Experimental Evidence for Spatial Learning in Cuttlefish (*Sepia officinalis*)

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Laboratory mazes were used to study spatial-learning capabilities in cuttlefish (*Sepia officinalis*), using escape for reinforcement. In preliminary observations, cuttlefish in an artificial pond moved actively around the environment and appeared to learn about features of their environment. In laboratory experiments, cuttlefish exited a simple alley maze more quickly with experience and retained the learned information. Similar improvement was not found in open-field mazes or T mazes, perhaps because of motor problems. Cuttlefish learned to exit a maze that required them to find openings in a vertical wall. The wall maze was modified to an arena, and simultaneous discrimination learning and reversal learning were demonstrated. These experiments indicate that cuttlefish improve performance over serial reversals of a simultaneous, visual–spatial discrimination problem.

Cephalopod mollusks have complex nervous systems and highly diverse behaviors. Sensitization, habituation, associative learning, and spatial learning have all been demonstrated (for reviews, see Bitterman, 1975; Hanlon & Messenger, 1996; Mather, 1995; G. D. Sanders, 1975). Because cephalopods' behavioral abilities have been compared with those of lower vertebrates and because they are evolutionarily distant from species more commonly used in learning experiments, cephalopods are worthwhile test species for functional explanations of the evolution of complex nervous systems (Budelmann, Bullock, & Williamson, 1997; Packard, 1972).

Many octopus species forage away from a home den that they return to repeatedly for shelter (e.g., Ambrose, 1982; Boyle, 1983, 1988; Forsythe & Hanlon, 1997; Hartwick, Ambrose, & Robinson, 1984; Mather, 1991). Studies of detours and maze learning have supported field observations suggesting spatial learning (Boal, Dunham, Williams, & Hanlon, 2000; Mather, 1991; Moriyama & Gunji, 1997; Wells, 1964). Other complex learning behaviors observed in octopuses include avoidance learning (Boycott, 1954), discrimination learning (Sutherland & Muntz, 1959), and reversal learning (N. J. Mackintosh & Mackintosh, 1964). Octopuses learn relatively quickly and retain the learned information. It is clear that learning is an important aspect of the natural history of octopuses.

Neurobiological evidence suggests that cuttlefish, like octopuses, could be capable of complex learning. Cuttlefish have a larger overall brain to body size ratio than do octopuses (Maddock & Young, 1987). Furthermore, the vertical lobe in the common European cuttlefish, a brain area thought to be involved in learning and memory (Young, 1960, 1965), occupies roughly 24% of the total brain volume, whereas the vertical lobe of the common octopus occupies about 13% of the total brain volume (Maddock & Young, 1987; Wirz, 1959). In the common European cuttlefish, an improvement in learning has been correlated with increases in the volume of the vertical lobe during postembryological development (Dickel, Chichery, & Chichery, 1998; Messenger, 1973). This finding suggests that vertical lobe size could be associated with learning. Thus, learning and memory could play an important role in cuttlefish natural history.

Cuttlefish are clearly capable of associative learning. Through negative reinforcement, cuttlefish can be trained to not strike at prey items (e.g., Agin, Dickel, Chichery, & Chichery, 1998; Chichery & Chichery, 1992; Dickel et al., 1998; Messenger, 1968, 1977).

There are no published studies of spatial learning in cuttlefish; however, the natural history of cuttlefish provides little evidence for good spatial-learning ability (Boletzky, 1983; Hanlon & Messenger, 1988). Unlike octopuses, cuttlefish do not take shelter in home dens but instead rely primarily on crypsis for defense (Boletzky, 1983). Seasonal onshore–offshore migrations have been documented in the common European cuttlefish (Boletzky, 1983), and there is evidence that Australian cuttlefish return seasonally to a specific breeding site (Hall & Hanlon, 2002). However, because of their short lifespan (1–2 years) and typical semelparity, it is likely that learning is not involved in these migrations. Cuttlefish in nature frequently swim in and around vertical barriers, and tagging experiments indicate that Australian cuttlefish forage away from and then return to particular rocks (O'Dor, personal communication, January 2002). Spatial learning may be useful in negotiating these obstacles (F. K. Sanders & Young, 1940). There is still much to be discovered about the role of spatial learning in the natural history of cuttlefish.

