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Rapid taste aversion learning in adult cuttlefish, *Sepia officinalis*

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The common cuttlefish is an opportunistic predator with certain prey preferences. The literature suggests that learning plays a role in the predatory behaviour of cuttlefish. However, nothing is known about taste aversion learning in cephalopods. We developed a learning procedure in which the preferred prey of the experimental cuttlefish was made distasteful by a bitter taste (quinine). In the training session, the modified prey was repeatedly presented until the experimental cuttlefish stopped attacking it. Of 32 experimental cuttlefish, 26 attacked a different prey from the originally preferred one when both were presented in a choice test 24 or 72 h after learning. In contrast, matched control cuttlefish that had not been subjected to negative reinforcement continued to choose the initially preferred prey under identical test conditions. These results are the first demonstration of taste aversion learning in cephalopods. They underline essential adaptive functions in cuttlefish and the flexibility of their feeding behaviour. Cuttlefish were able to learn that a prey is not acceptable food, even if they usually preyed on it, to recognize it and to avoid it for several days and as a result to eat a usually nonpreferred prey.

The interaction between predator and prey is a complex process. When a predator forages it has to make crucial decisions as to which kind of prey to hunt. Prey choice may be affected by prey defence mechanisms, such as the presence of toxins, escape strategies and the availability of prey (Davies & Krebs 1979). According to foraging theory, choice of prey is based on the relation between energy gain and handling time (Stephens & Krebs 1986). Furthermore, the predator's choice may be affected by its own preference, or by the avoidance of a prey species through previous experience of undesirable characteristics. The ability to learn an unpleasant experience associated with the potentially damaging ingestion of a food may influence subsequent food choice and intake in a variety of animals (rodents: reviewed in Welzl et al. 2001; molluscs: reviewed in Carew & Sahley 1986). The animal may learn that a certain stimulus (novel taste or food) predicts a subsequent event such as illness (conditioned taste or food aversion). In other cases, the animal can learn to predict the consequences of its own behaviour (instrumental conditioning); data of this kind on feeding behaviour remain scarce. In cephalopods, no studies on taste aversion learning have been reported.

Cephalopods are voracious carnivores, feeding on live prey, detected mainly through visual or tactile inputs. They are considered to be the most highly evolved marine invertebrates and, thus, they have been extensively studied for their learning abilities (reviewed in Sanders 1975; Fiorito & Scotto 1992 on observational learning) and the flexibility of their predatory behaviour (reviewed in Mather 1995). Observations of cephalopod behaviour suggest that learning influences their predatory behaviour and perhaps their selection of prey. For example, *Eledone moschata* ceased attacking hermit crabs, *Paguristes maculatus* and *Eupagurus prideauxii*, carrying sea anemones, respectively *Adamsia rondeletii* and *A. palliata*, after being stung (Polimanti 1910). *Octopus vulgaris* made no more attacks on the hermit crab *Eupagurus bernhardus* carrying the anemone *Calliactis parasitica*, but persisted with attacks on other prey, such as the crab *E. prideauxii* carrying *Adamsia palliata*, which suggests the latter may be less noxious (Boycott 1954). Our limited knowledge of cephalopods' prey choice has been derived mainly from indirect information rather than from direct observations in the sea. Some of the indirect approaches have consisted of analysing gut contents or performing laboratory experiments. In the case of some octopods, a third source of information on diet has come from counts of prey remains left in a 'midden' next to their 'homes' (Smale & Buchan 1981; Ambrose & Nelson 1983). The natural

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diet of cephalopods consists mainly of molluscs, crustaceans and teleost fish, so they are considered to be generalist predators (von Boletzky 1983; Guerra 1985; Nixon 1985, 1987; Hanlon & Messenger 1996). None the less, many studies have shown that the octopuses do have prey preferences (*Octopus bimaculatus*: Ambrose 1982, 1984; *O. vulgaris*: Mather 1991; *O. dofleini*: Vincent et al. 1998).

