BRIEF COMMUNICATIONS

Sign Tracking in Cuttlefish (*Sepia officinalis*)

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Two groups of cuttlefish (*Sepia officinalis*) were used to demonstrate classical conditioning in this species and to determine whether the resulting approach response would be that of sign tracking or goal tracking. For cuttlefish in the paired condition, a flashing light was presented at one end of a long tank followed by food dropped into the center of the tank. For cuttlefish in the unpaired condition, food was dropped into the center of the tank either before or after the flashing-light stimulus. Paired cuttlefish oriented to the light, positioned themselves within striking distance, and occasionally attacked the light. Unpaired cuttlefish showed no reliable response to either stimulus. The results demonstrate that cuttlefish are capable of signal learning and that, under the conditions tested, cuttlefish sign tracked. This study begins a comparative analysis of learning in cuttlefish and offers a possible ecological advantage for sign-tracking behavior.

Comparative analyses of learning between vertebrates and invertebrates are necessary to fully answer questions related to the evolution of intelligence (Bullock, 1984; Thomas, 1980). Although few dispute this claim, it is somewhat surprising that researchers have focused their efforts on vertebrate learning models even though invertebrates constitute 95% of all animals. Of the research that has been conducted with invertebrates, most has involved mollusks or insects. This research has focused on questions related to the neurobiology of learning in *Aplysia, Apis mellifera,* and *Hermissenda* (e.g., Carew & Sahley, 1986; Crow, 1988; Menzel, 1983; Rogers, Talk, & Matzel, 1994) and general learning phenomena in honeybees (e.g., Bitterman, 1988, 1996; Gould, 1984, 1993).

Recently, investigators have begun to examine the cognitive and behavioral abilities of coleoid cephalopods (cuttlefish, octopuses, and squid; Boal, 1996a, 1996b; Hanlon & Messenger, 1996; Mather, 1995). Such investigations show great promise. Among the invertebrates, the cephalopod brain is remarkably complex and is relatively large (Abbott, Williamson, & Maddock, 1997; Budelmann, 1995). In addition, the cognitive and behavioral repertoires of coleoid cephalopods are greater than those of *Aplysia* or *Hermissenda.* Habituation (Boycott, 1954; Wells & Wells, 1956),

operant conditioning (Crancher, King, Bennett, & Montgomery, 1972; Dews, 1959), discrimination learning (reviewed in Boal, 1996b), object permanence (Sanders & Young, 1940), lower levels of concept formation (Boal, 1991), and some forms of observational learning (Fiorito & Scotto, 1992) have been reported.

Although interest in learning in cephalopods is growing, investigators have virtually ignored the cuttlefish (*Sepia officinalis*). Cuttlefish would be expected to show strong evidence of learning because their nervous system is complex and controls sophisticated and effective sense organs as well as a complex muscle system capable of coordinated and finely tuned motor output (Budelmann, 1995). In addition, the ratio of brain to body weight in *Sepia officinalis* is the highest among coleoid cephalopods (Maddock & Young, 1987; Packard, 1972).

The question arises as to where to begin a systematic analysis of learning ability in cuttlefish. Thomas (1980) presented a hierarchy of learning abilities that provides one basis for a starting point. The first 3 levels of this hierarchy include habituation, signal learning, and stimulus–response learning. *Habituation* involves the waning of a response to a repeatedly presented stimulus and may relate to an animal's learning that certain stimuli are not followed by events of biological significance. *Signal learning,* or Pavlovian conditioning, involves arranging a contingency between a stimulus and an outcome. According to Gagné (1970), the animal "learns to make a general, diffuse response to a signal" (p. 63). *Stimulus–response learning,* or instrumental conditioning, involves arranging a contingency between a response and an outcome. Gagné (1970) argued that here the animal learns a "precise response to a discriminated stimulus" (p. 63).

A few studies have reported learning in cuttlefish, but it is unclear whether any of Thomas's (1980) three levels of learning ability have been demonstrated. Sanders and Young

(1940) placed a cuttlefish in a long runway that contained a glass barrier at one end. A prawn was placed behind the barrier but in full view of the cuttlefish. The cuttlefish would swim down the runway and repeatedly attack the prawn by striking its tentacles against the glass. Sanders and Young reported that this attack behavior decreased from approximately 10 shots per 2 min to 0 shots over a 30-min period. The problem is determining what form of learning was represented by this procedure. The decrease in attacks could be attributed to habituation, avoidance learning, or even extinction. The procedure used by Sanders and Young did not allow one to decide what form of learning, if any, was being demonstrated.

