



## Social recognition using chemical cues in cuttlefish (*Sepia officinalis* Linnaeus, 1758)

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### Abstract

Forty-five full-sized, virgin cuttlefish (*Sepia officinalis* Linnaeus) were tested for social discriminations on the basis of chemical cues alone. Subjects were tested by placing them in the base of a Y-maze and permitting them to choose between the two arms of the maze, each arm with a different water supply. Each subject was tested three times: once with water from a male versus a female conspecific, once with water from a mated versus a virgin conspecific of the opposite sex, and once using plain seawater in both arms of the Y-maze as a control for any bias towards one of the arms of the maze. Results fail to support hypotheses for chemical communication in cephalopods; difficulties in using approach behavior to measure chemical communication in cephalopod and other mollusks are discussed. © 1998 Elsevier Science B.V. All rights reserved.

**Keywords:** Communication; Mollusks; Pheromones; Reproduction; Social behavior

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### 1. Introduction

The coleoid cephalopods (octopuses, cuttlefishes and squids) have been considered to be primarily visual animals. In behavioral reviews, emphasis has been placed on the importance of visual body patterning for social communication (Hanlon and Messenger, 1996) and chemical cues have not been thought to be of great significance to cephalopod behavior (Budelmann, 1994; but see below). Sensory receptors on the suckers of octopus arms were described decades ago (Graziadei, 1964), however, and Wells showed that

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octopuses can learn to discriminate between objects on the basis of chemical cues alone (Wells, 1963; Wells et al., 1965). An absence of chemical-based social communication in cephalopods would be a noteworthy break with their molluscan phylogeny.

In most mollusks, chemical cues are important for social communication. Cues can be detected from both local ('touch') and distant ('smell') sources (Audesirk, 1975). Species-specific trail following has been demonstrated in terrestrial snails (Chase et al., 1978) and preferential following of individuals of the opposite sex has been shown in *Littorina* (Erlandsson and Kostylev, 1995). Ink induces avoidance behavior in *Aplysia* (Fiorito and Gherardi, 1990) with strong response to ink from conspecifics, weak response to ink from congeners, and no response to ink from other mollusks (Stopfer et al., 1993). In *Aplysia*, pheromones are clearly important to both the establishment of breeding aggregations (Audesirk, 1977; Painter, 1992) and the induction of mating behavior (Painter et al., 1989). Socially-induced taxis has been demonstrated also in *Aplysia* using approach behavior towards water-borne stimuli from conspecifics (Lederhendler et al., 1977). Individuals were more attractive sexual partners during and immediately following egg-laying (Audesirk, 1977).

Recent data suggests that chemical cues may be more important to cephalopods than has been previously thought. As in other mollusks, cephalopods can detect chemical cues from both local and distant sources (Hanlon and Messenger, 1996). Chemotaxis has been demonstrated in nautilus, octopuses, cuttlefish and squids using chemicals related to foods (Chase and Wells, 1986; Lee, 1992; Lee et al., 1994; Basil, Sheikh and Hanlon, in prep). Cephalopods probably use chemical cues for social communication also. Ink pipetted directly on the olfactory pit of squids elicits jetting, an escape response (Gilly and Lucero, 1992; Lucero et al., 1992). Boal (1996) found that male cuttlefish did not recognize their own mate from another mated female, but they did discriminate between mated and unmated females; a discrimination suggestive of the use of chemical cues. Similarly, in a modified y-maze design, Boal (1997) found that sexually receptive females preferred the more recently mated of two males. During trials, Boal (*ibid.*) used a semi-natural situation in which the cuttlefish could see and interact with each other. Interestingly, subjects showed the same preferences before the trial formally began, when an opaque barrier prevented the female subject from seeing the two males. This result again suggested that cuttlefish could be using chemical cues for social communication.

Chemical communication among cuttlefish makes sense. To the best of our knowledge, cuttlefish spend much of their lives dispersed and are social only for the purposes of reproduction (Corner and Moore, 1980; Hanlon and Messenger, 1996; Boal et al., in press). Chemical cues are a commonly used method for locating mates in widely dispersed species (Alcock, 1984).