The common cuttlefish, *Sepia officinalis*, is also an opportunistic predator with a flexible diet that allows it to adapt its choice of prey during its life cycle and to survive when its usual prey is unavailable (Najai & Ktari 1979; Pinczon du Sel & Daguzan 1997; Pinczon du Sel et al. 2000). Juveniles are miniature replicas of adults and, from hatching, use the same prey capture strategies as adults do (Messenger 1968; Chichery & Chichery 1991). However, diet changes markedly during ontogeny. As the cuttlefish grows, the size of its chosen prey increases and so cuttlefish may sample different types of prey. In the laboratory, when a cuttlefish attempts to attack a crab for the first time it is often unsuccessful and is frequently pinched by the crab's claws (Wells 1962). Boal et al. (2000) proposed that the cuttlefish's gradually improved performance in crab predation is the result of rapid learning. Hanlon & Messenger (1996) suggested that early prey choice depends on a 'hardwired' program and then on individual experience throughout life. Thus, in the wild, adult cuttlefish may learn to restrict themselves to prey that is safe as well as tasty and thus become selective in what they attack. In laboratory experiments, *S. officinalis* quickly learned not to attack shrimps presented behind glass, probably because of the pain incurred when the tentacles struck the glass (Sanders & Young 1940; Messenger 1971, 1973, 1977; Chichery & Chichery 1992; Agin et al. 1998; Dickel et al. 1998). Wells (1958) emphasized that most experiments on learning behaviour are performed on cephalopods caught after one or more years' growth in the sea. Thus, the possibility of wide differences in individual experience before capture must be taken into account when considering the behaviour of these cephalopods under training conditions in the laboratory.

We investigated selectivity in the predatory behaviour of subadult and adult *S. officinalis*. We first considered whether cuttlefish caught in the wild from the same area of the sea showed the same spontaneous food preference in choice tests, and we then developed a taste aversion learning procedure based on observed food preferences. Making their preferred prey distasteful with quinine, we tried to assess the flexibility of prey preference for each cuttlefish. Using this procedure, we estimated the importance of individual experience, and hence learning, in the development of choice of prey. Finally, we tested the long-term effects of learning on subsequent food preferences.

METHODS

Study Animals

We used subadult and adult *S. officinalis* (N = 66; 130–240 mm dorsal mantle length), of both sexes. They were trawled or fished with pots in the vicinity of Luc-sur-Mer, France, and kept in separate opaque plastic tanks (80 × 60 cm and 40 cm high). They were fed shrimps, *Crangon crangon* (collected on the shore with a fishing net), and crabs, *Carcinus maenas* (picked up under stones), ad libitum. We collected all these animals with the authorization of the commune of Luc-sur-Mer. Shrimps were housed in a circular tank (1500 litres) and crabs were maintained in tanks (1500 litres) with stones. All the tanks were supplied with running sea water maintained at 15 ± 1°C. All shrimps and crabs collected were used to feed all the cuttlefish kept at the marine station. To ensure that cuttlefish were motivated to feed in a training session, we carried out a simple test by attaching prey to a thread and hanging it inside the tanks. We selected cuttlefish that attacked the prey within 10 s of its introduction into the tank, the prey being removed before it could be seized. Attack latency is considered a good indicator of the level of feeding motivation (Messenger 1973; Chichery & Chichery 1991, 1992; Dickel et al. 1998). After the experiment, cuttlefish were killed by decapitation after being anaesthetized (immersion in sea water containing 2% ethanol and 17.5 g/litre magnesium chloride), to study any eventual neurobiological correlates underlying short- and long-term retention processes.

