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Distance chemoreception in the common cuttlefish, *Sepia officinalis* (Mollusca, Cephalopoda)

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Abstract

Cephalopods are highly visual animals; the importance of chemical perception to these complex mollusks is less well understood. In this experiment, ventilation rate was used to measure the perception of chemical stimuli by cultured juvenile cuttlefish. The test tank had opaque sides and top to visually isolate the cuttlefish. A clear bottom permitted direct observation of funnel movements associated with ventilation. Cuttlefish cannot see beneath them when resting on the bottom; trials began once cuttlefish had remained calmly on the bottom for at least 15 min. The chemical stimulus was placed in a tank located upstream from the test tank containing a single cuttlefish; the cuttlefish's ventilation cycles were measured by direct observation. Ventilation rate increased significantly after exposure to ink from a conspecific, water containing food, water containing a conspecific, novel seawater and water that had contained sea turtles, potential predators. Results were obtained despite any background chemicals remaining within the closed sea water system, suggesting findings are probably robust to the conditions cuttlefish would normally experience in the ocean. Results are consistent with those obtained using visual stimuli and extend previous research indicating that cephalopods are capable of using chemical cues to detect salient environmental features.

Keywords: Cephalopod; Invertebrate; Marine; Sensory perception

1. Introduction

The Coleoid cephalopods (the octopuses, cuttlefishes and squids; hereafter simply referred to as 'cephalopods') are notable for their excellent vision (Hanlon and Messenger, 1996); it is less well known that cephalopods are capable of both contact and

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distance chemoreception (Budelmann et al., 1997). Many cephalopods are either nocturnal or live at depths where little light penetrates. Chemoreception could be quite important to these species; however, the function and extent of cephalopod chemosensory abilities are poorly understood.

Evidence for contact chemoreception is most extensive for octopus. Contact chemoreception is probably important in the recognition of prey items; for example, many of the shallow water octopods hunt by exploring under rocks and in crevices with their arms (Hanlon and Messenger, 1996). Wells (1963) demonstrated that *Octopus vulgaris* could discriminate between objects soaked in plain seawater from those that had been soaked in seawater with hydrochloric acid, sucrose, or quinine sulfate, using tactile discrimination. The chemoreceptors responsible for this ability were discovered on the octopus' suckers (Graziadei, 1962). Similar receptors, at a much lower density, have been found in the suckers of cuttlefish and squids (Budelmann et al., 1997) and in the buccal lobes surrounding the beaks of both squids (Emery, 1975) and cuttlefish (Graziadei, 1965).

Distance chemoreception was first noted when experimenters observed that octopuses became active when fish juice was added to their tank water (Wells, 1963; Messenger, 1967). Chase and Wells (1986) demonstrated that a blinded octopus moved towards various stimulatory chemicals at concentrations of 10^{-3} to 10^{-6} M, perceiving them as a food source. In experimental trials, the octopus *Eledone cirrhosa* responded to common chemical constituents of arthropod prey items at concentrations of less than 10^{-4} M by increasing ventilation rate (Boyle, 1986). Lee (1992) demonstrated chemotaxis in *Octopus maya* in a Y-maze using proline (10^{-4} M), ATP (10^{-5} M) and crab extracts (5×10^{-5} g l^{-1}). In recent work, electrophysiological recordings from the olfactory pits of octopuses, cuttlefishes and squids have shown that these organs are lined with chemoreceptors sensitive to chemical concentrations as little as 10^{-5} M (reviewed in Budelmann et al., 1997). Cephalopods are clearly capable of using distance chemoreception to help locate food.