In a second series of experiments, Sanders and Young (1940) claimed to have demonstrated discrimination learning. Cuttlefish were housed in a long wooden tank. On negative trials, a glass barrier was positioned at one end of the tank to separate the cuttlefish from a prawn. The glass barrier had a white circle painted on it. On positive trials, a prawn was placed in the tank with no glass barrier. Each day the cuttlefish received three negative trials followed by a positive trial. The number of tentacle strikes at the glass barrier declined over days, and this was viewed as discrimination learning. However, the cuttlefish could have stopped striking the glass barrier because of habituation, extinction, or avoidance. The procedure did not require discriminating between positive and negative conditioned stimuli. In addition, there was potential for sequence effects. Rewarded and nonrewarded trials were not randomly presented, allowing for the possibility that the cuttlefish learned that its responses were not rewarded until late in a session.

Wells (1958) demonstrated that newly hatched *Sepia* do not begin to attack prey items until they are approximately 48 hr old. At this age, their reaction time to respond to a prey item (a mysid) decreased from 2 min to 5 or 10 s after five attacks. Wells argued that experience, not maturation, modified this behavior. He based his argument on the finding that hatchling cuttlefish that were kept for 5 days without eating also initially took 2 min to respond to a prey item. Consistent with cuttlefish that were not starved for 5 days, these cuttlefish reduced their latency to respond only after five or so attacks. Interestingly, in another manipulation, Wells allowed cuttlefish to attack a glass jar containing mysids. Reaction times to respond to the mysids also decreased even though the strikes were not rewarded in this case. Thus, the reduction in response time to attack may have reflected motor practice rather than associative learning.

Messenger (1973) assessed learning by placing a cuttlefish in a tank and allowing it access to prawns that were held in a transparent plastic tube. As in Sanders and Young's (1940) study, the cuttlefish initially struck the tube repeatedly, but after 3 min, the response waned. It appeared that the reduction in strike behavior was sensitive to experimental contingencies. If a cuttlefish was rewarded with a prawn for striking the tube, the strike response persisted, and if the cuttlefish was punished with electric shock, it stopped striking the glass much faster.

These results provide better evidence of associative learning, but not conclusive evidence. Messenger (1973) did

not use a noncontingent shock control group to assess whether the strike response was being punished or whether shock simply suppressed all behavior. Similarly, a noncontingent reward control was not used to assess whether the strike response was being rewarded. It is true that striking persisted for a longer period of time, but it did not increase over baseline levels. In addition, in the procedure, Messenger "reinforced" the cuttlefish only every fifth response during a single 20-min session. Thus, the cuttlefish received intermittent reward only three or four times. Its seems unlikely that an association between response and reinforcer could be achieved in that time period. It is more likely that the increased persistence of the strike behavior was a result of disinhibition. Use of the noncontingent reinforcement control could distinguish between these two alternatives.

In 1977, Messenger reported that cuttlefish had solved a size discrimination problem. Cuttlefish had learned to choose a large square over a small square at a distance of 60 cm in three sessions. Performance increased from approximately 60% to 85% correct. Interestingly, performance continued to improve over the next two sessions even though the small square was brought forward 30 cm relative to the large square. Messenger argued that the result constituted evidence of size constancy and that cuttlefish could learn to discriminate. However, from the description it could not be determined how many trials were run per session, whether position or size variables were counterbalanced, or whether the discrimination was conducted with responses to the negative stimulus being punished with electric shock, a common methodological procedure of the time. In addition, there appeared to be a bias toward responding to the large square.

From the published studies on learning in cuttlefish, it appears safe to conclude that cuttlefish can modify their behavior on the basis of past experience, but it is unclear what types of learning abilities they have. Thus, it is not certain whether cuttlefish are capable of habituation, signal learning, or stimulus–response learning. To begin a systematic and comparative analysis of learning in cuttlefish, clear demonstrations of each of the first 3 levels of learning ability identified by Thomas (1980) are needed. We chose to begin with signal learning. We chose signal learning, or classical conditioning, for two reasons. First, we could not find evidence of such learning in cuttlefish. Second, the classical-conditioning literature is extensive and contains references to a large number of species, thus allowing for comparative analyses.