Food Preferences

We conducted tests to determine the feeding preference of the cuttlefish, given the choice between a crab and a shrimp. Prey size varied from 45 to 60 mm (total length from acron to telson) for shrimps, to ensure that it was large enough to attract the cuttlefish, and from 40 to 55 mm (carapace width) for crabs, so that their claws were not too big (Duval et al. 1984). To control for choice based on prey position, we placed the prey at random on the left and right of a T support by a thread, 10 cm apart. They were then presented together in the cuttlefish's anterior visual field, to ensure that it could see them both. This apparatus was presented 20 times to each cuttlefish over 2–5 days, according to the prey chosen and individual feeding motivation. A cuttlefish will eat more shrimps than crabs in a day. To assess prey preference, we expressed the number of times a cuttlefish captured a particular type of prey as a percentage of the total number of prey choices presented. If the cuttlefish had a sufficient level of feeding motivation, training began the day after the determination of this preference; if not, the cuttlefish were fed according to their preference until the day of testing.

Conditioning

Before the experiment, we prepared a saturated solution of quinine dissolved in colourless nail polish and painted it on to animals used as prey to render it distasteful when presented in the subsequent tests. Since *S. officinalis* can detect chemicals in the water (Boal & Golden 1999), we carried out preliminary tests in which cuttlefish were found to attack coated prey immediately on presentation, indicating that they were unable to detect the quinine coating except by contact, and proving that the presence

of the chemical 'locked' in the coating did not disturb normal predatory behaviour. Crabs and shrimps did not respond to being coated with quinine.

Pairs of cuttlefish were trained simultaneously in their separate tanks. Figure 1 gives schematic view of the experimental procedure. For the experimental cuttlefish, we began training by presenting its preferred prey coated with the quinine solution with an intertrial interval (ITI) of 15 min. An attack was recorded whenever the cuttlefish caught the prey. Since cuttlefish usually attack prey within 10 s, a 2-min ceiling time for each trial was imposed for them to attack, after which we removed the prey from the tank. This training was continued to the point when no attack occurred during the 2-min period of two consecutive trials. We referred to this point as the learning criterion (LC). Therefore, during the training session, each trial terminated with an attack negatively reinforced by contact with the quinine, except for the final two trials at the point of the LC which each terminated after 2 min with no attack on the prey. Whenever the experimental cuttlefish attacked the prey, the matched control cuttlefish was presented with its preferred prey without quinine. Both experimental cuttlefish and the matched control cuttlefish were selected on the basis of their similar level of feeding preference for the same prey (Fig. 2). We systematically removed the prey from the tank just after the beginning of the attack of the control cuttlefish. We repeated this sequence until the experimental cuttlefish reached the LC, at which point we discontinued presenting prey to the control cuttlefish.

During a preliminary experiment, we checked that removing the prey from the tank immediately after an initial attack did not prevent the cuttlefish from attacking the prey in subsequent trials. For this we used three cuttlefish in 20 trials with an ITI of 15 min. These trials showed that cuttlefish would continue to detect and attack the prey even if prevented from eating it.

Finally, to perform a long-term retention test of this task, we examined the prey preference of the experimental cuttlefish either 24 or 72 h after the LC (these are the standard time windows used to test long-term memory in neurobiology). The test consisted of offering a choice between a crab and a shrimp without quinine, suspended at random on either side of the T support. An identical choice was presented to the matched control cuttlefish after the same delays. In the case of the 72-h retention tests, the length of the delay was too long to leave the cuttlefish without food, so we provided an interim feed during the resting interval. A third and different type of prey from those already used in the procedure was offered, in this case the fish *Blennius pholis* (length 50–60 mm). Only the number of fish necessary for this experiment was collected at low tide under stones. The fish were maintained in a circular tank (1500 litres) with running sea water. Each cuttlefish was used only once.