Preliminary observations of 7 cuttlefish placed individually in a large, outdoor artificial pond (13.4 m × 13.7 m; see Figure 1A) indicated that cuttlefish moved around a new environment in a manner consistent with an interpretation of exploration. There was

a barrier within the experimental pond with a small opening that allowed the cuttlefish to travel from one side of the pond to the other (see Figure 1A). Cuttlefish appeared to remember the location of this hole and returned to the site of the hole when it was blocked off (the open hole was approached an average of 14.3 times/hr; the closed hole was approached an average of 25.8 times/hr). The cuttlefish's repeated use of the hole in the barrier and frequent return to this hole suggest that the cuttlefish learned about features of the artificial pond and retained the information from one day to another. Thus, it seemed that cuttlefish could be used in laboratory experiments designed to evaluate spatial learning.

We attempted to provide cuttlefish with maze problems that were comparable with a natural spatial-learning problem, using escape as motivation. In Experiment 1, we asked whether cuttlefish would learn the simple task of exiting a straight alley when escape was the sole motivation. Experiments 2, 3, and 4 were initial attempts to design appropriate mazes that allowed for choice and to assess spatial learning in cuttlefish. Finally, in Experiment 5, we asked whether cuttlefish would show improvement over serial reversals of a two-choice, spatial–visual discrimination problem.

General Method

Experiments were conducted at the Marine Biomedical Institute (MBI) of the University of Texas Medical Branch, Galveston, Texas, and the Marine Resources Center (MRC) of the Marine Biological Laboratory, Woods Hole, Massachusetts. At the MBI, all 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). Salinity ranged from 31 parts per thousand (ppt) to 35 ppt, and water temperature ranged from 16 °C 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 during experimental trials. At the MRC, the water supply was drawn from a depth of approximately 10 ft (3 m) below the surface of Great Harbor and gravity fed to tanks throughout the MRC building. Salinity ranged from 31 ppt to 33 ppt, and the water temperature ranged from 15 °C to 21 °C.

All subjects were laboratory-cultured cuttlefish (*Sepia officinalis*) from the National Resource Center for Cephalopods (MBI, Galveston, TX). Cuttlefish were housed in small groups (4–7 individuals) in large experimental tanks (MBI, 122 cm long × 183 cm wide × 80 cm deep; MRC, 366-cm diameter × 90 cm deep). Gravel, large pieces of polyvinyl chloride pipe, and artificial plants were placed in each tank. Unless otherwise specified, experiments were conducted in the home tanks. The cuttlefish were fed a mixture of live and frozen fish, shrimp, and crabs twice a day in the morning and early evening. A complete description of cuttlefish mariculture can be found elsewhere (e.g., DeRusha, Forsythe, DiMarco, & Hanlon, 1989; Hanley et al., 1998). Data (time only) were log transformed and analyzed using parametric and nonparametric statistics as specified (Siegel & Castellan, 1988).

Figure 1. Illustrations of the mazes tested with cuttlefish as seen from above (except for E). Starting points are indicated with an S, and exit locations are shaded with diagonal lines. A: Artificial pond used for preliminary observations. B: Alley maze used in Experiment 1. C: Open-field maze used in Experiment 2. D: T maze used in Experiment 3. E: Wall maze used in Experiment 4 (left: side view) with detailed view of the wall and two exit doors (right). F: Two-choice discrimination maze used in Experiment 5.