In classical conditioning, one pairs a conditioned stimulus (CS) with an unconditioned stimulus (US). The typical conditioned response, at least to a localized appetitive CS, is one of approach. In most of these procedures, the CS and the US are not separated spatially, making it unclear whether the animal is approaching the CS or the US. Studies in which the CS and the US have been separated spatially have shown mixed responses. Sometimes animals approach the CS, a behavior known as sign tracking (Hearst & Jenkins, 1974), and sometimes animals approach the US, a phenomenon known as goal tracking (Boakes, 1977).

One variable that may affect whether an animal sign tracks or goal tracks is the nature of the US. Burns and Domjan (1996) showed that the dominant response of Japanese quail in a sexual-conditioning paradigm was sign tracking. In sexual conditioning, the US is not stationary, and the animal must track a moving stimulus in order to contact the US. Burns and Domjan argued that a moving US may lead to sign tracking whereas a stationary US may support goal tracking.

We conducted this study to determine whether cuttlefish are capable of signal learning and to see if such learning leads to sign tracking or goal tracking. Cuttlefish feed on moving organisms, including crabs, shrimp, and fish. As Messenger (1968) showed, to eat, the cuttlefish must orient to a potential prey item, position itself approximately 8 cm from the prey, and then attack either by rapid tentacle extension or by pouncing. Given that the US in this study involved live prey that would require follow-and-capture behavior, we predicted that cuttlefish would show signal learning and that they would sign track.

Method

Subjects

Sixteen experimentally naive cuttlefish (Sepia officinalis), with mantle lengths measuring between 8 and 14 cm, were obtained from the National Resource Center for Cephalopods (Galveston, TX). The cuttlefish were maintained in a closed water filtration system based on the system proposed by Oestmann, Scimeca, Forsythe, Hanlon, and Lee (1997). On arrival, they were housed in individual fiberglass tanks measuring 115 cm long × 56 cm wide × 30 cm deep. These home tanks also served as the experimental tanks. The cuttlefish were acclimated to the experimental tanks for 1 week and were fed goldfish that measured 4–5 cm in total length four times per day. To simulate conditioning trials, they were fed four fish spaced approximately 20 min apart. Three cuttlefish died during this week, and 1 cuttlefish failed to eat reliably. The experiment began with 6 cuttlefish randomly assigned to the paired group and 6 cuttlefish randomly assigned to the unpaired group.

Apparatus

Two 5-cm holes were drilled in the floor of each tank. These holes were positioned 10 cm from the front and the back of the tank and were centered laterally. The holes were covered with clear acrylic plastic that had been sanded with medium-grain sandpaper. We positioned a 4-W lightbulb beneath each hole. This light served as the CS. Presentations of the CS were controlled by an Apple IIgs microcomputer linked to an interface adapter (VIA r6522) manufactured by Life Science Associates (Bayport, NY). The computer was programmed to cause the light to flash at a rate of approximately twice per second. Each CS was presented for a total of 30 s. Live feeder goldfish, 4–5 cm in length, served as the US. The experimenter used a polyvinyl chloride pipe cup filled with water and connected to a 110-cm-long handle to deliver the goldfish. A monochrome video camera (Sony SSC-M370) and a videocassette recorder (Panasonic AG-5700) recorded the results of all trials. The camera was mounted 135 cm above the tanks and could be moved from one tank to the next without disrupting the cuttlefish.

Procedure

After the acclimation period, conditioning trials began. For half of the subjects in either group, the CS was presented at the front of the tank, and for the other half of the subjects, the CS was presented at the back of the tank. If necessary, at the start of each trial, the cuttlefish were gently moved to the opposite end of the tank from the CS.

For the cuttlefish in the paired condition, there was a 90-s delay, and then the CS was presented for 30 s followed by US delivery to the side of the tank. The goldfish were always delivered 50 cm from the location of the CS. The cuttlefish received four trials per day for 30 days. The intertrial interval was approximately 20 min, and the sessions were run daily between 10 a.m. and 1 p.m.

The cuttlefish in the unpaired condition also received four trials per day for 30 days. Trials consisted of two types. On half of the daily trials, following the 90-s delay, a goldfish was delivered to the side of the tank, and the CS was presented 2 min later. On the other half of the daily trials, following the 90-s period, the CS was presented. Two minutes after offset of the CS, the goldfish was delivered. The two trial types were randomly presented with the stipulation that two of each trial type occurred each day.