Ethical Note

Although analyses of cuttlefish gut contents have revealed the presence of many invertebrate species such
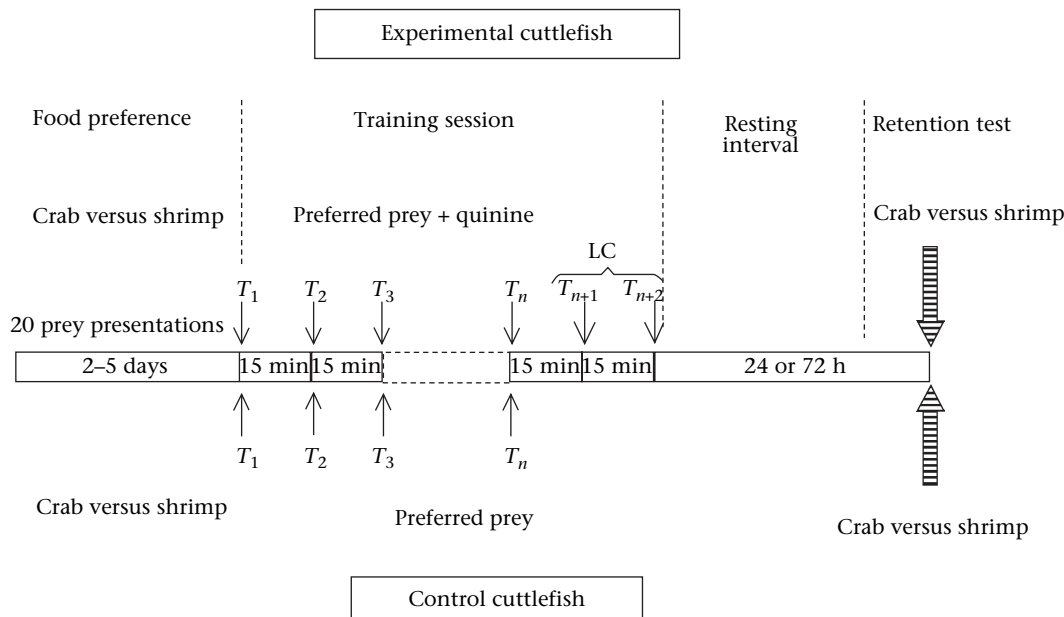
Figure 1. Schematic representation of the experimental procedure. Before the training session, the experimental cuttlefish and their matched controls were given a choice between a crab and a shrimp, to assess their feeding preference (N = 20); this phase lasted 2–5 days. The training session consisted of a series of trials (T_1–T_n), with a 15-min interval during which their preferred prey coated with quinine was presented to the experimental cuttlefish, and their preferred prey without quinine was presented to the matched control cuttlefish. LC symbolizes the last two trials of the session for the experimental cuttlefish (i.e. two presentations with no attack for 2 min each). A retention test was performed after a variable resting interval (24 or 72 h). The treatment applied to the experimental cuttlefish is represented in the upper part of the diagram and that of the matched control cuttlefish is represented beneath.
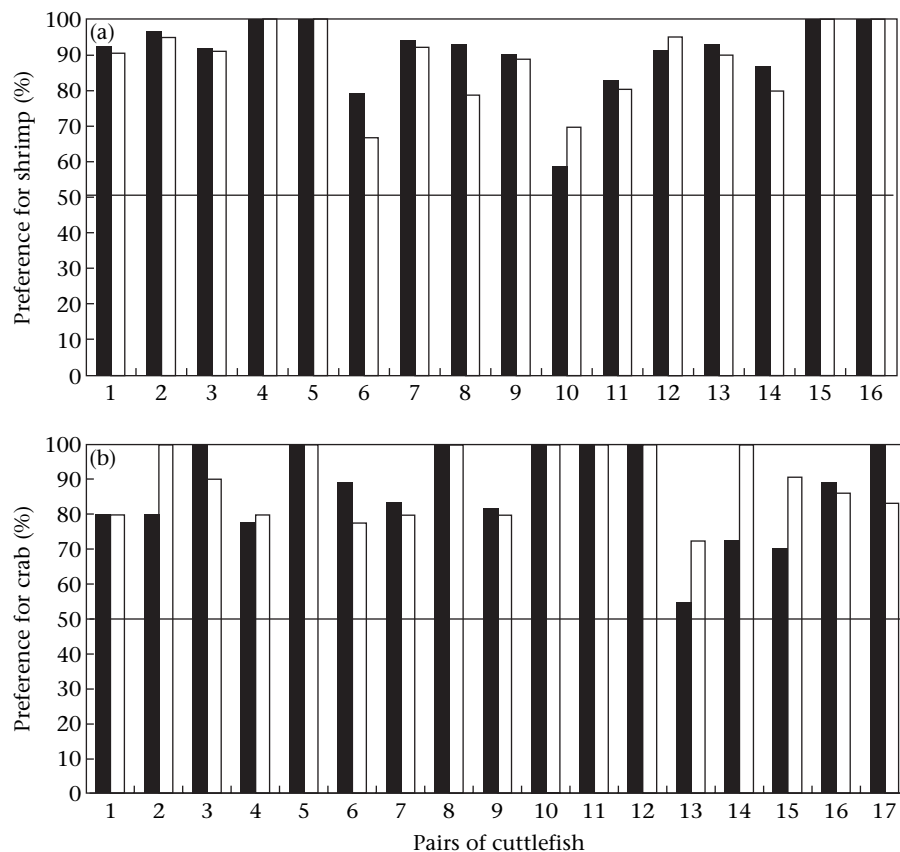
Figure 2. Feeding preference of experimental cuttlefish (■; $N = 33$) and their matched control cuttlefish (□; $N = 33$) determined after the choice tests preceding the training session. Experimental and matched control cuttlefish that preferred (a) shrimps ($N = 16, 16$) and (b) crabs ($N = 17, 17$).