Experiment 1

Method

This experiment tested the feasibility of using a simple escape maze with cuttlefish. Seven subadult cuttlefish (9–15-cm mantle length [ML]) were
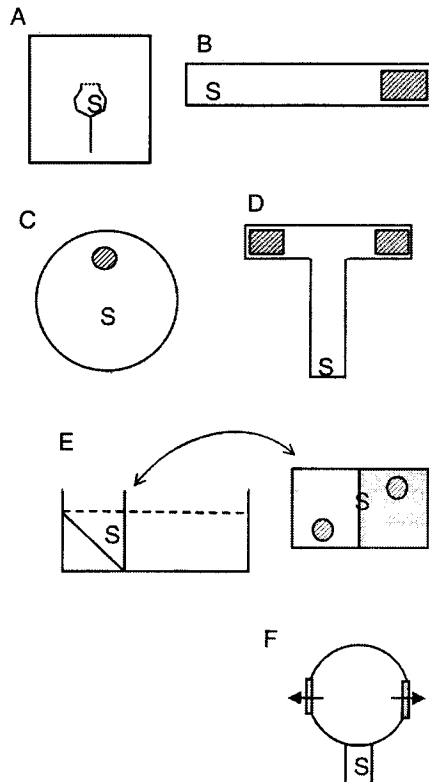
used. An alley (150 cm long × 20 cm wide × 20 cm deep) was constructed with wooden sides and a clear, Plexiglas bottom (see Figure 1B). The alley was suspended over and submerged in a home tank, such that the water depth in the alley was 10 cm. The last 20 cm of the alley had no bottom so the cuttlefish could escape by swimming down into the tank below.

Cuttlefish were placed at the closed end of the alley and allowed to swim to the open end to escape into the home tank below. Cuttlefish are highly visual and like to settle (and bury) on the bottom in a large, open space. They did not settle on the clear bottom of the alley but swam until they found their way out.

There were four stages to the experiment. In Trials 1–15, the open end of the maze faced north. In Trials 16–20, the open end faced south. In Trials 21–25, the open end again faced north. During Trials 26–30, the open end was reversed on each trial.

Results

The performances of all cuttlefish are plotted in Figure 2. The cuttlefish showed significant overall reduction in escape time from a mean of 123 s in Trial 1 to a mean of 20 s in Trial 30: repeated measures analysis of variance (ANOVA), six blocks of five trials, $F(5, 30) = 6.74$, $p < .001$. Differences between individuals were not significant: repeated measures ANOVA, six blocks of five trials, $F(5, 30) = 1.10$, $p > .25$. There was no detectable effect on maze-escape performances from reversing the maze orientation.

Discussion

The cuttlefish quickly learned the simple task of exiting a straight alley with escape as the only motivation. Results were similar to those obtained by Walker, Longo, and Bitterman (1970) using octopuses in an alley with a food reward at the end of the maze. Whereas octopuses required extensive shaping before readily pursuing the food, cuttlefish required no pretraining in this escape maze. The increase in escape time observed between Trials 21 and 25 was probably due to a water quality problem resulting from a blower failure.

Overall, this experiment suggests that learning in cuttlefish can be evaluated using a simple escape maze. Additionally, the lack of effect of maze reversal (Trial 25) suggests that the cuttlefish did not rely on visual features around the laboratory to solve this simple maze problem.
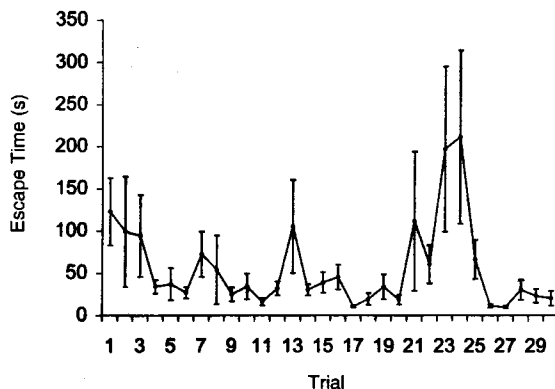

Figure 2. Mean escape time for cuttlefish in the alley maze (Experiment 1; N = 7). The maze orientation was reversed at Trial 16, Trial 21, and Trials 26–30. Error bars represent standard errors.