Distance chemoreception could also play a role in social communication. Gilly and Lucero (1992) demonstrated that the squid *Loligo opalescens* responded with a jet-escape response when chemical substances including squid ink (concentration unknown), L-Dopa, and agents that block voltage-dependent potassium channels were introduced near the olfactory organ. In laboratory experiments, male cuttlefish, *Sepia officinalis*, guarded recently mated females and attempted to mate not-recently mated females (Boal, 1996), while female cuttlefish preferred to approach recently mated males rather than ones that had not recently mated (Boal, 1997). These experiments demonstrate that cuttlefish can detect the reproductive status of potential mates. Although these two experiments did not rule out visual cues, a more plausible explanation for the results is that cuttlefish detect chemical cues from conspecifics. Boal and Marsh (in press) failed to demonstrate discrimination of either sex or reproductive condition in cuttlefish using a Y-maze apparatus, however.

Ventilation rate appears to be closely related to the behavioral state of arousal and can be used to measure the effect of both chemical and visual stimuli on cephalopods (Boyle, 1983; see also Chase and Wells, 1986). Two methods for measuring ventilation rate have been used. The first method is direct observation; the observer counts the

inhalation and exhalation cycles by directly observing the subject's funnel (Boyle, 1983; Boal and Ni, 1996). This method is well-suited to cuttlefish whose funnels remain visible from beneath at all times. The second method is indirect; the electrical impedance of the water surface can be measured. The impedance changes with the turbulence associated with each ventilation cycle (Boyle, 1983). This method is better suited to octopuses whose funnels extend laterally and are frequently moved from one side of the octopus to the other. Using the first method, Boal and Ni (1996) determined that the juvenile cuttlefish *Sepia officinalis* became aroused after the general disturbance of being moved to a different tank, the sight of prey, and the sight of a conspecific. Using the second method, Boyle showed that *Octopus vulgaris* became aroused after exposure to an extract of crab tissue (Boyle, 1983) and that the octopus *Eledone cirrhosa* became aroused after exposure to chemical constituents of arthropod prey items (Boyle, 1986).

In this study we used direct observation of ventilation movements to evaluate juvenile cuttlefish's perception of ecologically salient chemical cues. We were interested in evidence for perception (increase in ventilation rate) and, further, evidence for the relative salience of odors (more arousing, less arousing). We predicted the following ranking of responses, as measured by increase ventilation rate: (1) ink from a conspecific, because the ink would indicate a serious disturbance of a conspecific and possible immediate danger, (2) odor from a predator, a potential immediate threat, (3) odor from food, (4) odor from a conspecific (our subjects were not yet sexually mature; mature animals might be expected to respond more strongly to conspecifics than to food. A larger conspecific could be perceived as a predator, however, since cannibalism among cephalopods has been documented (Hanlon and Messenger, 1996)).

2. Materials and methods

Subjects were 24 juvenile cuttlefish, *Sepia officinalis*, that had been reared at the National Resource Center for Cephalopods at the University of Texas Medical Branch in Galveston, Texas. All cuttlefish were from the same cohort and had mantle lengths from 8.0–11.5 cm during the time of trials.

The cuttlefish were housed in a 1.5 m × 1.2 m × 0.6 m deep holding tank prior to trials and were moved to a separate, similar tank after trials. Cuttlefish were fed live shrimp in the morning and evening, ad libitum. For each subject, morning feedings were withheld on the day of testing.

All housing and experimental tanks were interconnected on the same 13,000 l recirculating water system, dedicated to holding cephalopods and their live food. The system housed all experimental cuttlefish plus octopuses, non-experimental cuttlefish, and the cephalopods' live food (shrimp and fish). Water was a mixture of natural seawater from the Gulf of Mexico and artificial seawater made from Fritz brand salts; salinity ranged from 32 to 35 ppt and water temperatures ranged from 19 to 21°C. In this closed, continuous-flow system, water exiting each tank passed through mechanical, chemical and biological filters, and was treated with ultraviolet light to kill pathogens (Fig. 1). Water entering experimental tanks was not further filtered; any detection of test