In this study, our goal was to attain the control necessary to conclusively demonstrate chemical communication through behavioral displacement. For this reason, a y-maze apparatus was chosen. The only cues available to subjects were those present in the water flowing down the two arms of the maze. The discriminations we investigated were sex (water from a virgin male versus a virgin female) and mate status (water from a virgin versus a recently mated conspecific of the opposite sex).

## 2. Materials and methods

### 2.1. Subjects

Subjects were 22 male and 23 female virgin *Sepia officinalis* Linnaeus that had been reared at the National Resource Center for Cephalopods at the University of Texas Medical Branch in Galveston, Texas. Additional males and females from the same cohort were used for comparison animals (see below). Methods used in culturing the cuttlefish are described fully elsewhere (Forsythe et al., 1991, 1994). All cuttlefish were between 19 and 31 cm in mantle length and were presumed to be sexually mature adults.

### 2.2. Apparatus

Between trials, cuttlefish were housed in six large tanks with water as similar to that of the y-maze as possible (temperature within 2°C, salinity within 2 ppt). Females and males were housed separately and individuals were distinguished using the unique banding patterns on their mantles (Boal, 1996).

The y-maze apparatus consisted of a base compartment 49 cm wide, 63 cm long and 20 cm deep connected to two arms separated by an angle of 60° each 24.5 cm wide × 70 cm long × 20 cm deep (Fig. 1). The maze was filled with water to a depth of 10 cm. A perforated gate located between the base and the arms of the maze was operated manually with a rope and pulley system. The y-maze was surrounded by a black curtain to eliminate visual distractions and was lit indirectly by incandescent lamps aimed at the white ceiling overhead. Cuttlefish are attracted to darker, covered places. The arms of the maze were covered with perforated plastic covers, both to increase the likelihood that subjects would enter one of the arms of the y-maze and to decrease the likelihood that subjects would choose one arm over the other on the basis of a lighting difference that we had failed to detect.

Trials were viewed using a video camera suspended directly over the maze and connected to a monitor and VCR in an adjacent room (Panasonic color video camera WV-3255/8AF, Panasonic Omnivision III video cassette recorder NV-8950).

### 2.3. Water

The water in the y-maze was obtained from the Gulf of Mexico. Water was pumped into the outermost end of each arm at a rate of 8.5 l per min per arm; water drained passively from the farthest end of the base section into a reservoir below (see Fig. 1). Water from the reservoir passed through biological, mechanical, and chemical filters before being pumped back up into the arms of the y-maze (details in Forsythe et al., 1991). Complete details of the y-maze apparatus can be found in Lee (1992).

During trials, test water was added to the inflow of each arm of the y-maze using a separate, peristaltic pump; a uniform flow rate of 1 l/min from this pump was verified weekly using a flow meter. Water in the reservoir was not changed between trials; subjects were required to make discriminations against any background odors which