Experiment 2

Method

An open-field maze was constructed of a round tank (100-cm diameter × 7 cm deep) with a clear Plexiglas bottom and opaque, blue sides (see Figure 1C). A hole (20 cm diameter) was cut into the bottom of the maze 11 cm from one side. This hole allowed the cuttlefish to swim out of the bottom of the maze into the home tank below. For Group 1, a landmark was provided (6-cm × 6-cm × 2-cm piece of Styrofoam tethered and floating directly above the hole in the maze). No specific landmarks were provided for Group 2.

Individual subadult cuttlefish (N = 18; 7–9-cm ML) were placed in the maze and allowed to swim until escaping into the home tank (no time limit). Trials were repeated twice daily for 20 days. For the first 25 trials, training proceeded as described above. For Trials 26–30, the location of the opening was rotated 180°. In Trials 31–40, the location of the maze exit was assigned randomly to one of the four cardinal directions, with the constraint that each direction was presented at least twice.

Results

No significant improvement in maze escape time was found: repeated measures ANOVA, $F(4, 52) = 2.35$, $p = .67$.

Discussion

In this experiment, problems arose from the peculiar way that cuttlefish swim (see Figure 3). Cuttlefish swim slowly forward and backward by using their fins and swim quickly backward by jetting with their funnels. Fine directional control is not possible when jetting, and jetting cuttlefish move haphazardly around the mazes. A number of forward-swimming cuttlefish turned around once they found the maze exit and attempted to jet backward through the exit hole. At times, they missed the hole and had to turn around and again search for the exit. Other times, the cuttlefish would find the escape hole on a forward approach, but on contacting the hole, they became excited or agitated and jetted backwards. Some of the cuttlefish repeatedly forward approached, touched, and jetted backward, appearing "frustrated" with their inability to get through the maze. These various motor constraints probably interfered with maze learning.

Experiment 3

Method

A T maze (100 cm long × 20 cm wide × 10 cm deep) was constructed with black Plexiglas sides and a clear Plexiglas bottom (see Figure 1D). Exits (20 cm × 20 cm) were cut through the bottom at the end of each arm of the T and fitted with removable clear Plexiglas doors. These holes allowed the cuttlefish to swim down into the home tank below. White panels on the walls of the right arm of the T and green panels on the left arm were provided as directional cues (i.e., bright vs. dark).

Subadult cuttlefish (N = 15; 9–13-cm ML) were first pretrained with 12 trials in an alley maze (the central alley of the T maze; see also Experiment 1). After runway training, the cuttlefish were then pretrained with 12 trials with the open arm of the maze varied (forced turn; six right and six left turns in semirandom order; Fellows, 1967). The cuttlefish were then divided into three groups and given 24 training trials as follows: For Group 1, the exit was on the right (white) arm of the T maze. For Group 2, the exit was on the left (green) arm of the T maze. For Group 3, the exit was
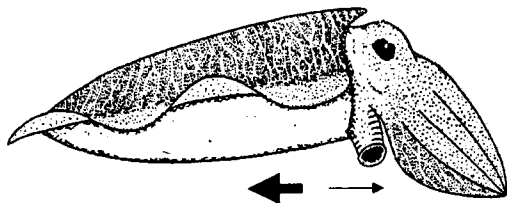
Figure 3. Cuttlefish use fins for slow, forward movement (small arrow) and jet propulsion for rapid, backward swimming (large arrow). From "*Sepia*," by D. H. Tompsett, 1939, *Liverpool Marine Biology Committee Memoirs, 32,* Plate I. Copyright 1939 by the University Press of Liverpool. Adapted with permission from Trevor Norton, Director, Port Erin Marine Laboratory.

located on either the right (white) or left (green) arm of the maze, varied semirandomly from trial to trial.

Trials were conducted twice a day with a 6-hr intertrial interval. Immediately after training, learning was tested in two ways. First, cuttlefish received one trial with both exits open (Test 1). This tested the possibility that cuttlefish could detect the location of the open exit using an unintended cue (e.g., water current). Second, the cuttlefish received one trial with the exits to both maze arms open and the wall panels reversed (right arm green, left arm white; Test 2). This tested the relative importance of turning direction versus wall panel cues.