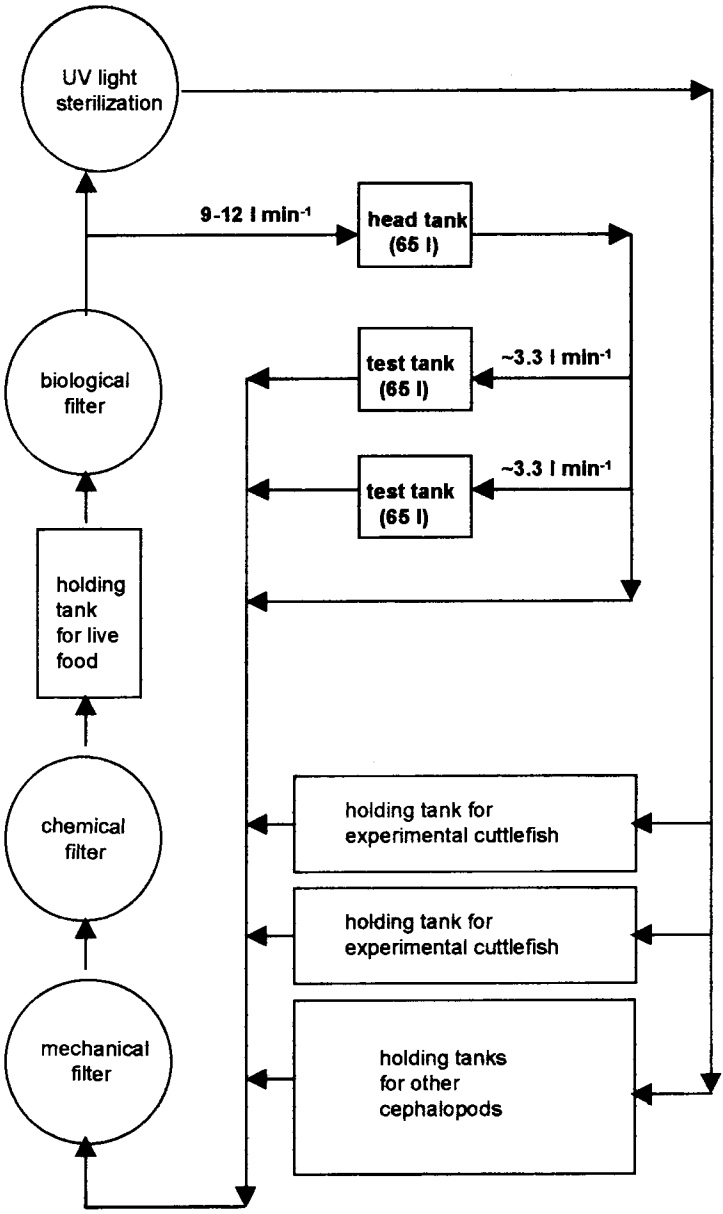

Fig. 1. Schematic showing water circulation pattern for all tanks. Water circulated continuously, including during experimental trials. Total volume of water in the system was approximately 13,000 l.

stimuli occurred against the background of any chemicals remaining despite filtration. Water flow was continuous at all times, including throughout trials.

The experimental tanks consisted of three tanks (91 cm × 46 cm × 43 cm deep) with

glass bottoms and opaque sides and covers. The first tank was raised 30 cm higher than the other two tanks; water was pumped into this tank at a rate that varied from about 9 l min^{-1} to about 12 l min^{-1}. The water from this head tank flowed directly (without filtration) into the two test tanks by gravity (Fig. 1). Each of the tanks held 65.2 l of water. Flow rates into the test tanks were regulated by 1-inch PVC ball valves; flow rates were adjusted before each trial to maintain a rate of 3.24 to 3.42 l min^{-1} (20 min exchange rate). Test tanks were supported by stout beams at either end; perforated, movable PVC partitions prevented the cuttlefish from settling directly above the beams (out of view of the experimenter). A 60-watt red light was placed beneath each test tank to facilitate viewing; cephalopods are not sensitive to light of this wavelength (Hanlon and Messenger, 1996).