Results

We measured three different behaviors exhibited by cuttlefish in foraging situations. These behaviors, attention, positioning, and seizure, were first classified by Sanders and Young (1940) and were later refined by Messenger (1968, 1977). Attention is observed when a prey item is first introduced. The cuttlefish's eye or eyes move toward the prey and fixate on it. Head movements and body movements (a result of funnel and fin movement) cause the cuttlefish to directly face the prey. In addition, color changes may occur on the cuttlefish's arms, head, and mantle. The end result of the attention phase is that the cuttlefish is facing its prey and the prey is fixated binocularly. We recorded an attention response if the cuttlefish moved its head and body in such a way as to direct its head toward the CS. If the cuttlefish was already oriented toward the CS, we recorded an attention response if the cuttlefish began to move its fins during the CS presentation.

Positioning involves maintaining a distance of approximately 8 cm from the prey. This typically requires movement toward the prey. However, if the cuttlefish is too close to strike, it may remain stationary until the prey moves, or the cuttlefish may retreat to a distance of 8 cm. We recorded a positioning response if the cuttlefish, during the CS presentation, moved at least one half of its body length toward the CS or otherwise positioned itself within striking distance of the CS. If the cuttlefish moved toward the CS, we assumed it had also produced an attention response.

Seizure occurs either through rapid extension of the tentacles or by pouncing. We recorded a seizure or an attack response if, after an attention and a positioning response, the cuttlefish either pounced on the CS during its presentation or moved to within 8 cm of the flashing light and shot its tentacles at the flashing light.

To determine the reliability of these response measures, we had two observers independently record the responses by cuttlefish from 175 randomly selected trials. The interob-

server reliabilities for attention, positioning, and seizure responses were 88%, 94%, and 98%, respectively.

Three of the cuttlefish in the unpaired condition died during the course of the experiment. Thus, the data reported were collected from 6 cuttlefish in the paired condition and from 3 cuttlefish in the unpaired condition. Attention and positioning data were averaged over two session blocks and were analyzed using a repeated measures analysis of variance design. Groups (paired vs. unpaired) was the between-subjects variable, and session blocks (Blocks 1–15) served as the within-subjects variable.

With respect to the attention response, cuttlefish in the paired condition oriented to the CS significantly more than did the cuttlefish in the unpaired condition, $F(1, 7) = 7.15$, $p < .05$. Cuttlefish in the paired condition oriented to the CS on 29% of all trials, whereas cuttlefish in the unpaired condition oriented to the CS on only 3% of all trials. The Groups × Blocks interaction was significant, $F(14, 98) = 3.44$, $p < .05$. Figure 1 shows that cuttlefish in the paired group did not differ from cuttlefish in the unpaired group for the first 5 blocks. Beginning in Block 6, cuttlefish in the paired group showed an increasingly greater percentage of attention responses to the CS, whereas cuttlefish in the unpaired group did not.

A simple main effects test of the interaction (Kirk, 1968) confirmed the visual impression provided by Figure 1. The difference between the paired condition and the unpaired condition was significant for Blocks 10, 11, 12, and 13. The F values ($df = 1, 105$) were 14.52, 10.79, 10.79, and 14.52, respectively. In addition, the simple main effects test showed

that there was no effect of trial blocks for the unpaired group, $F(1, 98) = 2.17$. In contrast, the effect of trial blocks was significant for the paired group, $F(1, 98) = 317.23$. All simple main effects differences were tested at $p < .003$ to correct for error rate.

The results were similar for the positioning data. Cuttlefish in the paired group positioned themselves to the CS significantly more than did those in the unpaired group, $F(1, 7) = 6.01$, $p < .05$. Overall, paired cuttlefish positioned themselves to the CS on 20% of all trials, whereas unpaired cuttlefish positioned themselves to the CS on only 4% of the trials. The Groups × Blocks interaction was also significant, $F(14, 98) = 3.19$, $p < .05$. Beginning in Block 6, paired cuttlefish positioned themselves to the CS on an increasingly greater percentage of trials (see Figure 2). Unpaired cuttlefish made very few positioning responses to the CS.

A simple main effects test of the interaction showed that paired cuttlefish positioned significantly more often than the unpaired cuttlefish beginning with Block 10, $F(1, 105) = 12.21$. The differences between the paired and unpaired groups were also significant for Blocks 11, 13, and 14 (all $Fs > 10$). In addition, the simple main effects test showed that the differences between the trial blocks were not significant for the unpaired group, $F(1, 98) < 1$, but the differences between the trial blocks for the paired group were highly significant, $F(1, 98) = 250.46$. Again, the simple main effects tests were conducted at $p < .003$ to correct for error rate.