as polychaetes, nemertines or bivalves, we were never able to persuade *S. officinalis* to eat such invertebrates in laboratory conditions. Furthermore, although it is possible to train laboratory-reared juveniles to eat dead prey (von Boletzky & Hanlon 1983), pilot observations showed that wild-caught cuttlefish refuse to capture and consume it. Because these other interim feeding options appeared likely to affect their health, we decided to feed cuttlefish on live fish. At this stage we also restricted the sample size for the 72-h delay to 15 experimental cuttlefish plus 15 matched control cuttlefish (Huntingford 1984), to mini-mize the numbers of fish fed. We gave two fish to each cuttlefish on the day after the training session. Fish provided as food were killed and eaten as soon as they were detected, shortly after their introduction into the tank. No specific licence was required for the study.

Analysis of Behavioural Data

Throughout the training session, we recorded attack latencies for each trial for experimental cuttlefish and their matched control cuttlefish, and the number of trials necessary to reach the LC for experimental cuttlefish. To evaluate the long-term retention of this learning, we compared the food preference of the experimental cuttle-fish before the training session with their preference 24 or

72 h later. The food preference of the matched control cuttlefish was also checked.

Statistical Analyses

All data were analysed with nonparametric tests (Siegel & Castellan 1988) and computed using SYSTAT software (SYSTAT Inc., Evanston, Illinois, U.S.A.). We used two-tailed statistical tests.

To evaluate the inhibition of the predatory behaviour of experimental cuttlefish towards their preferred prey, we focused on the mean attack latencies during the training session. We used Wilcoxon signed-ranks tests to compare attack latencies at the first trial (T_1) with attack latencies at the last trial before the LC (T_n), to evaluate any changes that occurred with training in both experimental and control cuttlefish, and to compare attack latencies be-tween the first two trials (T_1 and T_2), to evaluate any immediate changes in performance in experimental and control cuttlefish. Finally, attack latencies in the two groups at T_2, and then at T_n were compared using the Mann–Whitney U test. In each case of multiple compar-isons, the alpha criterion was adjusted according to the number of comparisons (α divided by the number of comparisons).

To evaluate whether learning had a long-term effect on the behaviour of the experimental cuttlefish, we compared their prey preference before the training session with that observed during the retention test 24 or 72 h later (binomial test, with $P = 0.5$), with an identical comparison being made for the control cuttlefish after the same delays. We also used a chi-square test to compare experimental cuttlefish's prey choice during the retention test at 24 and 72 h with that of the control cuttlefish after the same delays.