The procedures for this experiment were modeled after those described in Boal and Ni (1996). One subject was placed into each of the two test tanks and allowed to acclimate for at least one hour before trials began. Ventilation cycles, as indicated by movements of the funnel, were recorded for 60 s every 3 min by the experimenter, who lay quietly underneath the tanks. Measurement intervals for the two subjects were offset by 1.5 min so that one experimenter could record the responses of two subjects.

Trials began once subjects had been calm for 15 min (five measured intervals). When cuttlefish are disturbed, their ventilation rates increase; consequently no trials were begun until subjects were resting calmly on the tank bottom and ventilation rates were averaging about 40 cycles per min, with no measures greater than 55 cycles per min. Six treatments were given for each subject:

1. Control. Seawater from the experimental system was added to the head tank. The transfer was accomplished using a 25 cm × 16 cm × 12 cm deep, hard-plastic box, filled to a depth of 6 cm (1.7 l volume of water).
2. Presence of Ink. Six grams of ink obtained from a frozen, dead adult cuttlefish was dissolved in 100 ml of seawater from the experimental system. Using a syringe, 10 ml of this solution was injected directly into the water inflow of each test tank. Subjects could not see the experimenter or the syringe because of the opaque tank lid. Subjects probably could not see the ink, either, because the tank was dark and the ink was dilute.
3. Presence of Conspecific. One conspecific from same holding tank as the subject was transferred into the head tank. The transfer was accomplished using the same hard-plastic box as in #1, again filled to a depth of 6 cm (1.7 l volume of water and cuttlefish, combined).
4. Presence of Food. Six thawed (dead) shrimp (approx. 22 g) were placed directly into the head tank. (Cuttlefish were normally fed live shrimp.)
5. Novel seawater. Seawater from the Gulf of Mexico was taken from the National Marine Fisheries Service facility in Galveston, Texas. Water was pumped from directly off-shore (salinity 23 ppt, temperature 26°C). The water was collected in a 2 l hard-plastic water bottle and was refrigerated overnight for trials the following day. One hour before a trial, the water bottle was floated in the experimental system to bring the sample up to the same temperature as the water in the rest of the experimental system. Water was transferred to the same 25 cm × 16 cm × 12 cm

hard-plastic box as in previous trials (1.7 l volume of water) for introduction into the head tank.

6. Presence of Potential Predator. Water was taken from a holding tank containing 14 loggerhead sea turtles, *Caretta caretta*, at the National Marine Fisheries Service facility in Galveston, Texas. The turtle holding tank (2 m × 7 m) contained approximately 5000 l of water from the Gulf of Mexico (see novel seawater, #5, above). Water in the turtle holding tank was changed completely each morning; water for trials was collected in the afternoon (approximately 6 h later), stored, and used as in #5.

Once the stimulus was added, ventilation rates were recorded for 24 min (eight measured intervals). A new trial did not begin until 30 min after the previous treatment or until the subject was calm again, whichever was longer. Up to four subjects (two pairs) were tested per day. The second pair of subjects was not put into the experimental tanks until at least 30 min after the previous two subjects had been removed.

The subjects did not readily settle and sit calmly on the bottom. Consequently, we were unable to run all trials for a subject in a single day. Trials were performed in three different blocks, therefore. The food trials were the first to be performed; 24 animals were tested over a six day period. Next, the control, ink, and conspecific trials were performed together, over a ten day period ($N = 24$). Lastly, trials were performed using the water from the National Marine Fisheries Service, with and without sea turtles ($N = 20$). The order of presentations of treatments within blocks were randomized. Ventilation rates during swimming are complicated by the use of jets of water for propulsion (Bone et al., 1994); for this reason, no measurements were taken when subjects were actively swimming. Swimming bouts rarely lasted for more than one minute.