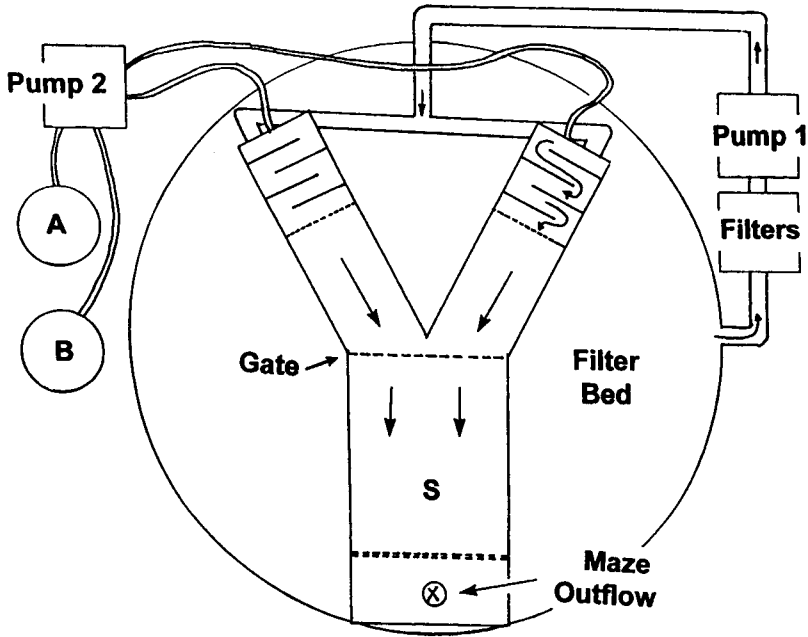


Fig. 1. Schematic of the y-maze. Water was pumped into the arms of the y-maze (Pump 1) at a rate of 8.5 l/min for each arm. At the base of the y-maze, the water passed through a grate and passively drained back into the biological filter bed located below; it then passed through biological and chemical filters and an ultraviolet light sterilizer before returning to the y-maze. Water for trials was pumped into the maze separately using a peristaltic pump (Pump 2) at a rate of 1 l/min from each source (A and B). Trials proceeded by, (1) placing a subject (S) in the base section of the maze, (2) turning on the peristaltic pump, and (3) raising the gate to allow the subject to enter either arm of the maze. Behavior was recorded using a video camera suspended overhead.

might remain despite the extensive filtration. Previous experiments suggesting chemical communication (Boal, 1996, 1997) used much less control for background 'noise'.

One hour before the trial was run, 20 l of water from the y-maze were placed in each of two large, hard-plastic basins and an appropriate comparison animal was placed into each basin, along with an air stone, and left for 30 min. A small hard-plastic container was used to move the cuttlefish into and out of the basins. The volume of water plus cuttlefish moved in each transition (in and out of the basin) was 5 l; thus, some water from the comparison animals' home tanks was present in the test water used in trials. At the conclusion of a trial, both basins were thoroughly rinsed with fresh water from a high-pressure hose.

In trials for discrimination of sex, cuttlefish used for comparison were virgins of similar size, one male and one female. In trials for discrimination of mate status, both cuttlefish were of the opposite sex from the subject. The mated cuttlefish had mated, usually within the previous 24 h, but always within the previous 72 h; the other cuttlefish was a virgin of similar size.

## 2.4. Procedure

Each day, a single subject was placed into the base of the maze facing towards the arms. The subject was allowed to acclimate for 40 to 60 min before trials began. At the start of each trial, the peristaltic pump was turned on and allowed to run for 5 min before the gate between the base of the y-maze and the arms was lifted. This delay served to increase the likelihood that the subject had been exposed to both water sources before it made a choice of which source to approach. Ten minutes after the gate was lifted, the trial was terminated by turning off the peristaltic pump.

Each subject received all three trials on a single day: (a) control, (b) sex, and (c) mate status. The order of trials was balanced across subjects (i.e., abc, bca, acb, cba, bac, cab), and the side of the maze that each comparison was assigned (right/left) was alternated between subjects. The interval between successive trials was at least 1 h. Thirty-nine of the 45 subjects entered one of the maze arms in at least one of the three trials (20 females and 19 males): 26 entered at least one arm during control trials, 30 during sex trials and 25 during mate status trials.

A subject's exact location was chosen a priori to be the point midway between its eyes. We scored the subjects' choices four ways: the arm of the maze that was first entered (First Entry), latency to entering each arm (Latency, in sec), total time in each arm (Total Time, in sec, continuous), and the arm of maximum total time (Maximum Time, dichotomous). Number of switches between arms (Switches) was recorded as a possible indication of searching behavior.

Statistical significance was determined using chi-square goodness of fit (Siegel and Castellan, 1988), Kruskal-Wallis nonparametric analysis of variance or a paired analysis of variance (Sokal and Rohlf, 1969). For purposes of analysis, arms never entered were assigned a Latency of 600 s. Trials in which neither maze arm was ever entered were not included in statistical analyses because we could not definitively interpret this trial outcome.