RESULTS

Food Preferences

Whichever their preferred prey, the cuttlefish showed a strong overall preference for a given prey ($\overline{X} \pm \text{SEM} = 88.8 \pm 1.4\%$; Fig. 2). Apart from two pairs, individual preferences were greater than 70%.

Behavioural Observations Throughout Training

During the first trials, experimental cuttlefish attacked the prey coated with quinine as soon as it was introduced into the tank. However, as soon as they touched it, they quickly released it and withdrew to a corner of the tank. Occasionally a few cuttlefish were observed attempting to remove the quinine from the prey with their arms although they eventually released the prey. During the later training trials, we observed that instead of attacking the prey by the usual attack strategies (tentacle strike or 'jump'), a few experimental cuttlefish slowly approached the prey and extended their arms or tentacles to touch it. Finally, during the LC trial, some experimental cuttlefish pulsed jets of water towards the prey and moved away from it.

All experimental cuttlefish reached the learning criterion within a mean $\pm$ SEM of 8.1 ± 0.7 trials ($N = 33$). Individual cuttlefish varied in their pattern of response during the training session, with one cuttlefish reaching the criterion after only one trial and three after a maximum of 15 trials. Furthermore, for 15 of 33 experimental cuttlefish no attack on the prey was made for 2 min during a particular trial but they attacked again in later trials before reaching our LC of two presentations with no attack. All matched control cuttlefish attacked the prey every time it was presented.

Attack Latencies During Training

Attack latencies gradually increased from the beginning to the end of the training in experimental cuttlefish but appeared to remain constant in control cuttlefish (Fig. 3). In this analysis we discarded the data for one cuttlefish that reached the LC in one trial. Attack latencies were significantly higher during T_n than during T_1 in experimental cuttlefish (Wilcoxon signed-ranks test: $Z = 4.664$, $N = 32$, $P < 0.001$) but not in control cuttlefish ($Z = -0.057$, $N = 32$, $P = 0.955$).
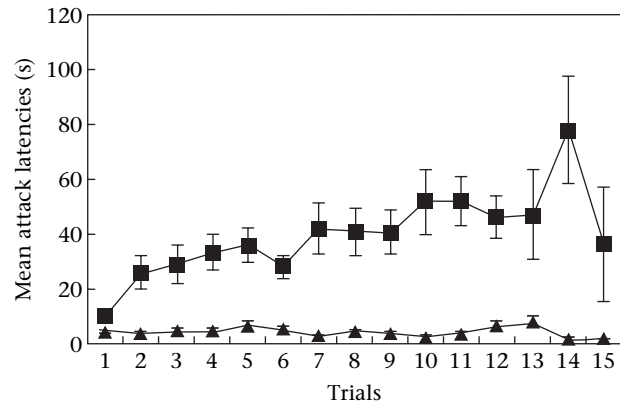
Figure 3. Effect of quinine on attack latencies in experimental cuttlefish. Cuttlefish were trained over a series of trials (abscissa). The ordinate represents mean $\pm$ SE attack latencies during the training session. ■: Experimental cuttlefish; ▲: matched controls. Numbers in matched groups on each trial: $N_1 = 33$; $N_2 = 32$; $N_3 = 31$; $N_4 = 29$; $N_5 = 27$; $N_6 = 22$; $N_7 = 19$; $N_8 = 16$; $N_9 = 15$; $N_{10} = 12$; $N_{11} = 10$; $N_{12} = 8$; $N_{13} = 6$; $N_{14} = 5$; $N_{15} = 3$.