To evaluate our results, we calculated the mean ventilation rate for the five sampling intervals before the stimulus was added and for the five sampling intervals immediately after the stimulus was added for each subject in each trial. To determine the significance of differences in mean ventilation rates before and after treatments, paired Student's *t*-tests were used. When comparing the magnitude of responses between treatments, we compared the change in ventilation rates (mean after − mean before) for the different treatments. Paired *t*-tests were used for trials performed within a block. Unpaired t-tests were used for comparisons between blocks because we did not tag individuals and did not know which data came from which subject.

3. Results

Mean ventilation rate before treatments was 39.9 cycles per min and did not differ between time intervals ($F_{4,420} = 1.32$, $P > 0.25$) or treatments ($F_{5,130} = 1.48$, $P > 0.20$), but did differ between subjects (for treatment control, conspecific, ink; $F_{23,112} = 1.89$, $P < 0.05$).

When ventilation rates 3 to 15 min after the stimulus were compared with those 3 to 15 min before the stimulus was added (paired *t*-tests), a significant increase in

ventilation rate was observed for all treatments excluding the control: water containing food ($t_s = 4.35$, df = 23, $P < 0.0005$), ink from a conspecific ($t_s = 4.59$, df = 23, $P < 0.0005$), water containing a conspecific ($t_s = 3.20$, df = 23, $P < 0.005$), novel seawater ($t_s = 2.68$, df = 19, $P < 0.01$) and water from turtles ($t_s = 2.63$, df = 19, $P < 0.01$) (Fig. 2). No significant change was observed with the addition of water from the subjects' own holding tank (control; $t_s = 1.08$, df = 23, $P > 0.15$).

Responses varied between treatments ($F_{5,130} = 4.79$, $P < 0.001$; Fig. 3), with the response to ink being significantly greater than responses to all other treatments except food, and the response to food being significantly greater than the response to the control treatment. Response to a conspecific was also significantly different from response to the control (paired $t_s = 1.84$, df = 23, $P < 0.05$). Responses to the remaining treatments