Results

No improvement in exit time was found: arcsine transformed proportions, repeated measure ANOVA, for group, $F(2, 11) = 0.55, p > .50$; for trial, $F(3, 33) = 0.28, p > .80$; for the interaction, $F(6, 33) = 1.33, p > .25$. Individual performances were examined for evidence of learning. Three cuttlefish from Group 2 that chose the left–green arm in their initial choice and in Test 1 chose the right–green arm in Test 2.

Discussion

Motor constraints may have again interfered with learning. The cuttlefish often swam down the runway portion of the maze, but when they got to the top of the T, they often rested on the bottom and did not move much thereafter. At this point, they needed to make a 90° turn right or left in a small space, interrupting momentum toward finding the exit in the maze. A Y-shape maze could work better.

The 3 cuttlefish that chose the green arm in both Test 1 and Test 2 may have chosen the maze arm on the basis of visual landmarks rather than directional cues. However, this result is uncertain because no evidence for learning was found.

Experiment 4

Method

Observations from the pond suggested that cuttlefish could learn to use openings in vertical barriers. Consequently, a wall maze was constructed by placing a vertical, opaque Plexiglas wall 50 cm from the short end of a rectangular experimental tank, creating a small testing arena and a larger home tank (see Figure 1E). The side of the wall facing the testing arena was covered with material: artificial sea grass on the left and camouflage mesh on the right. Two holes (20 cm diameter) were cut into the wall: one on the left and one on the right. The hole on the left side was 10 cm above the

bottom of the tank, and the hole on the right side was 60 cm above the bottom of the tank. Both exit holes remained open throughout the experiment. A piece of opaque, plastic sheeting the exact width of the tank was angled at 45° from the base of the wall to the water surface on the opposite side of the testing arena (see Figure 1E). Thus, within the testing arena, there was no horizontal surface on which the cuttlefish could settle, providing increased motivation for escape. A gravel substrate was provided in the home tank.

Individual subadult cuttlefish ($N = 18$; 9–13-cm ML) were placed in the testing arena midway between the openings and facing the back wall. The time to exit the arena (maximum 10 min) and the exit used were recorded. If a cuttlefish did not escape, the escape time was recorded as 1,000 s.

Results

Cuttlefish demonstrated a significant decrease in exit time within 10 trials: repeated measures ANOVA, $F(9, 135) = 7.47, p < .001$ (see Figure 4). The mean escape time in the 1st trial was 15.6 min (only 3 of 18 cuttlefish escaped), whereas the mean escape time in the 10th trial was 4.0 min (15 of 16 escaped). This was not a result of an improvement in maze escape time (mean first escape time $= 154.0$ s, $SEM = 33.2$; mean last escape time $= 154.0$ s, $SEM = 40.3$). Thirteen of 18 cuttlefish preferred the left–lower hole, and cuttlefish exited through their preferred hole an average of 78.00% of the time (range $= 50.00\%–100.00\%$, $SD = 16.17$).

Discussion

Cuttlefish learned to escape from this two-choice maze. They did not escape more quickly; time to escape the small arena was simply the time it took the cuttlefish to turn around and swim out. Initially, those that did not exit swam rapidly around the testing arena, repeatedly approaching the corners. At the end, those that did not escape wedged themselves between the plastic sheeting and the wall and remained still for the full 10 min.