Because multiple measures of subjects' behavior in each trial were recorded, the usual criterion for statistical significance ( $P < 0.05$ ) is not sufficiently stringent to indicate significant deviation from chance. Probability criterion are not magic; we were interested in overall patterns as much as performances measured on any one single variable. We present a summary of our results in raw form, therefore, so that readers can better evaluate our results. In the interests of brevity, statistics for variables with an associated probability of 0.10 or greater are not listed.

## 3. Results

During control trials, both male and female subjects showed a non-significant bias towards the left arm of the maze (Table 1). This non-significant bias was observed in all four variables, for males, for females and for all subjects combined (First Entry, 16 L:10 R; Total Time average, 127 L: 54 R; Maximum Time, 18 L:8 R; Latency average, 223 L: 324 R).

In sex discrimination trials, both male and female subjects showed a non-significant

Table 1  
Tallies of maze arm first entered (First Entry) for 23 female and 22 male virgin subjects

| Trial          | Choice               | Subjects |      |
|----------------|----------------------|----------|------|
|                |                      | Female   | Male |
| 1. Sex         | Virgin Female        | 11       | 9    |
|                | Virgin Male          | 3        | 7    |
|                | No Movement          | 9        | 6    |
| 2. Mate Status | Mated, Opposite Sex  | 7        | 8    |
|                | Virgin, Opposite Sex | 6        | 5    |
|                | No Movement          | 10       | 9    |
| 3. Control     | Right                | 6        | 4    |
|                | Left                 | 8        | 8    |
|                | No Movement          | 9        | 10   |

bias towards odors from females (Table 1). For females, this non-significant bias was observed in all four variables (First Entry, 11 F:3 M,  $\chi^2 = 4.57$ ,  $P < 0.05$ ; Total Time average, 94 F: 79 M; Maximum Time, 8 F:6 M; Latency average, 298 F: 346 M). For males, this bias appeared only for First Entry (9 F:7 M) and Total Time (average, 99 F: 67 M). For both Maximum Time and Latency, males showed a preference for whichever odor was on the left (Maximum Time, 13 L:3 R; Latency average, 282 L: 378 R).

In trials presenting a choice of mate status, both male and female subjects showed a non-significant bias towards odors from mated conspecifics of the opposite sex for three out of the four variables measured (First Entry, 15 M:11 U; Total Time average, 122 M: 63 U; Latency average, 260 M: 312 U; where M = mated and U = unmated) (Table 1). Curiously, for Maximum Time, both male and female subjects showed a preference for whichever odor was on the right (Maximum Time, 16 R:10 L).

Subjects were not significantly more likely to explore both arms of the maze (Switches) during trials when test water had held animals (sex or mate status, averages 4.3 and 4.4, respectively) than when it had not (control) (average 3.8), nor did they spend more time in the arms of the maze (Total Time) when test water had held animals than when it had not (averages: sex 84 s, mate status 93 s, control 90 s). Subjects were slower to enter an arm of the maze, either right or left, during control trials than they were during sex or mate status trials (minimum Latency,  $\chi^2 = 5.61$ ,  $df = 2$ ,  $P = 0.06$ ).

#### 4. Discussion

This experiment was conducted in a y-maze with no cuttlefish actually located at the end of either arm of the maze. This highly artificial method was chosen to insure that the only cue subjects could receive would be any residual chemical remaining in the water from conspecifics. In a previous, more behaviorally realistic experiment, cuttlefish appeared to demonstrate discrimination on the basis of chemical cues alone (Boal, 1997).

These experiments tested social preference on the basis of chemical information and did not directly test whether subjects could detect a conspecific on the basis of chemical

cues (no trials using water from a conspecific versus plain water were given). Detection would be inferred, however, on the basis of choices differing significantly from chance.