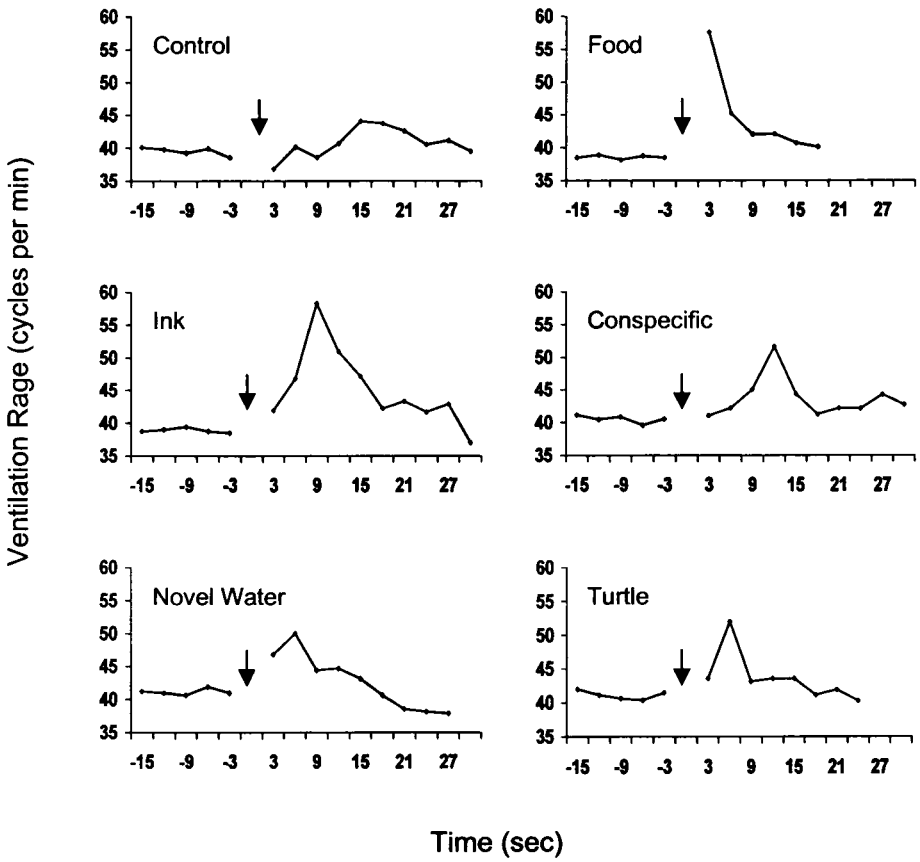

Fig. 2. Mean time course for ventilation rate during trials. At time 0 (arrow), the stimulus was added into the head tank, except for ink, which was added directly into the test tank inflow. In each of these graphs (but not in the statistical analyses), individual response curves were shifted so that the time of peak response coincided for all of the subjects. Standard errors of all plotted points before treatment were less than 0.5 and after treatment were less than 1.5.

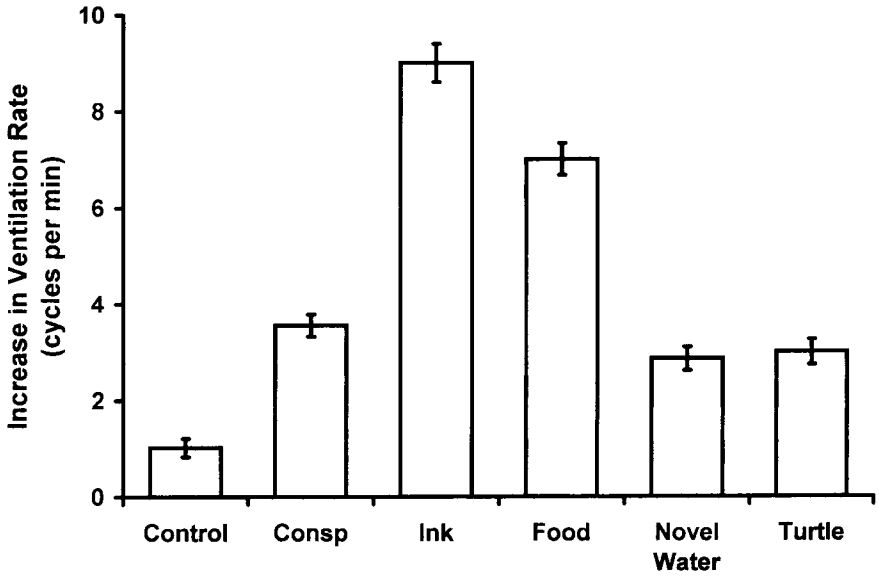

Fig. 3. Increase in ventilation rate (mean after − mean before the stimulus was added, ±SE) for cuttlefish exposed to ecologically salient stimuli ($n = 24$ except in the case of the turtle experiment when $n = 20$).

were not significantly different from each other; however, important statistical power was lost because we were unable to perform paired comparisons and subjects differed significantly from one another even before treatments were added.

There were no significant differences between treatments in the time course of responses (3 to 15 min after treatment; $F_{4,599} = 0.84$, $P = 0.50$); time to peak response varied widely between subjects.

4. Discussion

This study clearly confirms that juvenile cuttlefish are capable of detecting ecological salient substances using chemical cues alone. Our results were obtained despite any background chemicals remaining within the closed system, suggesting that this level of sensitivity to chemical cues may extend to the natural marine environment.

Our data provide evidence that cuttlefish can detect conspecifics using chemical cues. The largest increase in ventilation rate occurred after subjects were exposed to ink. Ink from a conspecific elicits a jet-escape response from squids (Gilly and Lucero, 1992) and elicits avoidance behavior from the sea slug *Aplysia fasciata* (Fiorito and Gherardi, 1990). Ink is used by most cephalopods, and some other mollusks, as a means for escaping predators. Our results suggest that ink could function similarly to the alarm substance of some fishes. This alarm substance is released from epidermal cells upon injury, and causes a fright response in neighboring conspecifics (Hara, 1993).