Only 1 cuttlefish in the paired condition and none in the unpaired condition consistently attacked the light. The
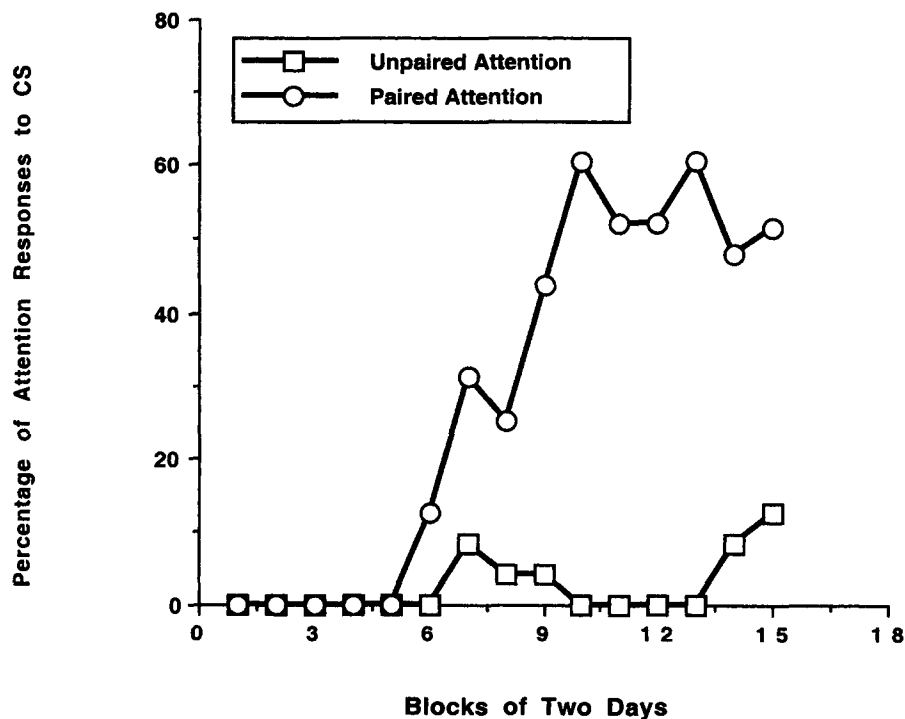

Figure 1. Percentage of attention responses to the conditioned stimulus (CS) for the paired and unpaired conditions.
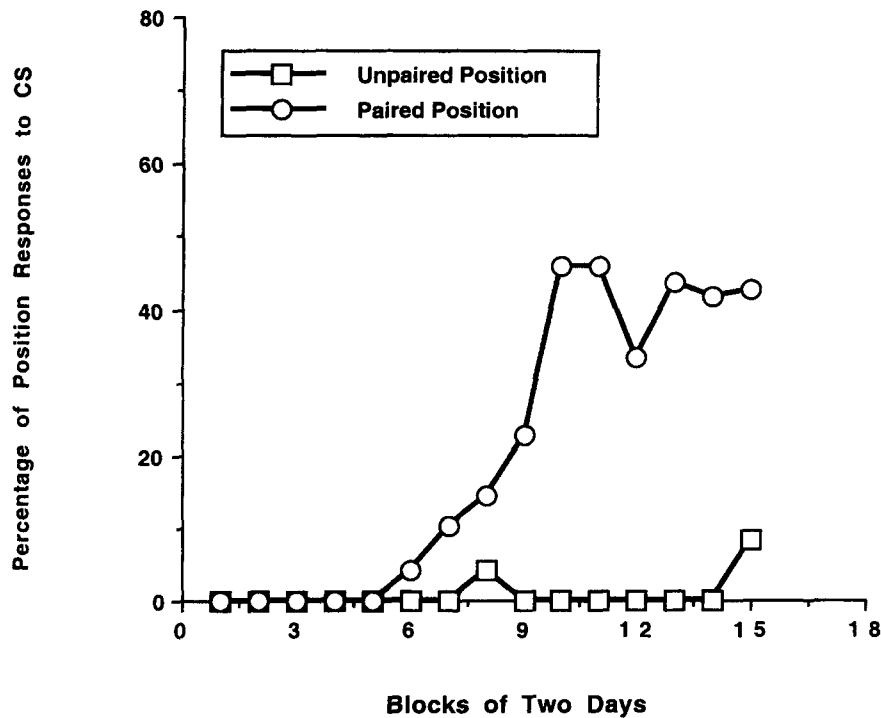
Figure 2. Percentage of position responses to the conditioned stimulus (CS) for the paired and unpaired conditions.

consistent cuttlefish attacked the light on 75% of the trials over the last 10 days of training.