Results from this experiment indicate that the problem with the open field and T mazes lies not with the cuttlefish learning abilities but instead with the maze design and cuttlefish motor behavior. In both the wall maze and the alley maze, cuttlefish exited while swimming slowly forward, and thus, motor constraints did not interfere with learning.
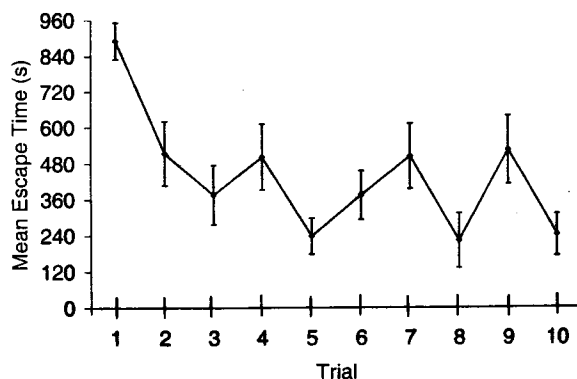
Figure 4. Mean escape time for cuttlefish in the wall maze (Experiment 4; $N = 18$). Cuttlefish demonstrated a significant decrease in exit time within 10 trials. Error bars represent standard errors.

Cuttlefish are generally benthic; thus, the greater preference for the left–lower hole may have resulted because cuttlefish remained near the bottom of the testing arena and the lower hole was easier to locate.

Experiment 5

Method

The purpose of this experiment was to further evaluate learning of a simultaneous, visual–spatial discrimination task. Subsequently, reversal learning of this problem was tested. Twenty cuttlefish were used in this experiment: 13 adults at the MRC (15–25-cm ML) and 8 subadults at the MBI (10–15-cm ML). A circular testing arena was constructed from a large, plastic barrel (71 cm deep × 56 cm diameter; see Figure 1F). A start tube (16 cm diameter) with doors on both ends was placed through one side of the arena, 17 cm below the top edge (12 cm below the water surface). Two exit holes (16 cm diameter) were cut on opposite sides of the arena, 6 cm below and perpendicular to the start tube. A panel of striped fabric (36 cm × 36 cm) surrounded the exit located on the right side of the start tube, and a spotted panel of fabric (36 cm × 36 cm) surrounded the exit located on the left side of the start tube. Exits were fitted with movable, clear Plexiglas doors. The bottom of the arena was fitted with a plastic mesh cone (point up, 12 cm high) such that, like the wall maze, there was no horizontal surface on which the cuttlefish could settle. The maze was placed within the home tank at the beginning of each set of trials.

In each trial, 1 cuttlefish was herded into the start tube. After 1 min, the door to the testing arena was opened. The cuttlefish was given 3 min to exit the tube and enter the arena. If the cuttlefish did not enter the arena, the experimenter chased it into the maze using a net. Once the cuttlefish was inside the arena, the start tube was blocked off. The cuttlefish was given 7 min to escape the arena before the experimenter chased it out of the open exit with a net. The escape time for each trial was recorded. Any trial in which the cuttlefish failed to escape was assigned an escape time of 10 min. In each trial, the maze was positioned in a random direction within the home tank to control for the possibility that cuttlefish used cues around the laboratory to locate the open exit.

There were four stages to this experiment: pretraining, preference testing, training, and reversal. Individual cuttlefish (N = 21) were pretrained with both exit doors open. Trials were repeated until the cuttlefish independently exited the maze once through each exit. After pretraining, exit preference was determined by observing the exit most frequently used in five further escapes. After pretraining and preference testing, experimental trials began. In the first set of training trials (Reversal 0), the cuttlefish's preferred exit remained closed. Each cuttlefish received six trials per day (at least 45-min intertrial interval) until six of seven consecutive escapes were achieved in less than 1 min. Once this criterion had been reached, the cuttlefish were given a probe trial with both exits open. This probe tested the possibility that cuttlefish could detect the location of the open exit using an unintended cue (e.g., water current). If the cuttlefish did not escape through the trained exit, they were given two more training trials and then another probe trial; this occurred only three times, in 3 different cuttlefish. Once the cuttlefish was trained, the open door was closed, the opposite door was opened, and the training procedure repeated. Training and door reversal continued as time permitted.

