter (triangles; Blocks 1–8), suggesting that octopuses had learned the location of the open burrow. Performances remained at their previous low level after a week with no trials (square; Block 9), indicating they had retained the memory of the burrow's location. When the location of the open burrow was reversed 180°, performances were disrupted but subsequently improved (circles; Blocks 10–15), demonstrating relearning.

they maintained this level of success thereafter. We conclude that the octopuses did learn to solve this maze problem, Wilcoxon signed ranks test, $T = 70$, $p < .01$.

To determine whether octopuses had retained what they had learned for a week with no trials, performances of octopuses on their retention trials (Block 9) were compared with their initial performances (Block 1). Eight of the 11 octopuses that responded on retention trials performed better on the retention trials than on their initial trials. The other 3 were the same exceptional individuals mentioned above, and they again went directly to the open burrow during the retention trials. We conclude that the octopuses retained what they had learned for at least 1 week, Wilcoxon signed ranks test, $T = 48$, $p < .05$.

To determine whether octopuses learned the location of the open burrow or just used a strategy for finding the open burrow, performances of octopuses on their initial reversal trials (Blocks 10–11) were compared with their previous, apparently asymptotic performance (Blocks 2–9). Eight of 10 octopuses that completed at least two blocks of reversal trials performed worse on the reversal than on their previous trials. The 2 exceptions performed nearly twice as well on the reversal; 1 of these octopuses was one of the exceptional ones above. We conclude that most of the octopuses learned the location of the open hole and were disrupted by the reversal, Wilcoxon signed ranks test, $T = 49$, $p < .05$. Had they simply learned a strategy, they should have done as well as previously.

To determine whether the octopuses had learned the new location of the open burrow, performances of octopuses on the first half of the reversal trials they completed were compared with their performances on the second half of reversal trials they completed. Eight of 10 octopuses that completed at least four reversal trials showed such improvement. One of the 2 exceptions was the octopus that had been exceptional in every analysis; its performance was about the same throughout the entire experiment. We conclude that the octopuses successfully learned a reversal of the initial maze problem, Wilcoxon signed ranks test, $T = 49$, $p < .05$.

Discussion

The octopuses demonstrated clearly that they had learned the location of the open burrow and that they could remember its location for at least a week. Learning was most evident when the burrow location was reversed 180°, and, as with *O. maya* in a T-maze (Walker et al., 1970), more pronounced learning was evident during relearning, when the spatial task was reversed. Heavy pruning of the data (in this case, use of median scores in three-trial blocks) was required to detect trends in highly variable individual performances, and asymptotic performances were considerably worse than the optimal 0.17 circumferences of a direct line of travel. For reasons that are not clear, erratic and low asymptotic performances seem to be characteristic of octopuses in learning experiments (Boal, 1996; Sanders, 1975). It would require more strongly aversive conditions to evaluate whether the octopuses cannot perform more accurately or whether they are not motivated to do so under experimental conditions.

General Discussion

These experiments demonstrate that (a) octopuses show exploratory learning, (b) within 1 day they can learn the location of an

environmental feature that is not needed at the time of exploration but that could have value at another time, and (c) this learning can be trained and is retained for at least a week.

Results confirm and extend previous experimental studies (e.g., Mather, 1991; Mather & Anderson, 1999; Papini & Bitterman, 1991; Walker et al., 1970) and support field observations suggestive of long-term spatial learning by octopuses (Forsythe & Hanlon, 1997; Mather, 1991; Mather et al., 1985). The learning evident in these experiments may not be spatial; instead, the octopuses could have learned to associate a particular landmark with the burrow (Mather, 1991). The impressive distances at least some octopuses appear to travel in a straight line (Forsythe & Hanlon, 1997) certainly suggest that spatial learning is possible in these mollusks. However, it remains to be determined what exactly octopuses are learning when they learn to orient in space.

This demonstration of learning in octopuses is not a great step forward in and of itself; similar learning has been demonstrated in numerous other invertebrates (see reviews in Abramson, 1994; Gallistel, 1990). Unlike other invertebrates, however, octopuses have complex, vertebrate-like brains that raise interesting questions about the evolution of complex nervous systems (Budelmann, Bullock, & Williamson, 1997). Interest in cephalopod, particularly octopus, nervous systems is long standing and includes a prodigious volume of work addressing the neurobiology of learning (see reviews in Boal, 1996; Boycott, 1954; Boycott & Young, 1950; Chichery, 1992; Mather, 1995; Sanders, 1975; Wells, 1962, 1978; Young, 1961, 1964, 1977). A chief roadblock in investigations of octopus learning abilities has been their relative intractability as experimental subjects. The methods used here were simple to execute and were free from the problems associated with food delivery, stimulus presentation, handling of subjects, and inadvertent experimenter cueing that have complicated many appetitive experiments (Bitterman, 1975; Boal, 1996). Spatially related learning is clearly of biological significance to octopuses. These methods provide a simple way to approach spatial learning questions with octopuses, and the methods are similar enough to open field, radial arm, Morris water, and other mazes used with other species to facilitate comparative studies. For these reasons, we think these experiments offer a step forward in the objective assessment of learning in cephalopods.

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