Our data also provide support for the hypothesis that cuttlefish can detect non-inking

conspecifics using chemical cues alone (Boal, 1996, 1997); this is the first experimental evidence for such chemical perception of a conspecific in cephalopods.

The juvenile cuttlefish responded more strongly to the odor of food than the odor of conspecifics. Boal and Ni (1996) obtained similar results using visual cues alone. These findings are consistent with research indicating that cuttlefish are probably solitary, at least until sexual maturity (Boletzky, 1983).

Our results suggest that chemical cues could also function in prey and predator detection. We obtained significant increases in ventilation rate in response to both the odor of food and the odor of turtles. These results are consistent with previous research; much of the evidence for distance chemoreception derives from the attractant properties of foods (Wells, 1963; Messenger, 1967; Boyle, 1983, 1986; Chase and Wells, 1986; Lee, 1992) and octopuses displayed body patterning associated with alarm to water from a tank in which a Moray eel had been living (MacGinitie and MacGinitie, 1968). Oddly enough, we did not see a greater response to odors associated with turtles in novel water than we did to novel water alone. It could be that our samples were too dilute, although previous experiments indicate detection of chemicals at concentrations as low as 10^{-5} M (Boyle, 1983, 1986; Chase and Wells, 1986; Lee, 1992). It is possible that turtles do not normally feed on cuttlefish, although these particular turtles had been fed frozen squid at the time of trials. It would be interesting to try using water taken very soon after the turtles had fed.

We are intrigued at our evidence for discrimination of novel water. Both the water in the experimental system and the novel water originated in the Gulf of Mexico; differences in chemistry could have been subtle. Discrimination between different sources of water has been demonstrated previously in fish (Hara, 1993) and could be useful for the seasonal inshore-offshore migrations that have been documented in cuttlefish (Boletzky, 1983; Boucaud-Camou and Boismery, 1991). In what could be a related phenomenon, Wells et al. (1965) showed that octopuses detected potassium chloride at concentrations of as low as 10^{-5} M. A potential third role for chemical cues is navigation, therefore.

It is interesting to note that ventilation rates responded most strongly to significant familiar stimuli (food, ink) and less distinctly to non-significant familiar stimuli (conspecifics) and novel stimuli (novel water, turtles). It is possible that changes in ventilation rate are responses to learned relationships between perceived stimuli and salient events.

In this experiment, the largest increase in ventilation rate occurred in response to ink, followed by odors from food, a conspecific, turtles and novel water. Only the responses to ink, food and conspecifics were significantly different from the control; however, other differences between treatments might have been revealed had we marked individuals, permitting paired statistics throughout. Several complications limit our ability to further compare responses between treatments and to draw definitive conclusions about the relative salience of these odors. First, we could not control exactly when the odor of a particular stimulus would reach each subject; the exact timing depended upon unspecified flow variables and the location of the subject at the time that the stimulus was added. Second, we did not attempt to precisely quantify the amount of odor subjects received, either between subjects within the same treatment, or between

treatments. In octopuses, the level of response obtained was dependent on the concentration of the chemical substance (Boyle, 1986). Third, mean response over a 15 min interval was clearly a crude measure; responses varied substantially within the 15 min interval (Fig. 2). We believe this experimental design is not sensitive enough to permit fine comparisons of the relative salience of odors to the cuttlefish.

5. Conclusion

This study provides strong evidence that cuttlefish detect ecologically salient chemical cues including predators, prey, conspecifics both alarmed and calm, and variations in general water chemistry. The experiment was not sensitive enough to differentiate between responses to these various stimuli except to note that odors from a conspecific's ink and from food elicited the strongest responses. Discriminations were performed against the background of chemical cues inherent to a closed sea water system, suggesting findings are probably robust to the conditions cuttlefish would normally experience in the ocean. It remains for future experiments to determine the degree of specificity of cuttlefishes' discrimination abilities.

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