Furthermore, although attack latencies did not differ between T_1 and T_2 in control cuttlefish (Wilcoxon signed-ranks test: $Z = -0.693$, $N = 32$, $P = 0.488$), a significant increase in latencies was observed in experimental cuttlefish ($Z = 2.455$, $N = 32$, $P < 0.05$). The increase in latencies observed from the second trial on was significant in experimental cuttlefish compared with that of control cuttlefish and attack latencies at T_n were significantly higher in experimental cuttlefish than in control cuttlefish (Mann–Whitney U test: at T_2: $Z = 4.592$, $N_1 = N_2 = 32$, $P < 0.001$; at T_n: $Z = 6.311$, $N_1 = N_2 = 32$, $P < 0.001$).
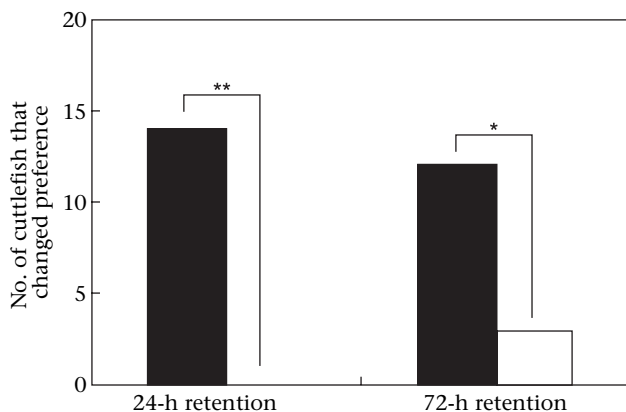
Retention Performance

Retention performances at 24 h

At 24 h after the training session, 14 of 18 experimental cuttlefish changed their initial preference, three kept their initial preference and one made no choice. Experimental cuttlefish significantly switched their feeding preference after the training session, whatever prey they originally preferred (binomial test: $P < 0.01$). In contrast, all control cuttlefish that attacked prey always chose the prey originally preferred, while the four remaining made no choice. There was a significant change in feeding preference during the retention test between experimental cuttlefish that learned the association between quinine and their preferred prey and control cuttlefish that did not (chi-square test: $\chi_1^2 = 14$, $P < 0.001$; Fig. 4).

Retention performances at 72 h

At 72 h after the training session, 12 of 15 experimental cuttlefish changed their preference, only one chose its initial preference and two made no choice. Among the 12 experimental cuttlefish that changed their preference, two had not shown a marked feeding preference in the preference tests (scarcely more than 55%; Fig. 2) and their

Figure 4. Retention performances at 24 and 72 h in experimental (■) and control (□) cuttlefish. At 24 h, $N = 18, 18$; at 72 h, $N = 15, 15$. The figure shows the number of experimental and matched control cuttlefish that changed preferred prey during the retention test. Asterisks indicate a significant difference between experimental and control cuttlefish (chi-square test: *$P < 0.05$; **$P < 0.001$).

behaviour is difficult to interpret. The training session modified the experimental cuttlefish's original choice of prey; whichever prey they originally preferred, their preference changed significantly after training (binomial test: $P < 0.01$). Eleven of 15 control cuttlefish continued to choose their preferred prey, three spontaneously changed prey preference and one made no choice. Control cuttlefish significantly continued to choose their original prey (binomial test: $P < 0.05$). Although three control cuttlefish spontaneously switched their preference, the experimental cuttlefish significantly changed their feeding preference more often during the retention test (chi-square test: $\chi^2_1 = 5.4$, $P < 0.05$; Fig. 4).

DISCUSSION

Food Preferences

Although our cuttlefish came from the same fishing ground, they did not all have the same food preference, some preferring shrimps and others crabs. Since cephalopods are generally considered to be generalist predators, one can only speculate on the reasons for these preferences: perhaps preferences depend on prey profitability or on the predator's own experience (e.g. cuttlefish that have been pinched by crabs may prefer shrimps). Vincent et al. (1998) suggested that O. dofleini included in its diet whichever bivalve and crab species were available locally. However, O. dofleini exercises some discrimination between prey types, since it actively avoids some species such as large crabs. Vincent et al. proposed that this selectivity could be explained by several factors such as predation risks or interspecific competition.