Discussion

The results confirmed the hypothesis that cuttlefish are capable of signal learning, and they provide the first controlled demonstration of associative learning in this species. The hypothesis that cuttlefish would sign track was also confirmed. The cuttlefish in the paired condition oriented to and then positioned themselves toward the CS significantly more often than did the cuttlefish in the unpaired condition. There was no tendency for either group to orient to or move to the side of the tank where the food was introduced. Thus, the cuttlefish approached the CS but not the US in response to the flashing light. This sign-tracking behavior is consistent with a variety of vertebrate species, including crows (Powell & Kelly, 1976), Japanese quail (Burns & Domjan, 1996), monitor lizards (Loop, 1976), pigeons (Silva, Silva, & Pear, 1992), and rats (Locurto, Terrace, & Gibbon, 1976).

Cuttlefish sign tracked under conditions in which the CS and the US were separated by 50 cm. In rats, separating the CS from the US by more than 30 cm disrupted sign tracking (Holland, 1980), and in pigeons, separating the CS from the US by 60 cm reduced sign tracking (Silva et al., 1992). The present findings are similar to those of Burns and Domjan (1996), who showed that the dominant response of Japanese quail in a sexual-conditioning paradigm was that of sign tracking. Burns and Domjan used a live sexually receptive female as the US. To copulate with the female, the male had to orient and then track the female. This behavior was followed by grab and mount behavior.

The US in Burns and Domjan's (1996) study shared many characteristics with the US in the present study. Although we used a foraging paradigm as opposed to sexual conditioning, both USs required that the animal orient to, move toward and follow, and capture or secure the US. Such characteristics may lead to sign tracking. For stationary USs, the predominate conditioned behavior might be goal tracking. If a given CS always predicts a stationary US to occur in a certain location, the animal could be predisposed to goal track. It is interesting to note that most of the studies of sign tracking have used a stationary US.

Sign tracking might make sense when it is viewed from an ecological perspective. Shrimp, small fish, and crabs make up the majority of the diet for a cuttlefish. These prey avoid being eaten by hiding, moving, or both. As a result, they are not always going to be in sight of the predator. One way for a cuttlefish to find food would be to look for stimuli that have been associated with prey. Such stimuli could include different types of plants, rocks, and so forth. When the cuttlefish approaches such stimuli, it is sign tracking.

Support for this idea comes from Sanders and Young (1940), who maintained a cuttlefish in a large rectangular tank that contained an enamel pail and an enamel wall at one end. In the experiment, a shrimp was tied to a string and placed in front of the cuttlefish. The shrimp was then dragged around behind the pail and then behind the wall.

The cuttlefish tracked the shrimp even though it was moved out of the visual field. Sanders and Young commented, "After a prawn has disappeared round a corner that corner exerts an attraction which it did not possess before" (p. 522). It could be argued that the ability to approach a stimulus that has been associated with food might be important for an animal that hunts live and cryptic prey.

With respect to a comparative analysis of sign tracking, it appears that differences may exist between large-brained invertebrates (the coleoid cephalopods) and invertebrates with less developed nervous systems. Cuttlefish may behave more like vertebrates than more primitive mollusks in their responses to CSs. Kemenes and Benjamin (1989) examined autoshaping behavior in pond snails (*Lymnaea stagnalis*). They presented a tactile stimulation to the lip of the snails as the CS, and a concentration of sucrose water directed through small tubes into their dish served as the US. Snails in the paired group moved toward the location where sucrose water was injected into their dish and thus showed goal tracking.

The present experiment provides clear evidence that cuttlefish sign track. The experiment does not address the underlying mechanism for this behavior. It may be that the cuttlefish formed a stimulus–reinforcer connection and that this association supported sign tracking. In this model of association, the CS elicits an approach response because presentation of the CS activates a representation of the US. Consistent with that idea, the cuttlefish oriented to, approached, and occasionally attacked the CS in the same manner as they attack prey. It is also possible that the cuttlefish formed a response–reinforcer association. In this second model, the response of moving toward the flashing CS was reinforced. To determine the nature of the association formed in this paradigm, omission studies are necessary (Williams & Williams, 1969). Future research should address this question.

Much research remains to be done, but it is clear that cuttlefish sign track whereas more primitive mollusks may not. This study provides a beginning for a systematic analysis of learning in cuttlefish.

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