Results

All cuttlefish completed pretraining successfully (range = 5–16 trials). There were no notable performance differences between cuttlefish tested at MBL and MBI or between female and male cuttlefish. Nine cuttlefish preferred the striped (right) exit and 12 cuttlefish preferred the spotted (left) exit. Fourteen cuttlefish had strong preferences (4 or 5 out of 5 trials). These strong preferences

were split evenly between the two exits (8 cuttlefish preferred the striped exit, and 6 preferred the spotted exit).

For the 20 cuttlefish that completed Reversal 0 (training against preference), the mean number of trials was 36 (range = 13–72), the mean escape time was 5 min 8 s (range = 2 min 50 s to 6 min 24 s), and the mean percentage of escapes in less than 1 min was 36.2% (range = 13.9%–64.7%). One cuttlefish died during the course of training for Reversal 0.

There was a marked improvement in performance for cuttlefish that completed subsequent reversals. For cuttlefish completing Reversal 2, the mean number of trials during Reversal 2 was 17 (range = 6–28), the mean escape time was 2 min 48 s (range = 1 min 4 s to 4 min 6 s), and the mean percentage of escapes in less than 1 min was 61.9% (range = 33.3%–76.9%).

Four cuttlefish completed six reversals and showed a significant improvement in maze performance. Improvement was indicated by a significant decrease in the number of trials per reversal, a significant decrease in the percentage of errors per reversal, and a significant increase in the number of escapes in less than 1 min (see Table 1 and Figures 5 and 6). The apparent decrease in average escape time across all reversals was not significant (see Table 1).

For further analyses, performances on Reversals 0, 2, 4, and 6 (against original preference) were considered separately from performances on Reversals 1, 3, and 5 (consistent with original preference). For all variables, there was significant improvement when trained against original preference but not when trained with original preference (see Table 1).

Two of the cuttlefish that completed Reversal 6 showed performances suggestive of one- to two-trial learning in later reversals: One cuttlefish completed Reversals 3 and 6 in just eight trials per reversal, and the other cuttlefish completed Reversals 5, 6, and 9 in eight trials per reversal. Because criterion level performance was six of seven consecutive escapes in less than 1 min, the absolute minimum possible number of trials in a reversal was seven.

Table 1

Results of Analyses of the Effects of Serial Reversals on Learning (N = 4)

Variable	k	L	p
No. trials per reversal			
Overall	7	505	**< .01**
Against preference	4	115	**< .01**
With preference	3	50	> .05
% error			
Overall	7	521	**< .001**
Against preference	4	114	.01
With preference	3	53	> .05
No. escapes in less than 1 min			
Overall	7	497	**< .025**
Against preference	4	112	**< .05**
With preference	3	46	> .05
Mean escape time			
Overall	7	480	> .10

Note. Results (L) are based on the Page test for ordered alternatives (Siegel & Castellan, 1988). Boldface type indicates significant results. k = the number of reversals.

Discussion

Previous authors have established that cuttlefish can learn a simultaneous discrimination task (Messenger, 1977). This experiment is the first to establish that cuttlefish improve over serial reversals of a simultaneous discrimination problem. Results are consistent with those found in octopuses trained simultaneously (N. J. Mackintosh & Mackintosh, 1964; Young, 1962) but not successively (J. Mackintosh, 1962). Improvement over serial reversals may indicate that cuttlefish are learning how to learn (Harlow, 1949). This ability allows animals to update or relearn solutions to problems when previous solutions are no longer relevant.

Significant improvement in escape performance was observed across reversals in which the cuttlefish were trained against their original door preference; only minor (statistically insignificant) improvement was observed across reversals in which the cuttlefish were trained consistent with their original door preference. This is similar to findings from octopus discrimination-learning experiments (Boal, 1996).

The performances of 2 cuttlefish were indicative of two-trial learning. N. J. Mackintosh and Mackintosh (1964) also observed an octopus that showed one-trial learning. One-trial learning has been attributed only to vertebrates (see reviews in Bitterman, 1975; N. J. Mackintosh, Wilson, & Boakes, 1985). The few published studies on reversal learning in marine invertebrates (e.g., crabs: Datta, Milstein, & Bitterman, 1960; isopods: Thompson, 1957) did not show one-trial learning, but anecdotes with octopuses suggest that very rapid learning of some tasks should be investigated more thoroughly.