Rapid Taste Aversion Learning and Long-term Retention

Our finding that as early as after the second trial, attack latencies began to increase gradually in experimental

cuttlefish, while remaining below 10 s in control cuttlefish throughout the training session, suggested that learning occurred early (Fig. 3). Furthermore, our procedure led to the complete inhibition of all the experimental cuttlefish's predatory behaviour towards their preferred prey within 10 trials, thereby providing evidence that this new paradigm involved a rapid acquisition of associative learning. In comparison, Barlow & Sanders (1974) trained octopuses, O. vulgaris, on a passive avoidance task. The octopus was given an electric shock on the arms each time it attacked a crab. Barlow & Sanders obtained a total inhibition of the predatory behaviour in about seven trials. Our results suggest that quinine is as intense and effective a reinforcing agent as electric shock for promoting good acquisition of the task. In a study on appetitive conditioning in O. cyanea (Papini & Bitterman 1991), performance in acquisition was more effective with continuous reinforcement; and animals trained with a small reward took about twice as long to complete training as did those trained with larger ones.

Associative learning has been demonstrated in cephalopods (Boycott & Young 1955; Maldonado 1963, 1964; Messenger 1973). The negative reinforcement used to produce learned changes in the predatory behaviour (electric shock in octopus or glass tube in cuttlefish), however, were events that the animal would not encounter in its natural environment. The relevance and the intensity of the reinforcement are important factors, because animals generally learn to associate events that are biologically meaningful to their survival. Our procedure is the first demonstration of taste aversion learning in cephalopods using quinine, a natural and widespread chemical, as the aversive agent. In addition, our results suggest that the associative learning processes involved may influence food selection of cuttlefish in their natural environment. The cuttlefish used in this study had been living in the sea for at least a year and would have experienced both crab and shrimp. Compared with conditioned taste aversion (CTA), where subjects associate a novel taste with nausea in a single trial, the time taken for the cuttlefish to learn to avoid their preferred prey can appear quite long. In our experiment, however the learning is different from that induced by CTA. First, it involves the modulation of a feeding response based on chemosensory input, via the receptors spread over the suckers and the lips (Graziadei 1964; Emery 1975a, b), and not on postingestive consequences. This is supported by the behaviour observed in our experimental cuttlefish once they experienced the quinine, such as a slow approach or a slow attack with the tip of the arms or tentacles, and by behaviour in octopuses reported by Boycott (1954) as 'cautious'. Furthermore, in our study the quinine was not ingested and so, while not noxious, was distasteful and sufficiently relevant to inhibit the normal predatory behaviour of the cuttlefish towards their preferred prey.

Finally, our results highlight the good long-term retention of a new and original instrumental learning. Long-term memory of associative learning in the cuttlefish has been demonstrated with the 'prey behind the glass tube' protocol (Messenger 1973; Chichery & Chichery 1992;

Agin et al. 1998; Dickel et al. 1998, 2000). Our result has adaptive implications since it shows that cuttlefish are able to store for a long time information that is crucial to their survival and welfare.

Implications of Taste Aversion Learning

In cuttlefish, choice of prey may be affected by many factors, and may depend on the predator's feeding history. This point is of special interest. Changes in feeding behaviour have been widely studied and have been attributed to associative aversive learning in gastropod molluscs (Gelperin 1975; Mpitsos et al. 1978; Sahley et al. 1981; Susswein et al. 1986). Our results support this hypothesis and prove experimentally, for the first time, the relevance of learning in food choice and, therefore, in predatory behaviour in cephalopods. It is not difficult to consider such capacities of learning being used in the natural environment by the predator to select prey. This selectivity implies capacities for discrimination. Cephalopods have good visual discrimination learning abilities (Sanders 1975) and visual control is important in the predatory behaviour of cuttlefish (Messenger 1968). Our experiment showed that once cuttlefish have experienced inedible prey, they can recognize and avoid it for a long time, emphasizing the flexibility of their feeding preference. On the other hand, if a cuttlefish simply fails in its attempts to capture its preferred prey without any negative reinforcement other than that failure, as was the case for our control group, it will attack the same prey on subsequent occasions.

Acknowledgments

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