We found no statistically significant evidence that cuttlefish discriminated by either sex or mating status using chemical cues. In captivity, sexually aroused males will attempt to mate another male if the other male does not respond with the body pattern termed an 'Intense Zebra Display' (Tinbergen, 1939; Messenger, 1970). It is conceivable that male cuttlefish cannot distinguish sex through chemical cues alone. Our results do not support Boal's experiments (Boal, 1996, 1997), however, that suggested cuttlefish can distinguish mate status using chemical cues. Indeed, our results provide no indirect evidence for even detection of chemical cues from conspecifics, because subjects were not more responsive to water from conspecifics than they were to control water.

It is not clear from this experiment whether cuttlefish do not use chemical cues for social communication or whether this experiment simply did not reveal this ability. Our consistent trends (preference for females over males and mated conspecifics over unmated conspecifics) leave us with more questions than answers.

One possible reason for the conflict between our results and those of Boal (1996, 1997) is that our cuttlefish may not have been as mature as they appeared. Our subjects were all large enough to be sexually receptive; females of this size appear to have mature ova when autopsied. In cuttlefish, behavioral receptivity does not always correlate closely with size, however. Males normally mature sooner than females; we have observed males with a mantle length (ML) of as little as 12 cm mating while other males are still not interested at 30 cm ML. First receptivity of females has appeared when females were as small as 18 cm ML or as large 28 cm ML. This lack of correlation between size and maturity could be an artifact of captive conditions or it could be normal for this species. Discrepancies between physical appearance and sexual maturity have been reported in other invertebrates (Prete, 1995). Few of our females mated willingly when placed with a male after trials (unwilling females flee and ink when approached by a displaying male). Our males and females were housed completely separately before the experiment while those in Boal, 1997 were in chemical contact with each other (water shared directly without intervening filtration). If chemical cues are important in sexual behavior, it is possible that this separation delayed sexual maturity in our subjects, as happens for isolated *Aplysia* (Painter et al., 1989). In short, we suspect that our subjects were not all sexually mature.

Similarly conflicting results have been attained in studies of chemical communication in *Aplysia*. For both *Aplysia* and cephalopods, subjects performed well in a y-maze when food was used as an attractant (Audesirk, 1977; Lee et al., 1994), and behavioral observations indicated preference for some sexual partners over others (Audesirk, 1977; Boal, 1997). Nevertheless, sexually mature conspecifics of both species failed to be a significant attractant in a y-maze (Audesirk, 1977; this data). Social discrimination was demonstrated in *Aplysia* only by relative taxis (Lederhendler et al., 1977) using a rectangular apparatus with one stimulus presented at a time; subjects approached the source of water containing odors from multiple conspecifics more than they did with plain water but showed no discrimination on the basis of types or numbers of conspecifics. It would be useful to attempt this alternate method with cuttlefish.

In *Aplysia*, the pheromonal sexual attractant appears to derive from atrial gland

products secreted onto the egg cord on as it passes through the oviduct (Painter et al., 1989; Painter, 1991). Adult cuttlefishes (pers. obs.) and squids (Arnold, 1962, 1965) take great interest in eggs and handling them appears to elicit mating behavior (R.T. Hanlon, pers. comm.). Any potential significance of the eggs themselves, or products of females' oviducal glands, does little to explain apparent preferences of receptive females for recently mated males (Boal, 1997), however, or the trend in this experiment for both males and females to approach other virgin females (data presented here).

In future work, it would be useful to devise a more sensitive behavioral assay than physical approach. Behavioral tests for sexual receptivity could be used prior to experiments to insure that subjects were truly sexually mature. A larger sample size could more easily detect behavioral discriminations, although it may not be attainable in practice, and the use of new water in each trial would insure that chemical signals from comparison animals were not lost in background noise from previous trials.

## 5. Conclusion

Our work does not support hypotheses for chemical communication in cephalopods. We find our experiments inconclusive, however, and look forward to future work for more definitive answers.

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