It remains unclear which cue the cuttlefish used to locate the open exit: direction relative to the start box or panel pattern surrounding the exit. Further experimentation to distinguish between these alternatives is currently in progress.

General Discussion

This is the first set of experiments to examine spatial and reversal learning in cuttlefish. Specifically, this set of experiments demonstrated that cuttlefish (a) can solve an experimental maze problem with escape as the sole motivation, (b) have particular
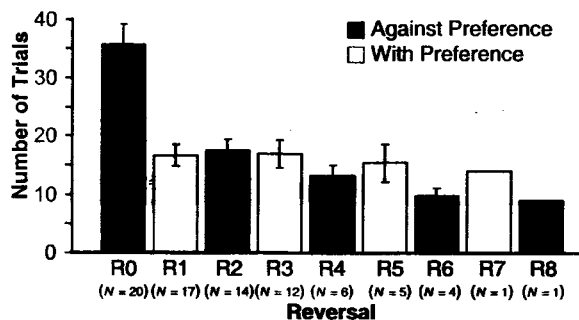

Figure 6. Mean percentage of errors (nonescapes) per reversal (Experiment 5; $N = 20$). Cuttlefish showed a significant decrease in the percentage of errors per reversal when trained against original preference (shaded bars) but not when trained in the direction consistent with original preference (open bars). Error bars represent standard errors. R = Reversal.
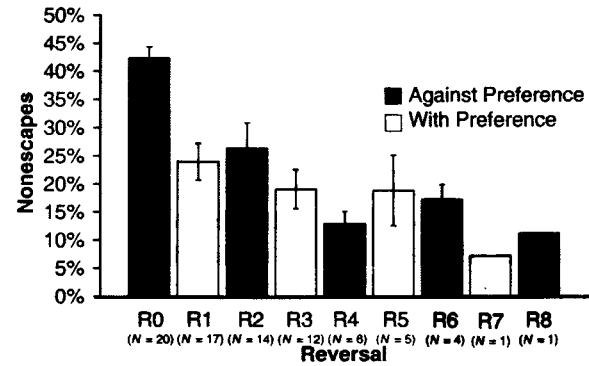
motor needs that can confound the results of spatial-learning experiments, and (c) show spatial learning and improvement across serial reversals when these confounders are overcome.

It is unclear how cuttlefish may use such learned spatial information in the natural environment. Unlike many octopuses, which probably use learning to relocate home shelters, cuttlefish rely primarily on crypsis for defense. Cuttlefish constantly move in and around vertical obstacles in the natural environment, and spatial learning may help them negotiate these obstacles (F. K. Sanders & Young, 1940). Alternatively, perhaps cuttlefish use spatial learning to relocate good foraging patches or return to a prominent landmark between forages (O'Dor, personal communication, January 2002). Unfortunately, we have no field data that address these particular hypotheses.

Spatial learning is widespread among animals. Spatial-learning studies have focused on mammals and birds but have also been successful in reptiles, amphibians, and fish as well as in invertebrate groups such as arthropods and octopuses (for reviews, see Capaldi, Robinson, & Fahrbach, 1999; Golledge, 1999; Sherry, 1998; Wehner, 1981). Spatial problems typically encountered by different animals, such as returning to home or finding food sources, are remarkably constant across different species. Locating food resources, shelter, and escape routes are each facilitated by spatial learning. It remains unclear which aspects of cephalopod life history might have caused their great cognitive divergence from other mollusks. These mazes could provide a tool for future studies addressing this question more precisely.

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Figure 5. Mean number of trials until reversal (criterion-level performance; Experiment 5; $N = 20$). Cuttlefish showed a significant decrease in the number of trials per reversal when trained against original preference (shaded bars) but not when trained in the direction consistent with original preference (open bars). Error bars represent standard errors. R = Reversal.

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